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ROOT PRODUCTION IN FOUR COMMUNITIES IN THE GREAT DISMAL SWAMP[1]

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A sequential coring approach was used to measure root biomass and production over 1 year in four different communities within the Great Dismal Swamp. A second method, an implanted bag technique, was also used to measure root production, and values were generally lower using this technique. On all sites, fine roots were the most dynamic root component. Both biomass (1,887 g/m^2) and production (354–989 g m^{-2} yr^{-1}) were highest on the mixed hardwood site, the least flooded site, and second highest on the cedar site, the site with the longest duration of soil saturation (1,033 g/m^2 and 274–366 g m^{-2} yr^{-1}). The maple-gum (696 g/m^2 and 59–91 g m^{-2} yr^{-1}) and cypress (824 g/m^2 and 68–308 g m^{-2} yr^{-1}) sites had similarly low amounts of biomass and rates of production. Environmental parameters that influenced production include frequency and duration of flooding, and soil type. Peaks in belowground production were observed on the most productive sites (mixed hardwood and cedar) in summer and late fall-winter; the other two sites exhibited little seasonal variability. The least flooded stand appears to allocate a greater percentage of net primary production belowground than the more extensively flooded stands. The ratio of above- and belowground allocation appears to change in response to a flooding gradient. This has major implications for ecosystem functions as carbon allocation patterns determine the array of litter types generated (leaves vs. roots) which affect decomposition rates and nutrient availability.

Roots are a large, dynamic component of an ecosystem, and a significant portion of net primary production (NPP) in temperate forests is allocated to roots (Harris, Kinerson, and Edwards, 1977; Santantonio, Hermann, and Overton, 1977; Persson, 1978; McClaugherty, Aber, and Melillo, 1982; Vogt, Grier, and Vogt, 1986). Yet of all components of a forested ecosystem, roots have received the least attention, especially forested wetland ecosystems. Santantonio and Grace (1987) reported that fine root production has been estimated in fewer than 30 stands worldwide. Only within the last two decades have there been any attempts to understand roots as part of the entire forest system (Hermann, 1977; Santantonio, Hermann, and Overton, 1977). This lack of attention is most likely due to methodological and logistical problems associated with studying roots. Observation normally causes disturbance which leads to an atypical picture of belowground processes (Hermann, 1977; Santantonio, Hermann, and Overton, 1977; Kane, 1981), and the time needed for processing makes such studies difficult.

The major objective of this study was to estimate biomass, necromass, and net production of three sizes of roots in four distinct plant communities in the Great Dismal Swamp. A sequential core approach and an implanted soil mass technique were used to measure production of fine roots. The size categories chosen were fine (<2 mm diam), small (2–5 mm), and coarse (>5 mm) roots exclusive of main root stocks. A second objective was to evaluate the effects of hydroperiod and other environmental parameters on these belowground features. The sites used in this study differed from each other in community composition, soil, and hydroperiod. They had served as long-term ecological study sites for more than a decade (Day, 1984).

SITE DESCRIPTIONS

The Great Dismal Swamp is an 85,000 ha, palustrine wetland situated on the Coastal Plain of southeastern Virginia and northeastern North Carolina. The Great Dismal Swamp has been subjected to various human disturbances such as logging, land clearing, and canal digging for transportation and drainage. As a result of these disturbances a drying trend has been accelerated throughout the swamp and much of the natural vegetation has been replaced. De-

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tails of the geology, hydrology, and vegetation of the Great Dismal Swamp as well as of each site may be found in Kirk (1979), Gomez and Day (1982), and Day, West, and Tupacz (1988).

The cedar site is dominated by Atlantic white cedar (*Chamaecyparis thyoides*), with black gum (*Nyssa sylvatica*) and red maple (*Acer rubrum*) as subdominants. The understory biomass was 1,852 kg/ha, and low shrubs and herbs were 30 kg/ha (Dabel and Day, 1977). The stand was estimated to be approximately 57 yr old in 1978 (Train and Day, 1982). Because fires are suppressed in the Dismal Swamp, the cedar trees are senescing naturally and leaving a large amount of woody material on the forest floor. Soil on this site is a dysic, thermic, Typic Medisaprist (J. Rule, unpublished data). Soil and soil water pH ranges from 3.2 to 4.4 (Bandle and Day, 1985). Flooding above the surface does not occur often on the cedar site; however, water levels do remain within 10 cm of the soil surface for at least 50% of the year (Day, West, and Tupacz, 1988).

The mixed hardwood site is a raised mesic area dominated by laurel oak (*Quercus laurifolia*), white oak (*Quercus alba*), sweet gum (*Liquidambar styraciflua*), black gum, and red maple. Understory biomass was 803 kg/ha, and low shrubs and herbs were 188 kg/ha (Dabel and Day, 1977). The oldest white oak was reported to be 78 yr old (Train and Day, 1982). The soil is a moderately permeable, fine, loamy, mixed, thermic Typic Ochraquult. Soil and soil water pH ranges from 3.2 to 4.4 (Bandle and Day, 1985). Flooding above the surface does not typically occur on this site, although winter water levels remain within 10 to 30 cm below the surface. Summer water levels drop to 1.75 m below the surface (Day, West, and Tupacz, 1988).

