Journal of Ecology (1983), **71**, 489–501

EFFECT OF WATER-TABLE DEPTH ON SHOOT GROWTH, ROOT GROWTH, AND NODULATION OF *MYRICA GALE* SEEDLINGS

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SUMMARY

(1) Seedlings of *Myrica gale*, an actinorhizal dinitrogen-fixing shrub, were grown in two boxes with a gradient of water-table depth from 3–79 cm The boxes were outdoors but sheltered from rain by translucent roofs One box was filled with sand and the other with peat The seedlings were harvested in autumn shortly before leaf-fall

(2) The plants produced maximum biomass at water table depths between 10 cm and 35 cm on both substrata but the total amounts produced were substantially greater on peat than on sand

(3) Shoot–root quotients decreased with increasing water-table depth on both substrata but were much larger on sand

(4) The roots did not penetrate below the water table and the orientation of the major lateral roots changed from primarily horizontal to semi-vertical with increasing water-table depth

(5) Nodules formed 6–7% of the total seedling biomass in the wettest soils and decreased to 1% in the driest

(6) Nodule roots showed maximum development in the wettest soils where they were relatively long and thick, and emerged through the surface into the air above This is consistent with a functional role in enhancing nodule oxygen uptake under oxygen limiting conditions

(7) The considerable phenotypic plasticity in response to moisture and aeration exhibited by *Myrica gale* appears to be a valuable adaptation in its natural habitat where the water level often fluctuates

INTRODUCTION

Myrica gale L is an actinorhizal, dinitrogen-fixing shrub commonly found in open, minerotrophic peatlands and along the shores of lakes and streams in the northern United States, Canada and Europe It is capable of fixing substantial amounts of nitrogen (24–34 kg N ha^{-1} $year^{-1}$) in dense stands (Schwintzer 1979) and may be able to increase forest productivity on peat soils (Sprent & Scott 1979)

The root nodules consist of clusters of much-branched, modified lateral roots (nodule lobes) which house the actinomycetous endophyte *Frankia* sp Uninfected negatively geotropic roots (nodule roots) arise from the tips of most nodule lobes Recent studies of *Myrica gale* nodules describe oxygen relations within the nodule lobes (Tjepkema 1983) and seasonal patterns of nodule and endophyte growth and also give a summary of the literature (Schwintzer, Berry & Disney 1982)

The ecological response of a species to environmental variables like moisture and aeration often does not correspond to its physiological response (Mueller-Dombois & Ellenberg 1974). In Scotland, Sprent and Scott (1979) have observed that *Myrica gale* grows more profusely at drained or well aerated sites than at poorly aerated 'boggy' areas They suggest that its common association with 'boggy' sites may be due to tolerance of,

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0022–0477/83/0700–0489 $02 00 © 1983 British Ecological Society

rather than preference for these conditions, as well as reduced competitive pressure Bond (1976) reports that *Myrica gale* plants are usually well nodulated at a variety of sites in Canada and Europe but that plants without nodules have been found in Scotland, France and Canada In Scotland only about half of the plants at relatively dry sites had nodules whereas all plants at wetter sites were nodulated, suggesting that soil water content may affect nodulation

We report here on the growth of *Myrica gale* seedlings on two experimental soil-moisture gradients to determine in relation to moisture and aeration (i) their physiological response, (ii) the extent of phenotypic plasticity and (iii) the production of nodule biomass and hence capacity for nitrogen fixation

MATERIALS AND METHODS

Experimental moisture gradients were established outdoors, following the ideas of Mueller-Dombois (1964) Two rectangular wooden boxes were constructed with level bottoms, sloping surfaces, and translucent roofs Each contained a large wedge of soil in which a gradient of water-table depth was produced One was filled with sand and the other with peat (Fig 1) The boxes were 1 0 × 3 7 m, and were placed on a level lawn with their sloping surfaces facing west They were lined with two layers of 0 1 mm thick polyethylene sheeting and the water table was maintained at 43 cm above the floor by means of an outlet pipe at the lower end The roofs were made of wooden frames covered with clear 0 1 mm thick polyethylene sheeting and extended 0 4 m beyond the edges of the boxes They were open at the sides and lower ends but closed at the higher ends except for a 10 cm strip along the roof All exposed wooden surfaces were painted white