Dominants on the cypress site include bald cypress (*Taxodium distichum*), red maple, and black gum. Biomass of understory and low shrubs and herbs was 63 kg/ha and 178 kg/ha, respectively (Dabel and Day, 1977). The oldest trees were 86 yr old in 1978 (Train and Day, 1982). Soil on this site is a very heavy, massive, silty clay loam (a clayey, mixed, acid, thermic Typic Fluvaquent). pH ranges between 4.5 and 4.7 (Bandle and Day, 1985). The cypress site experiences the deepest aboveground flooding (10 cm above the soil surface) and longest duration of winter flooding of all sites. However, in the summer, the water table drops the lowest of all sites (3.25 m below the soil surface) (Day, West, and Tupacz, 1988).

The maple-gum site is dominated by water gum (*Nyssa aquatica*), red maple, and black gum. Biomass of understory and low shrubs and herbs was 658 kg/ha and 26 kg/ha, respectively (Dabel and Day, 1977). The oldest water gum was 52 yr old in 1978 (Train and Day, 1982). The soil is a fine, silty, mixed, acid, Thermic Histic Fluvaquent with 39% organic matter (J. Rule, unpublished data). Soil and soil water pH ranges between 4.3 and 5.6 (Bandle and Day, 1985). Surface flooding occurs in winter and spring on this site but is not as continuous as on the cypress site. Water levels on this site also drop to 1.75 m below the surface in summer (Day, West, and Tupacz, 1988).

MATERIALS AND METHODS

Sequential cores—Ten soil cores were extracted each month from each of the four sites from March 1985 through February 1986. A 39-m × 30-m (1,170 m^2) grid was laid out on each site with stations 3 m apart. Soil cores were obtained with a 7-cm-diam bucket auger in 10-cm sections taken to a depth of 40 cm. Although coring locations were randomly placed within the four study areas, care was taken to ensure that they were at least 60 cm from the base of any nearby tree. This allowed the exclusion of roots associated with the bole or stump of trees (McGinty, 1976; Montague and Day, 1980; Kane, 1981). Once collected, all soil core sections were placed in marked plastic bags and stored either frozen or refrigerated in the laboratory until processed.

A jet of water was used to facilitate sieving the sections through nested sieves with pore openings of 2 mm and 0.6 mm. Only extremely fine roots (less than 0.5 mm) were lost through the screens. No attempt was made to quantify this loss. The roots were sorted into six categories based on the diameter of the root and whether the root appeared alive or dead. The three diameter categories included fine (<2 mm diam), small (2–5 mm), and large (>5 mm). Determination of live vs. dead roots was often difficult and represented a source of error in the study. Live roots were resilient, flexible, and normally contained many lateral branches. Dead roots were often inflexible and fragmented or crumbled easily. Color was sometimes used as a supplementary test to resilience. Live roots were sometimes white internally, whereas dead roots were normally dark. The larger roots were sorted and oven-dried at 70 C for 48 hr. The remaining material, which contained the fine roots, was split into small aliquots that were sorted microscopically. Roots sorted from the aliquots were placed in small weighing pans and oven-dried at 70 C for 24 hr. All roots were weighed after drying.

An attempt was made to compute belowground NPP by the Wiegert and Evans (1964) model. The sequential core data, however, were too variable due to sampling error for this approach to be valid. There were no significant seasonal patterns in the necromass data, and others have stressed the importance of including only significant increases in mass difference models (Singh et al., 1984; Vogt et al., 1986; Symbula and Day, 1988). An estimate of belowground NPP was derived from the sequential core data by summing significant increases in biomass throughout the year.

Implanted soil mass technique—Bags (7 cm in diam and 40 cm long) were constructed of 4.8-mm aperture nylon mesh material sewn with polyester thread. A hole with the same dimensions as the implant bag was excavated with a hand auger. For each hole, soil was hand-sifted to remove large roots and placed into the bag. The bags were then implanted into the vacant hole. Two sets of ten implanted bags were randomly set out on each site. The first set remained implanted for approximately 4 mo during late summer and fall (from July 1985 through November 1985), and a second set remained implanted for about 3 mo during spring and early summer (from April 1986 to July 1986).

During the reexcavation process, care was taken both in the field and in the lab not to disturb or pull out roots that had grown into the bags. A large area of soil was excavated along with the bag to ensure that roots remained intact within the bag. Roots on the outside of the bag were trimmed away. The reexcavated bags were then divided into four 10-cm sections and washed through a set of sieves (as previoulsy described) to remove any soil from around the roots. After washing, only live roots were sorted since we could not identify dead fine roots that may not have been removed by the initial hand-sifting. Roots were separated into three diameter classes: <2 mm, 2–5 mm, and >5 mm. Once sorted, these roots were dried for 48 hr at 70 C and weighed.

Production was taken to be the dry mass of roots that had entered the implanted bags. For comparison, daily rates of production were calculated by dividing the dry mass of the roots by the total number of days implanted.

Environmental parameters—As described in Day, West, and Tupacz (1988), on each site one shallow (1.3 m) well was installed, and water levels were continuously recorded using a Stevens type F recorder. Chart papers were replaced approximately every 16 days (32 days over the last few months of the study). A deep (3.3 m) well was also installed on each site, and a chalked measuring tape was used to periodically determine water levels out of the range of the shallow well. Concentration of oxygen in soil air and soil water was measured using a YSI dissolved oxygen meter and probe. Specialized oxygen chambers were constructed as described by Carter et al. (1984). Two sets of oxygen chambers were buried on each site at depths of 5, 15, 25, and 35 cm below the surface. The chambers were designed such that approximately 60 cc of soil air or soil water, depending on water level, could be syringed out of each chamber. If soil water was available, it was sealed within a glass jar that contained a small stirring bar. The probe was then inserted into the glass jar and the water was stirred over a magnetic stirrer until a stable reading on the meter was obtained. Dissolved oxygen in water was recorded as parts per million. Temperature of the water was recorded as well. In order to measure oxygen concentration of soil air, a specialized adaptor (analyzer cell) was used. This analyzer cell was described by Patrick (1977) and attaches to the end of the oxygen probe. Air syringed out of the chambers was passed through the adaptor and over the membrane of the probe. Percent saturation of oxygen in air was measured.

Soil and soil water pH were measured using a portable pH meter and probe. Soil pH was measured at depths of 5, 15, 25, and 35 cm below the surface by mixing soil with deionized water (50:50). Temperature, dissolved oxygen, and pH readings were taken approximately every 16 days for the majority of the study period and every 32 days during the last few months.

Statistical analyses—Data were statistically analyzed using the Statistical Analysis System (SAS) versions 4 and 5 on an IBM 3090 mainframe computer. A supplementary procedure for SAS, the KSLTEST procedure, was used to test for normality. The results did not indicate the need for data transformation. One-way analysis of variance was used to test for significant ($P < 0.01$) variation in root mass among sites, depths, and sample dates. Duncan's multiple range tests ($P < 0.01$) were run a posteriori to compare means of root mass among sites, depths, and sample dates. These tests were also performed to compare averages of oxygen concentration, pH, and temperatures among sites, depths, and sample dates.

TABLE 1. *Mean (± 1 SE) root biomass (g/m²) for each site based on measurements taken monthly from May 1985 to February 1986*

	N[a]	Fine[b]	Small	Large	Total[c]
Cedar					
0–10 cm	110	a 345 ± 16	a 126 ± 12	a 150 ± 21	621 ± 32
10–20 cm	110	b 63 ± 4	b 36 ± 6	a 45 ± 16	143 ± 18
20–30 cm	110	b 48 ± 4	b 20 ± 5	a 84 ± 32	153 ± 32
30–40 cm	110	b 44 ± 4	b 23 ± 4	a 49 ± 18	116 ± 20
0–40 cm	110	500 ± 21	205 ± 17	328 ± 47	1,033 ± 53 B
Mixed hardwood					
0–10 cm	106	a 490 ± 34	a 222 ± 18	a 338 ± 49	1,050 ± 69
10–20 cm	105	b 182 ± 81	b 140 ± 16	a 218 ± 37	540 ± 88
20–30 cm	105	b 71 ± 6	c 51 ± 9	b 85 ± 35	207 ± 39
30–40 cm	99	b 51 ± 5	c 31 ± 6	b 21 ± 11	103 ± 15
0–40 cm	106	794 ± 86	444 ± 29	662 ± 73	1,887 ± 115 A
Cypress					
0–10 cm	110	a 139 ± 7	a 73 ± 7	a 127 ± 22	340 ± 25
10–20 cm	110	b 40 ± 6	b 27 ± 4	a 129 ± 27	195 ± 29
20–30 cm	110	b 27 ± 2	b 28 ± 5	a 115 ± 33	169 ± 34
30–40 cm	110	b 24 ± 2	b 17 ± 3	a 80 ± 22	120 ± 22
0–40 cm	110	230 ± 10	145 ± 11	451 ± 50	824 ± 55 BC
Maple-gum					
0–10 cm	109	a 135 ± 9	a 65 ± 7	a 70 ± 17	270 ± 22
10–20 cm	110	b 43 ± 3	b 27 ± 4	a 83 ± 21	152 ± 23
20–30 cm	110	b 33 ± 2	b 17 ± 4	a 107 ± 21	157 ± 22
30–40 cm	110	b 32 ± 3	b 12 ± 2	a 75 ± 29	119 ± 29
0–40 cm	110	243 ± 12	121 ± 10	335 ± 47	696 ± 53 C

[a] N = sample size.
[b] Means for each depth with different lowercase letters are significantly ($P < 0.01$) different within sites.
[c] Means for the entire 40-cm profile with different uppercase letters are significantly ($P < 0.01$) different between sites.