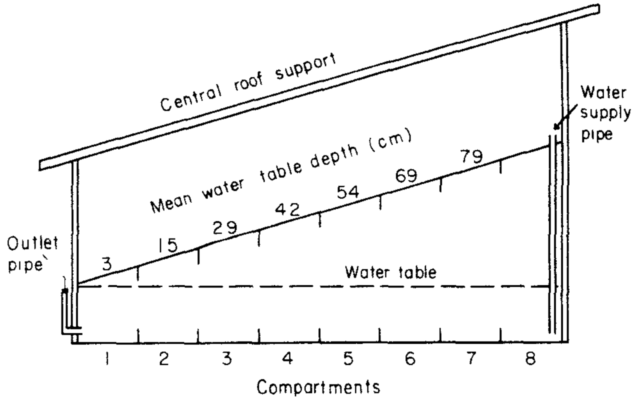

FIG 1 Longitudinal section through the centre of a soil-moisture gradient box

The boxes were filled with layers of coarse aggregate and soil in June 1979 as follows 10 cm of 1 3 cm diameter crushed stone, 5 cm coarse sand, and finally sand or peat to within 3 cm of the top on all sides Each gradient was divided into eight equal compartments with plywood panels driven 30 cm into the soil

After filling with soil, well water (pH 6 9–7·1), was added through the water supply pipes until the outlet pipes overflowed The water tables were then maintained by continuously dripping well water into the supply pipes at rates adjusted daily to maintain the water level within 1 cm of the top of the outlet pipe

Soils

Sand and peat soils were used to represent the streamside, lakeshore, and peatland soils on which *Myrica gale* grows naturally Because it was not feasible to take soils from *M gale* sites, conditions in these soils were simulated

The sand consisted of two parts of sand taken from a glacial deposit located within 100 m of the 'Pondside' *Myrica gale* site (Schwintzer 1979) and one part of locally obtained top soil These components were thoroughly mixed *Myrica gale* plants grown on the sand gradient in a preliminary experiment in 1979 made satisfactory growth In early June 1980 the upper 30 cm of soil was removed, thoroughly mixed to assure uniformity along the length of the gradient at the beginning of the experiment, and returned to the box The sand contained 5% small stones (determined by sieving) and the remainder comprised 94% sand, 3% silt and 2% clay (determined by the hydrometer method) It had a bulk density of 1 29 g cm^{-3} and a water content of 40% (vol /vol) at saturation Its water content was 6 2% at −33 kPa and 4 8% at −100 kPa (determined by the pressure membrane method) The pH (1 1 with water) was 6 0–6 2 in compartments 3–7 from mid-July until mid-September

The peat consisted of commercial milled Canadian peat supplemented with peat from the nearby 'Open Mat' *Myrica gale* site (Schwintzer 1979) added at a rate of 0 5 l per 30 l to introduce an appropriate microbial population *Myrica gale* plants grown on the peat gradient in a preliminary experiment in 1979 made very little growth because the peat was nutrient deficient Consequently, the upper 30 cm of peat was removed from the box in mid-June 1980 and Hoagland's nutrient solution, but without nitrogen salts (Hoagland & Arnon 1950), was added (5 l per 25 l of peat) The two were thoroughly mixed and returned to the box The peat had a bulk density of 0 063 g cm^{-3} and a water content of 83%(vol /vol) at saturation Its water content was 13 5% at −33 kPa and 9 5% at −100 kPa The pH (1 1 with water) was 3 5 in all compartments in mid-July and decreased to 3 2 in compartments 2–7 by mid-September but remained unchanged in compartment 1

Soil water content was measured in the middle of July, August and September on samples taken midway between the plants It was determined gravimetrically on a dry weight basis and multiplied by soil bulk density to convert to a volume basis

Seedlings

In April 1980 seeds collected at the 'Open Mat' site in November 1979 were germinated in washed sand after a 3-week cold treatment The seedlings emerged in mid-April and were transferred to 7 5 cm diameter pots in mid-May after inoculation with crushed nodule suspensions prepared from field-collected nodules Half of the seedlings were grown in 1 1 sand and milled peat and the remainder in sand from the sand gradient They were placed in a greenhouse for one month and then in a partly sheltered area outdoors for 2 weeks prior to planting in the gradients The seedlings were watered weekly with quarter-strength Hoagland's solution without nitrogen and with well water as required