RESULTS

Biomass and necromass—The mixed hardwood site had significantly ($P < 0.01$) greater mean total biomass than the other three sites (Table 1). The cedar site had significantly ($P < 0.01$) greater total biomass than the cypress or maple-gum sites. Fine roots constituted 48%, 42%, 28%, and 35% of total root biomass, while small roots constituted 20%, 23%, 18%, and 17% of total root biomass on the cedar, mixed hardwood, cypress, and maple-gum sites, respectively.

On all sites a significantly ($P < 0.01$) greater portion of fine and small root biomass was found in the top 10 cm of the soil (Table 1). An average of 67%, 58%, 57%, and 55% of fine and small root biomass was located within the top 10 cm on the cedar, mixed hardwood, cypress, and maple-gum sites, respectively. No differences in fine or small root biomass were found at depths below 10 cm for all sites except mixed hardwood. On the mixed hardwood site, significantly ($P < 0.01$) greater small root biomass was found within the 10–20 cm depth than the lower 20–40 cm.

Large roots constituted 32%, 35%, 55%, and 48% of total root biomass for the cedar, mixed hardwood, cypress, and maple-gum sites, respectively. A great deal of variability existed in the distribution of large roots among depths. For the cedar, cypress, and maple-gum sites, no differences between depths were found. In some samples no large roots were recorded. On the mixed hardwood site, only those sets of core samples taken in May, July, August, and September showed differences among depths. For all four dates, the 0–10 cm depth was significantly ($P < 0.01$) higher than the 20–40 cm depths.

The cedar, mixed hardwood, and maple-gum sites had about equal amounts of total necromass. The cypress site had significantly ($P < 0.01$) less total necromass than the other three sites (Table 2). Fine root necromass on the cedar, mixed hardwood, cypress, and maple-gum sites comprised 56%, 57%, 53%, and 39% of total root necromass, while small root necromass comprised 16%, 18%, 20%, and 17% of total root necromass, respectively.

For the cedar, mixed hardwood, and cypress sites, significantly ($P < 0.01$) more fine root necromass was found in the top 10 cm with no differences among depths below 10 cm. On all sites there was more small root necromass

TABLE 2. *Mean (± 1 SE) root necromass (g/m²) for each site based on measurements taken monthly from May 1985 to February 1986*

	N[a]	Fine[b]	Small	Large	Total[c]
Cedar					
0–10 cm	110	a 101 ± 11	a 27 ± 3	a 36 ± 10	163 ± 16
10–20 cm	110	b 20 ± 2	b 6 ± 1	a 11 ± 4	37 ± 5
20–30 cm	110	b 23 ± 3	b 5 ± 1	a 12 ± 4	40 ± 6
30–40 cm	110	b 21 ± 2	b 8 ± 2	a 24 ± 10	52 ± 11
0–40 cm	110	165 ± 12	46 ± 5	83 ± 16	292 ± 22 A
Mixed hardwood					
0–10 cm	106	a 114 ± 11	a 33 ± 5	a 42 ± 15	189 ± 22
10–20 cm	105	b 22 ± 3	b 12 ± 3	a 26 ± 11	60 ± 13
20–30 cm	105	b 16 ± 2	b 5 ± 2	a 4 ± 2	26 ± 4
30–40 cm	99	b 12 ± 2	b 2 ± 1	a 1 ± 1	15 ± 2
0–40 cm	106	164 ± 13	52 ± 7	73 ± 21	288 ± 29 A
Cypress					
0–10 cm	110	a 54 ± 5	a 23 ± 3	a 20 ± 6	97 ± 9
10–20 cm	110	b 10 ± 1	b 3 ± 1	a 7 ± 3	20 ± 4
20–30 cm	110	b 8 ± 1	b 2 ± 1	a 2 ± 1	12 ± 2
30–40 cm	110	b 8 ± 1	b 2 ± 1	a 12 ± 8	22 ± 8
0–40 cm	110	80 ± 6	30 ± 3	41 ± 12	150 ± 15 B
Maple-gum					
0–10 cm	109	a 49 ± 4	a 27 ± 3	a 32 ± 8	107 ± 10
10–20 cm	110	c 13 ± 1	b 6 ± 1	a 10 ± 4	29 ± 4
20–30 cm	110	bc 14 ± 1	b 6 ± 1	a 21 ± 6	41 ± 7
30–40 cm	110	b 24 ± 3	b 5 ± 1	a 50 ± 15	79 ± 16
0–40 cm	110	100 ± 7	44 ± 4	113 ± 18	255 ± 21 A

[a] N = sample size.
[b] Means for each depth with different lowercase letters are significantly ($P < 0.01$) different within sites.
[c] Means for the entire 40-cm profile with different uppercase letters are significantly ($P < 0.01$) different between sites.

in the top 10 cm than below. Large roots constituted 28%, 25%, 27%, and 44% of the annual mean total root necromass on the cedar, mixed hardwood, cypress, and maple-gum sites, respectively. For all sites, there were no differences in vertical distribution of large root necromass; however, much variability existed between sample dates.

Seasonal standing crops—On all sites except maple-gum, significant ($P < 0.01$) peaks or troughs in fine root biomass occurred in the top 10 cm of the soil. Both the cedar and mixed hardwood sites showed no significant temporal variation at depths below 10 cm. The lowest mean on the cedar site within the top 10 cm occurred in early November and was followed by a significant ($P = 0.0067$) increase in mid-December (Fig. 1). On the mixed hardwood site, a significant ($P = 0.0003$) increase was also recorded for mid-December and this was followed by a significant ($P < 0.01$) decrease in mid-February. The 20–30-cm depth on the cypress site displayed an increase from early April to early May. The maple-gum site displayed no significant seasonal variation in the 0–30 cm depth; however, the 30–40 cm depth did show a significant ($P = 0.0059$) increase from 17 g m^{-2} in early June to 57 g m^{-2} by late June.

No significant peaks or troughs in small or large root biomass were recorded at any depth on any site. Patterns in seasonal activity for all sizes of dead roots were extremely difficult to discern as much variability existed within the data. Because of this, no generalizations concerning necromass could be made.

Production estimates—Significant increases in root biomass during the core sampling period were summed to estimate belowground net primary production. The mixed hardwood site had the highest production estimate (989 g m^{-2} yr^{-1}) followed by cedar (366 g m^{-2} yr^{-1}), cypress (308 g m^{-2} yr^{-1}), and maple-gum (59 g m^{-2} yr^{-1}).

For both sets of implant bags, the mixed hardwood site had a significantly ($P < 0.01$) higher belowground production rate than the cypress or maple-gum sites (Table 3). The value for the cedar site was lower than for mixed hardwood, but the difference was not significant. Only the cedar and mixed hardwood sites displayed a significant decrease in production

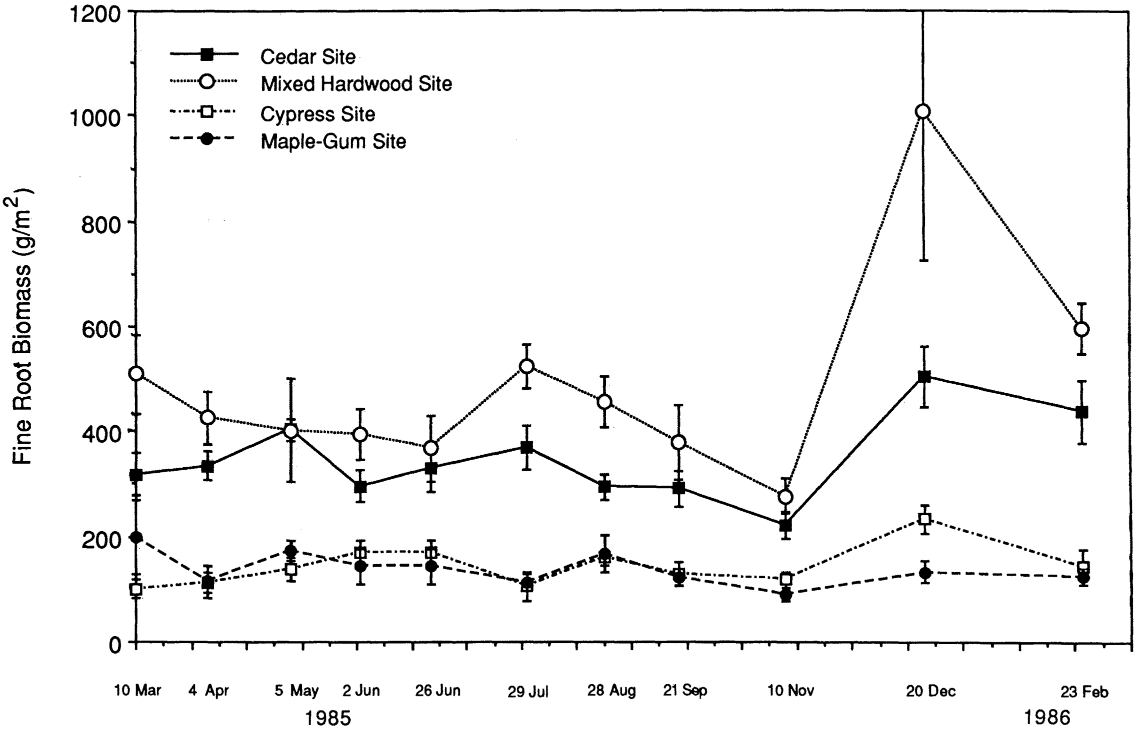

Fig. 1. Seasonal fine (<2 mm diam) root biomass in top 10 cm of soil. Vertical bars represent ± 1 SE.

with increasing depth. There was no significant difference between the two sets of bags. The mean daily production rate projected over a full year yielded annual production estimates that were generally lower than the estimates based on increases in biomass in sequential cores. These values were 354 g m^{-2} yr^{-1} for the mixed hardwood site, 274 g m^{-2} yr^{-1} for cedar, 68 g m^{-2} yr^{-1} for cypress, and 91 g m^{-2} yr^{-1} for maple-gum.