At the time of planting in late June the two groups of seedlings were sorted according to shoot length The largest and smallest (about one third of the total) were rejected and the remainder randomized Seedlings grown in peat were transplanted to the peat gradient together with the soil mass in the pot (hereafter called the original soil mass). Seedlings grown in sand were transplanted to the sand gradient When transplanted a few roots were just reaching the bottom of the pot Each compartment contained twelve seedlings arranged in two rows (15 cm apart) of six seedlings 15 cm apart

At harvest shortly before leaf-fall in late September (sand) and early October (peat) the seedlings were excavated with a water jet and the characteristics shown in Tables 1 and 2 were measured. Dry weights were determined after oven drying at 100 °C. Because it was impracticable to determine the depth of rooting and the depth of the nodules *in situ* during excavation, they were measured on root systems floating freely in large trays of water. A preliminary experiment comparing measurements in water and *in situ* in *Myrica gale* seedlings grown in the gradients in 1979 showed that measurements made in water were 27% ± 8% (mean ± S.E., $n = 7$) larger in compartment 2 and 8% ± 3% ($n = 35$) larger in compartments 3–7 than measurements made *in situ*.

RESULTS

Soil moisture content

As expected, soil moisture content decreased with increasing water-table depth (Fig. 2). On the sand gradient (Fig. 2(a)) the moisture content in compartments 1–3 remained unchanged and the soil surface was visibly damp until the end of the growing season. In compartments 4–7 the moisture content declined by about 1·5 percentage points in the upper 7·5 cm but remained unchanged in the next 7·5 cm. All water potentials corresponding to the measured moisture contents were higher than −100 kPa and most were higher than −33 kPa. Values below −33 kPa were found only in the surface 7·5 cm layer of soil in compartments 6 and 7 in August and September.

On the peat gradient (Fig. 2(b)) the moisture content of compartments 1–3 remained essentially unchanged and the peat surface was visibly damp until the end of the growing season. In compartments 5–7 the surface was visibly dry. In compartments 5 and 6 the moisture content remained unchanged and in compartment 7 it declined about 8 percentage points by late August in the upper 15 cm. All water potentials corresponding to the measured moisture contents were above −33 kPa up to late August.

Seedlings

The overall plant size at the end of the growing season as measured by total biomass (Fig. 3) and the individual plant characteristics in Tables 1 and 2 varied with both substratum and water-table depth. Shoot–root quotients (Fig. 4) and some nodule characteristics (Tables 1 and 2) also varied with substratum and water-table depth. The plants grown on sand were generally smaller than those grown on peat (Tables 1 and 2).

The water-table depth affected total biomass on both sand and peat (Fig. 3). The plants were smallest in compartment 1, largest in compartments 2 and 3, and the biomass decreased with increasing water-table depth above this. The decrease was large on sand but small and not statistically significant on peat.

When the seedlings were planted into the gradients in late June all had only primary shoots. Vigorous lateral shoots developed subsequently near the bases of the primary shoots and smaller lateral shoots appeared closer to the apex. Stolons also formed just below the soil surface on the main axis and on some of the basal lateral shoots. Several shoot characteristics at the end of the growing season are given in Tables 1 and 2. All show the same general response to water-table depth as total biomass.

The root systems consisted of a poorly developed primary root (taproot) ranging in length from 1·8 to 2·6 cm and several vigorous secondary (lateral) roots giving rise to higher order roots. On peat the roots were relatively thin and uniformly healthy in appearance. On sand, in contrast, they were relatively thick and some were dead. All

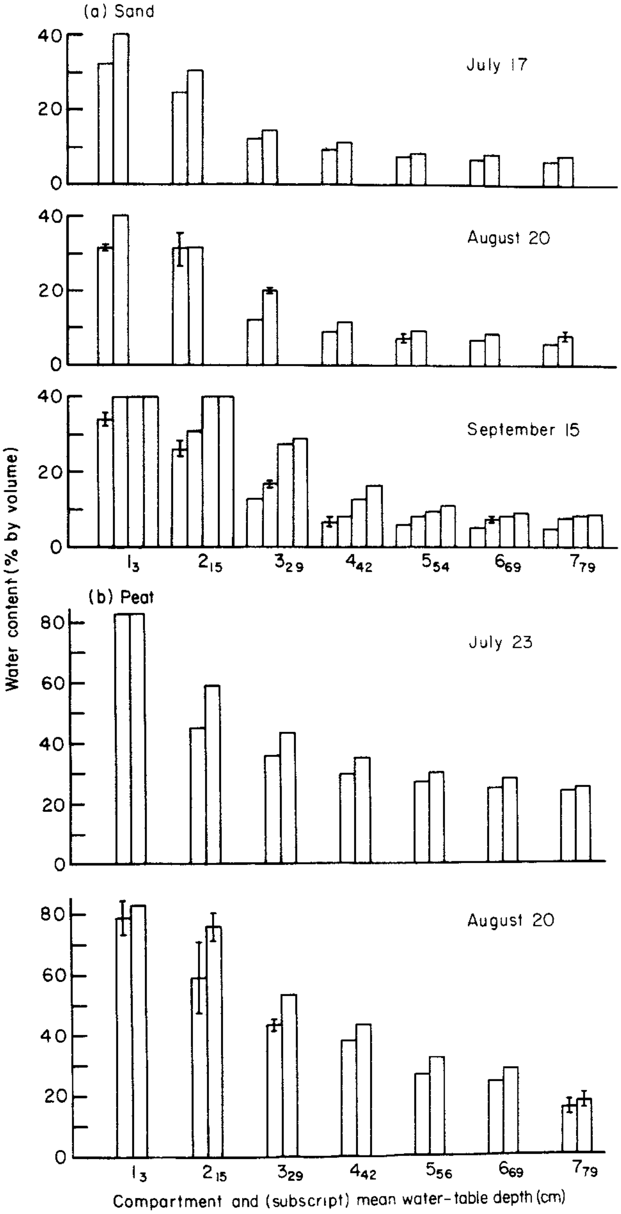

FIG 2 Relationship between water-table depth and soil moisture in (a) sand and (b) peat moisture-gradient boxes during the growing season of 1980 Bars represent the soil layers 0–7 5 cm (left) and 7 5–15 cm (right) For 15 September, 15–22 5 cm and 22 5–30 cm are also included in left to right sequence Values are means ± S E $n = 4$ except for July when $n = 2$

plants in sand compartment 1 had some dead roots, as did 83% in compartment 2, 50% in compartments 3 and 5, and 25% in compartment 7

The roots grew outward and downward except in the wet soils of compartments 1 and 2 where some roots grew upward, often emerging into the air above the soil and forming red

TABLE 1 Characteristics of *Myrica gale* seedlings grown on a sand soil-moisture gradient in Massachusetts The seedlings were harvested in late September 1980 Values are means ± S E , $n = 12$ All values are given per plant

Compartment	1 (wettest)	2	3	4	5	6	7 (driest)
Mean water-table depth (cm)	3	15	29	42	56	69	79
Shoots							
Length of main shoot (cm)	17 ± 1	32 ± 3	25 ± 2	23 ± 2	20 ± 1	19 ± 1	13 ± 2
Number of lateral shoots	3 2 ± 0 8	7 3 ± 1 1	7 3 ± 1 2	6 3 ± 0 7	5 8 ± 0 4	5 2 ± 0 5	3 5 ± 0 7
Total shoot length (cm)	33 ± 4	145 ± 15	129 ± 12	105 ± 10	78 ± 7	70 ± 13	32 ± 7
Leaf dry weight (g)	0 54 ± 0 06	2 84 ± 0 35	2 45 ± 0 22	2 11 ± 0 18	1 45 ± 0 16	1 20 ± 0 17	0 72 ± 0 19
Stem dry weight (g)	0 40 ± 0 05	2 34 ± 0 26	1 88 ± 0 16	1 21 ± 0 12	0 75 ± 0 09	0 63 ± 0 11	0 31 ± 0 08
Stolons							
Number of stolons	0 5 ± 0 3	0 4 ± 0 4	0 1 ± 0		0		0
Dry weight (g)	<0 01	0 01 ± 0 01	<0 01		0		0
Roots							
Maximum depth (cm)	2 7 ± 0 1	3 9 ± 0 3	7 4 ± 0 7		14 4 ± 0 7		12 5 ± 1 2
Length of major lateral roots (cm)	13 ± 1	27 ± 1	28 ± 1		32 ± 1		27 ± 2
Number of lateral roots	2 2 ± 0 3	12 6 ± 0 9	10 4 ± 1 1		6 1 ± 0 6		3 7 ± 0 8
Dry weight (g)	0 19 ± 0 03	1 09 ± 0 10	1 18 ± 0 09		0 85 ± 0 06		0 53 ± 0 12
Nodules							
Dry weight (g)	0 08 ± 0 01	0 27 ± 0 03	0 20 ± 0 03		0 07 ± 0 01		0 01 ± 0 00
Diameter of largest nodules (cm)	0 65 ± 0 04	0 66 ± 0 03	0 63 ± 0 03		0 37 ± 0 02		0 23 ± 0 02
Distance from surface to largest nodules (cm)	1 3 ± 0 2	1 7 ± 0 2	2 9 ± 0 7		8 7 ± 0 7		5 1 ± 1 0
Distance from surface to deepest nodules (cm)	2 5 ± 0 1	3 1 ± 0 3	6 9 ± 0 7		12 0 ± 0 4		9 0 ± 0 8
Longest nodule roots (cm)	2 4 ± 0 1	2 9 ± 0 2	2 7 ± 0 2		1 3 ± 0 1		0 6 ± 0 2
Number of roots with nodules outside the original soil mass	0 2 ± 0 2	6 8 ± 0 8	7 1 ± 1 0		4 0 ± 0 4		1 8 ± 0 5