Environmental parameters—Because the cypress site was inundated up to 25 cm above the soil surface during winter months, it was thought that soils within the rooting zone were saturated during the summer months as well. However, during the months of July, August, September, and October, water levels were lower on this site than on any other site (Fig. 2). The cedar site was flooded within the rooting zone for the longest duration, followed by the maple-gum site, the cypress site, and lastly the mixed hardwood site. All sites remained flooded to within the rooting zone (within 40 cm of the surface) at least 30% of the time (Day, West, and Tupacz, 1988).

The unflooded mixed hardwood site had the highest oxygen concentrations in soil water among sites for the 0–20-cm and 20–40-cm depths (Table 4). This difference was highly significant (ANOVA, $P < 0.01$) during more than half of the sample periods. The pH on the cedar site was significantly lower than on all other sites during all sample periods (ANOVA, $P < 0.0001$). The other three sites were not significantly different from each other.

DISCUSSION

Both saturation of soil and lack of water profoundly affect root growth (Hermann, 1977). Analysis of our data has shown that the mixed hardwood site had the greatest biomass, the second largest necromass, and the greatest production rate of all the study sites. Most importantly, this site was not flooded. Inundation above the soil surface on this site was limited to a few low-lying depressions and only occurred during the winter months. Saturation within the rooting zone (40 cm) occurred only 30% of the time. The soil remained aerobic (significantly higher oxygen levels than the other sites) but moist.

The cedar site was the wettest of all sites. Although inundation above the surface occurred very rarely, the soil within the rooting zone remained saturated nearly 75% of the time. Root biomass and production were second greatest and necromass was greatest on this site. Greater necromass could be the result of

TABLE 3. *Estimated production values (± 1 SE) using an implanted bag technique*

	July–December				April–July			
	N[a]	Production[b,c] (g m^{-2})	Days	Daily production (g m^{-2})	N	Production (g m^{-2})	Days	Daily production (g m^2)
Cedar								
0–10 cm	10	a 64 ± 23	124	0.52	8	a 33 ± 22	95	0.35
10–20 cm	10	ab 21 ± 9	124	0.17	8	ab 16 ± 5	95	0.17
20–30 cm	10	ab 14 ± 5	124	0.11	8	b 6 ± 1	95	0.06
30–40 cm	10	b 7 ± 2	124	0.06	8	b 4 ± 1	95	0.04
0–40 cm	10	107 ± 31 AB	124	0.86	8	61 ± 17 AB	95	0.64
Mixed hardwood								
0–10 cm	10	a 30 ± 8	133	0.23	10	a 51 ± 17	94	0.54
10–20 cm	10	a 46 ± 12	133	0.35	10	ab 24 ± 9	94	0.26
20–30 cm	10	a 23 ± 5	133	0.17	10	ab 12 ± 4	94	0.13
30–40 cm	10	a 22 ± 5	133	0.17	10	b 9 ± 1	94	0.10
0–40 cm	10	121 ± 22 A	133	0.91	10	97 ± 24 A	94	1.03
Cypress								
0–10 cm	10	a 12 ± 4	134	0.09	10	a 5 ± 1	99	0.05
10–20 cm	10	a 6 ± 2	134	0.05	10	a 7 ± 2	99	0.07
20–30 cm	10	a 3 ± 1	134	0.02	10	a 4 ± 1	99	0.04
30–40 cm	10	a 4 ± 2	134	0.03	10	a 3 ± 1	99	0.03
0–40 cm	10	25 ± 6 C	134	0.19	10	18 ± 3 B	99	0.18
Maple-gum								
0–10 cm	10	a 10 ± 3	137	0.07	10	a 11 ± 2	93	0.12
10–20 cm	10	a 9 ± 4	137	0.07	10	a 8 ± 6	93	0.09
20–30 cm	10	a 7 ± 3	137	0.05	10	a 4 ± 1	93	0.04
30–40 cm	10	a 5 ± 2	137	0.04	10	a 3 ± 1	93	0.03
0–40 cm	10	31 ± 8 BC	137	0.23	10	25 ± 9 B	93	0.27

[a] N = sample size.
[b] Means for each depth with different lowercase letters are significantly ($P < 0.01$) different within sites.
[c] Means for the entire 40-cm profile with different uppercase letters are significantly ($P < 0.01$) different between sites.