TABLE 2 Characteristics of *Myrica gale* seedlings grown on a peat soil-moisture gradient in Massachusetts The seedlings were harvested in early October 1980 Values are means ± S E , $n = 12$ All values are given per plant

Compartment	1 (wettest)	2	3	4	5	6	7 (driest)
Mean water-table depth (cm)	3	15	29	42	56	69	79
Shoots							
Length of main shoot (cm)	29 ± 1	37 ± 3	39 ± 3	36 ± 2	35 ± 2	35 ± 2	31 ± 1
Number of lateral shoots	7 6 ± 1 1	9 6 ± 0 9	8 2 ± 1 1	7 8 ± 0 9	8 6 ± 0 9	8 4 ± 1 0	7 8 ± 0 7
Total shoot length (cm)	140 ± 21	271 ± 24	266 ± 38	254 ± 28	246 ± 20	277 ± 42	215 ± 28
Leaf dry weight (g)	2 55 ± 0 46	5 74 ± 0 41	5 95 ± 0 82	5 80 ± 0 72	5 17 ± 0 41	6 63 ± 0 95	4 71 ± 0 60
Stem dry weight (g)	3 37 ± 0 49	7 85 ± 0 59	8 41 ± 1 39	8 12 ± 0 96	6 81 ± 0 67	8 76 ± 1 48	5 24 ± 0 54
Stolons							
Number of stolons	1 2 ± 0 4	2 1 ± 0 4	2 9 ± 0 9		1 2 ± 0 5		1 5 ± 0 5
Dry weight (g)	0 04 ± 0 01	0 14 ± 0 07	0 13 ± 0 04		0 12 ± 0 08		0 15 ± 0 09
Roots							
Maximum depth (cm)	5 8 ± 0 4	10 9 ± 0 5	20 2 ± 0 4		42 5 ± 0 8		48 3 ± 1 2
Length of major lateral roots (cm)	32 6 ± 1 7	42 2 ± 1 3	47 3 ± 1 4		57 0 ± 1 3		52 7 ± 1 5
Number of lateral roots	9 6 ± 1 2	20 0 ± 1 1	19 8 ± 1 5		18 2 ± 1 4		14 5 ± 1 2
Dry weight (g)	2 17 ± 0 44	6 03 ± 0 63	6 50 ± 0 75		7 91 ± 0 64		7 89 ± 0 95
Nodules							
Dry weight (g)	0 55 ± 0 10	0 90 ± 0 10	0 57 ± 0 07		0 20 ± 0 03		0 17 ± 0 02
Diameter of largest nodules (cm)	0 78 ± 0 03	0 77 ± 0 03	0 66 ± 0 04		0 55 ± 0 03		0 49 ± 0 02
Distance from surface to largest nodules (cm)	1 1 ± 0 2	2 2 ± 0 5	1 6 ± 0 2		1 2 ± 0 2		1 9 ± 0 2
Distance from surface to deepest nodules (cm)	3 7 ± 0 5	11 7 ± 0 6	21 2 ± 0 9		20 7 ± 2 1		19 9 ± 3 7
Longest nodule roots (cm)	4 4 ± 0 4	5 3 ± 0 5	4 0 ± 0 1		2 2 ± 0 3		2 3 ± 0 3
Number of roots with nodules outside the original soil mass	2 1 ± 0 7	9 1 ± 0 8	9 5 ± 1 4		4 0 ± 0 6		3 4 ± 0 8

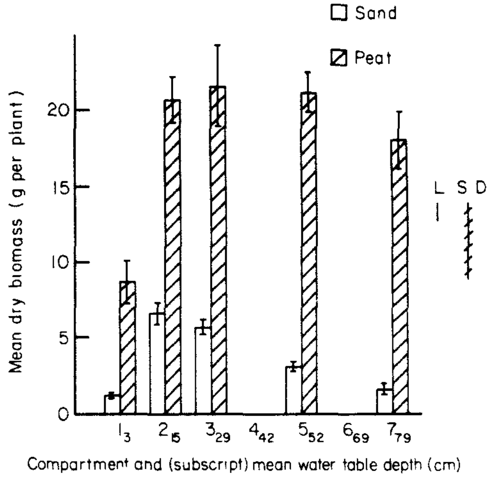

FIG 3 Effect of water-table depth in two soil moisture-gradient boxes on total dry biomass of *Myrica gale* seedlings at the end of the 1980 growing season in Massachusetts See text for further details Values are means ± S E $n = 12$ L S D = least significant difference ($P = 0\ 05$)

tips Upward-growing roots were common in compartment 1 on both substrata and occurred infrequently in compartment 2 on sand but were otherwise absent

The rooting depth (Tables 1 and 2) and the shape of the root system changed dramatically with increasing water-table depth on both substrata In compartment 1 the roots spread horizontally outward forming a shallow disk while in compartments 5 and 7 they grew downward, and to some extent outward, occupying a cone-shaped volume with a basal diameter similar to the lateral spread in the wetter soils Compartments 2 and 3 had intermediate root distributions All roots remained above the water table and only those in compartment 1 reached it

The proportion of the total biomass in shoots (Fig 4) decreased with increasing water-table depth on both substrata Nodules were excluded in the calculation of these shoot–root quotients because they do not take up significant amounts of water or nutrients other than nitrogen

Several nodule characteristics are also given in Tables 1 and 2 Nodule biomass was greatest in compartment 2 and declined strongly with subsequent increasing water-table depth on both substrata The proportion of biomass in nodules (Fig 5) was similar on both substrata even though nodule biomass was substantially greater on peat than on sand The proportion of biomass in nodules was greatest in compartment 1 where nodules constituted 6–7% of total seedling biomass and decreased with increasing water-table depth to 1% in compartment 7

Nodules were found on many roots outside the original soil mass (Tables 1 and 2) on both substrata indicating that nodulation had occurred in the experimental soils The number of roots bearing such nodules was greatest in compartments 2 and 3 and declined strongly with increasing water-table depth In compartment 1 almost no nodules formed on sand but a moderate number formed on peat Nodules were found at close to the maximum rooting depth in all compartments on sand and in compartments 1–3 on peat but were restricted to the upper half of the root system in peat compartments 5 and 7

The largest nodules formed in the wet to moist soils of compartments 1–3 on both

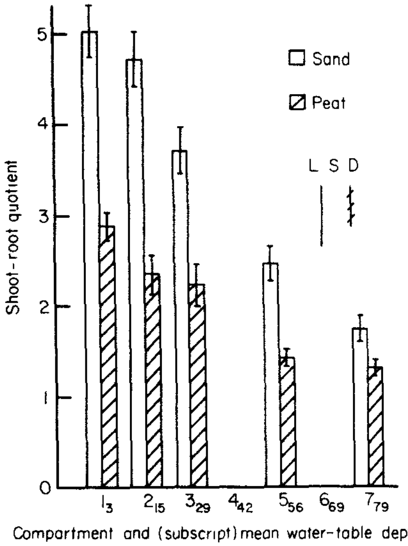

FIG 4 Effect of water-table depth in two soil moisture-gradient boxes on shoot–root dry weight quotients in *Myrica gale* seedlings Nitrogen fixing nodules excluded from root weight Values are means ± S E $n = 12$ L S D = least significant difference ($P = 0$ 05)

substrata (Tables 1 and 2) In the drier soils of compartments 5 and 7 nodule diameter decreased with increasing water-table depth The largest nodules were on the primary root and larger lateral roots in the original soil mass in all compartments on peat and in compartments 1–3 on sand, and thus were derived from the original inoculation In sand compartments 5 and 7 some of the largest nodules were found below 6 cm, the depth of the original soil mass, and thus arose from later infections