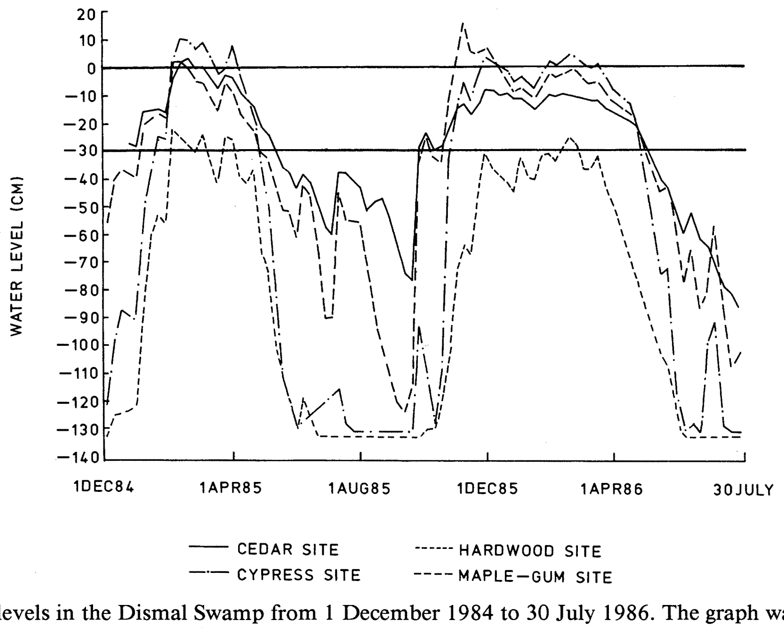

Fig. 2. Water levels in the Dismal Swamp from 1 December 1984 to 30 July 1986. The graph was generated from weekly means. Top horizontal line indicates soil surface; lower horizontal line indicates bottom of root zone. Depths to the bottom of the shallow wells were 124 cm (maple-gum), 131 cm (cypress), and 133 cm (mixed hardwood). The cedar well never had water levels near the bottom.

TABLE 4. *Range of environmental factors for each site by depth. These are not mean values but represent actual measurements taken at two different depths within each depth category. They are summarized this way because root mass and production differed most between surface and bottom with few gradients evident. Annual means are in parentheses*

Site	Depth[a]	O_2SW[b]	O_2SA[c]	Temp[d]	pH[e]
Cedar	1	0.63–11.36	96–99	8.56–19.65	3.48–3.97
		(3.08)	(98.53)	(11.18)	(3.68)
	2	0.31–9.94	78–99	8.32–23.85	3.44–4.01
		(2.41)	(93.99)	(12.75)	(3.69)
Maple-gum	1	0.36–10.0	80–99	6.43–19.93	4.38–5.03
		(4.05)	(94.29)	(11.39)	(4.69)
	2	0.29–6.36	93–97	6.33–20.93	4.53–5.23
		(1.93)	(94.76)	(12.39)	(4.90)
Cypress	1	1.07–9.06	95–99	5.84–21.73	4.58–5.14
		(2.87)	(96.86)	(11.52)	(4.76)
	2	0.57–7.93	89–97	6.03–20.38	4.54–5.25
		(2.16)	(92.69)	(12.10)	(4.89)
Mixed hardwood	1	1.0–11.96	96–99	7.95–20.60	3.97–5.08
		(7.16)	(97.98)	(11.65)	(4.49)
	2	0.63–9.68	75–98	8.44–22.00	4.57–5.61
		(3.73)	(92.98)	(12.07)	(5.14)

[a] 1 = 0–20 cm and 2 = 20–40 cm.
[b] mg/l oxygen in soil water.
[c] % air saturation with oxygen when chambers were dry.
[d] Temperature of soil water in °C.
[e] Soil pH taken as 50:50 mixture of soil:deionized water.

lower decomposition rates reported for this site (Tupacz and Day, 1990). High biomass and production values could be partly attributable to high density of trees and a dense shrub layer (Dabel and Day, 1977; Montague and Day, 1980).

The cypress and maple-gum sites had similar amounts of root mass and rates of production, yet conditions on these sites were very different. Soils present on the cypress site are thick clays that harden as flooding recedes. This hardened clay may act as a mechanical resistance to root growth and may partially account for relatively low standing crops and production rates. Also, even though the cypress site floods to approximately 20–30 cm above the surface in winter and spring, and is the most extensively flooded site during that period, it has a perched water table, and water levels can drop extremely low during the summer. The cypress site may have experienced drought stress during the growing season. The maple-gum site, in contrast, contains a mucky soil, high in organics and lacking in zonation. The maple-gum site remains saturated a greater percentage of the year than does the cypress site, yet mean oxygen levels are higher on this site.

Standing crops of live roots obtained by the core technique were similar to Symbula and Day's (1988) for the maple-gum site using the same method and were consistent with other estimates reported in the literature (Lugo, Nessel, and Hanlon, 1978; Montague and Day, 1980; Brown, 1981; Kane, 1981). Symbulla and Day's estimate of mean annual biomass for 0–40 cm was 583 g/m^2 based on 12 samples taken over a period of 335 days in 1983 and 1984. This is similar to our estimate of 699 g/m^2 based on 11 samples over 343 days.