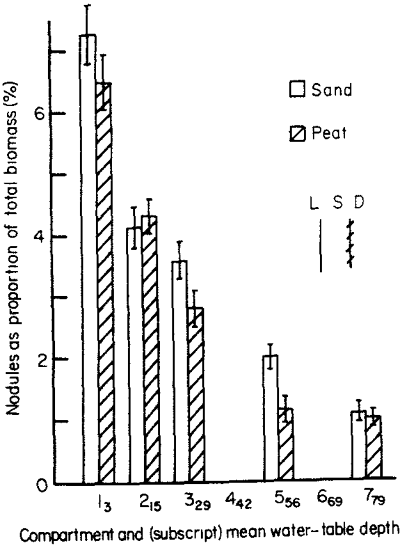

FIG 5 Effect of water-table depth in two soil moisture-gradient boxes on proportion of total biomass in nitrogen-fixing root nodules in *Myrica gale* seedlings Values are means ± S E $n = 12$ L S D = least significant difference ($P = 0$ 05)

The negatively geotropic nodule roots attained their greatest length and diameter in the wet to moist soils of compartments 1–3 on both substrata (Tables 1 and 2) In the drier soils of compartments 5 and 7 the nodule roots were thinner and their length decreased with decreasing moisture In the wetter soils they penetrated the surface, turned red above it, and their exposed tips were often desiccated Red nodule roots were conspicuous in compartment 1 where they were numerous and occurred on all plants They were much less developed in compartment 2 where they were found on only 67% of plants in sand and 33% of plants in peat They were otherwise absent Most nodule roots produced short, slender branches at various points along their length Branching was most extensive in compartments 2 and 3, and decreased with decreasing moisture in compartments 5–7

DISCUSSION

Many *Myrica gale* seedling characteristics showed similar responses to water-table depth on the peat and sand soils in spite of important differences between these soils including nutrient concentration, bulk density, and water-holding capacity Some interesting differences also developed between plants grown on the two soils including a large difference in the total biomass and shoot–root quotient These will not be considered further because their causes cannot be deduced from the data available due to the confounding effects of the numerous differences between the two soils

Water-table depth gradients are complex for they involve not only soil water content soil water potential and aeration, but also nutrient availability to the extent that it is determined by aeration and water potential. In our experimental gradients, the soil below the water table was probably completely anaerobic because the water table was below the surface and there was no lateral water movement (Armstrong & Boatman 1967, Armstrong 1975, Boggie 1977) The soils above the water table were probably well aerated except for a relatively narrow zone adjacent to the water table because the soils lacked structure and oxygen readily diffuses through soils with continuous air-spaces when the air-filled porosity exceeds 10% of the total soil volume (Stolzy & Fluhler 1978)

Although each plant characteristic examined had its own pattern of response to water-table depth, two general patterns can be identified The first is limited growth on very wet soils (compartment 1), maximum growth in wet soils (compartments 2 and 3), and increasingly limited growth as the soils become drier Characters showing this pattern included whole plant biomass (sand, Fig 3), most shoot characters, most biomass components, and the number of lateral roots produced (Tables 1 and 2) Presumably this pattern is a result of limitation of growth by water availability in the drier soils and limitation in the very wet soils of compartment 1 by low aeration and the presence of a very narrow zone of well-aerated soil This limitation occurred even though *Myrica gale* roots have several adaptations to high water tables, namely presence of upward-growing branch roots, ability to form extensive internal airspaces (Fletcher 1955), and radial oxygen diffusion from the roots (Armstrong 1968) The second general pattern has a maximum at one end of the gradient with a continuous decline to a minimum at the other end Characteristics showing this response included nodule–total biomass quotient, shoot–root biomass quotient, and maximum depth of roots In a slight variation of this pattern two characters had high values in very wet and wet soils and declining values in drier soils

At the dry end of the gradient only 1% of the biomass was in nodules but at the wet end 6–7% was in nodules Similar values (6 0–7 3%) have been found in nitrogen-free water cultures (Stewart & Bond 1961, Stewart 1963) Individual nodules also attained their maximum size in the wetter soils These findings are consistent with field observations in Scotland (Bond 1976) where only about half of the plants at relatively dry sites but all plants at wetter sites are nodulated Thus, it appears that both nodule number and the extent of nodule development are affected by soil water content Whether this is due to water potential or is an indirect effect of soil water content cannot be deduced from our data However, water potential has been shown to affect nodule initiation and development in legumes (Sprent 1979)

The structure of nodule roots allows a relatively large flux of oxygen to the endophyte-containing nodule lobes and their presence has been shown to enhance nitrogen fixation (nitrogenase activity) when oxygen is limiting (Tjepkema 1978) The extent of nodule root development seen here is consistent with a role in enhancing oxygen supplies to the nodule lobes Long, thick nodule roots that penetrated the soil surface were produced in wet soils where oxygen is in least supply whereas only short, thin ones were produced in drier, well aerated soils Sprent & Scott (1979) also found nodule root development greatest in wet, poorly aerated soils at four sites in Scotland

Most previous descriptions of nodule roots (Bond 1952, Fletcher 1955, Torrey & Callaham 1978) are based on plants grown in water culture or aeroponic conditions (Zobel, Del Tredici & Torrey 1976) In such conditions nodule roots typically reach a length of 3–4 cm in first year plants and often reach 8 cm in second year plants in water culture Moreover, lateral branches are rare In contrast, our soil-grown first year plants produced nodule roots that varied in length from 0 6 to 5 3 cm depending on both substratum and water-table depth Further, they nearly always had a few lateral branches and sometimes many depending on water-table depth

The change in shoot–root quotient seen here in response to water-table depth (Fig 4) is generally consistent with observations in other plants In dry soils where water is limiting, the shoot–root quotients usually decrease with decreasing water potential because shoot growth is reduced more than root growth (de Wit 1978, Kozlowski 1982) In very wet soils where the oxygen content is low, the response is variable depending on species (de Wit 1978)

The root systems were shallow near the water table but became deeper as water-table depth increased In the field, *Myrica gale* typically grows at sites where the water table is relatively close to the surface in mid-summer (Spence 1964, Schwintzer 1978) and consequently can be expected to be shallow rooted Examination of its root systems at the nearby 'Open Mat' site showed them all to be shallow with well developed, laterally spreading secondary roots

The physiological and ecological optima of a species with respect to environmental factors such as soil moisture content often do not coincide (Mueller-Dombois & Ellenberg 1974) However, in the case of *Myrica gale* they appear to be similar In Michigan and Massachusetts vigorous stands were found on wet soils more than 10 cm above the water table in mid-summer whereas growth was less vigorous on soils closer to the water table (C R Schwintzer, unpublished) In spite of its relatively poor growth at water-table depths less than 10 cm below the surface, *Myrica gale* is most common in these conditions (Spence 1964; Schwintzer 1978) Although our results show that *M. gale* can grow on drier soils more than 40 cm above the water table, even in the absence of periodic surface recharge by rain, we have rarely seen it under these conditions in the field In Europe, however, some stands do occur on relatively dry sites (Hegi 1957, Bond 1976)

A number of herbaceous wetland plants show extreme phenotypic plasticity in response to water-table depth—a characteristic which may help them to adapt to the changing water levels found in most wetlands (Wallace & Srb 1964, Sculthorpe 1967) Heterophylly, the capacity to produce leaves that differ in shape, habit and anatomy, or some combination of these, is a conspicuous and well known example of this phenotypic plasticity The large changes in shoot–root quotients, shape of the root system, development of nodule roots, proportion of biomass in nodules, and production of upward growing roots seen here in *Myrica gale* indicate that it too shows strong phenotypic plasticity in response to water level although these changes are not as visibly obvious as heterophylly Coupled with various documented changes in root anatomy and physiology in response to flooding in wetland plants (Bristow 1975, Gill 1977, Hook & Scholtens 1978) these observations suggest that strong phenotypic plasticity in response to water level is a common characteristic among both woody and herbaceous wetland plants

ACKNOWLEDGMENTS

We thank J D Tjepkema for helpful discussions and comments on the manuscript, E M Gould for assistance in the design and construction of the moisture-gradient boxes, L D Disney and S Corey for technical assistance, and D Hillel and M Fayer for use of the pressure membrane apparatus This work was supported in part by NSF Grant DEB77-02249 and a Charles Bullard Fellowship to CRS

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(*Received 30 September 1982*)