The two studies differed in their estimate of production on the maple-gum site, as our estimates were considerably lower than Symbula and Day's. The present study estimated 59 g m^{-2} yr^{-1} based on biomass increases and 91 g m^{-2} yr^{-1} from implant bags. Symbula and Day (1988) reported 645 g m^{-2} yr^{-1} and 597 g m^{-2} yr^{-1} based on similar methods. Our estimates from two methods for all four sites, ranging from 59 to 989 g m^{-2} yr^{-1}, are on the low side of values reported from other studies (87 to 1,629 g m^{-2} yr^{-1}) (Reader and Stewart, 1972; McGinty, 1976; Harris, Kinerson, and Edwards, 1977; McClaugherty, Aber, and Melillo, 1982; Persson, 1983; Burns, 1984; Nadelhoffer, Aber, and Melillo, 1985). Kurz and Kimmins (1987) have suggested that the three major sources of uncertainty associated with root production estimates obtained from seasonal data will more often underestimate true turnover rates than overestimate. The three sources of uncertainty due to sampling error are the concurrence of production and mortality, accuracy of distinguishing live and dead roots, and whether sample dates coincide with peaks and troughs in the seasonal pattern.

Estimates of production using the implanted soil mass technique were generally lower than estimates using the sequential coring approach. Symbula and Day (1988) also obtained lower estimates by the implant bag technique. During the initial design stages of the present study, it was decided that all existing roots should be removed from the soil placed in the implant bag. This created a disturbed yet vacant space for roots to grow into. Also, in order to implant the bag, roots surrounding the hole were severed. Because of the available rooting space and possible stimulation of roots due to pruning, artificially elevated rates of production were expected. However, the low estimates seem to indicate this was not the case.

Hermann (1977), in his review of growth and production of tree roots, cited several investigations that reported distinct seasonal changes in roots with diameters less than 2 mm. The most frequent pattern within temperate climates was one of cessation of most activity in winter and resumption again in the spring. He also reported alternating cycles of activity and rest during the growing season. In the present study, fine root production peaked in summer and late fall-winter only on the mixed hardwood and cedar sites (the most productive sites); whereas, Symbulla and Day (1988) found a late spring and winter peak in production on the maple-gum site. Santantonio and Hermann (1985) suggested that pulses in production during certain times of the year may be attributed to the activity of one or two species. They also suggested that if such pulses cannot be explained by abiotic influences, perhaps the next step is to sort roots according to species.

Megonigal and Day (1988) recently published an organic matter budget for the same four sites used in the present study. They obtained estimates of belowground production by multiplying total root biomass values reported by Montague and Day (1980) by a production : biomass ratio of 1.2. This ratio was based on estimates of fine root net primary production and mean annual fine root biomass for the maple-gum site reported by Symbula and Day (1988). Megonigal and Day (1988) found aboveground production was significantly higher on the flooded sites than on the rarely flooded site (mixed hardwood). Belowground production was similar to aboveground on the flooded sites; however, on the rarely flooded site, belowground production was nearly three times greater than aboveground. In the present study, belowground production rates were lower than Megonigal and Day's estimates, but the same pattern held. The rarely flooded site still had the highest allocation belowground.

Megonigal and Day's (1988) data indicate that substantially more carbon was allocated to root growth than to aboveground production on rarely flooded sites (73% of total net primary production for the mixed hardwood site, compared to 53% for cedar, 46% for cypress, and 44% for maple-gum). The present study marginally substantiates their observation (54% of NPP in the mixed hardwood site was belowground based on sequential core estimates). Duration of flooding and soil saturation appeared to influence allocation patterns. Studies on red maple seedlings in the greenhouse (Day, 1987) and bald cypress trees in mesocosms (P. Megonigal and F. Day, unpublished data) also showed higher allocation belowground in treatments flooded for the least duration. The mesocosm data in particular show that cypress trees exposed to periodic flooding (comparable to the three flooded sites in the Dismal Swamp) allocate more belowground than continuously flooded trees. The field data from the Dismal Swamp and the mesocosm data seem to support a continuum of increasing belowground allocation from continuously flooded to rarely flooded but moist sites.

Raich and Nadelhoffer (1989) suggested that aboveground production and belowground carbon allocation are strongly interrelated in forests (one process controls the other or both are controlled by the same factors), but there is considerable uncertainty above whether the ratio of aboveground to belowground carbon allocation changes along production gradients. Our data suggest that the ratio does change in response to environmental gradients, e.g., flood duration. This is an important observation in the context of overall ecosystem structure and function. Carbon allocation patterns (above vs. belowground) determine the array of litter types generated (leaves vs. roots) which determine decomposition rates and nutrient availability (Aber et al., 1985).

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