

THE RELATIONSHIP BETWEEN VARIABLE HYDROPERIOD, PRODUCTION ALLOCATION, AND BELOWGROUND ORGANIC TURNOVER IN FORESTED WETLANDS

Frank P. Day, Jr.
Department of Biological Sciences
Old Dominion University
Norfolk, VA 23529

J. Patrick Megonigal
Department of Botany
Duke University
Durham, NC 27706

Abstract: Belowground processes in forested wetland ecosystems are exceptionally important, yet most attention seems to focus on surface flooding regimes and other aboveground features of these systems. Field studies in the Dismal Swamp and several manipulative experiments examined belowground dynamics in relation to a flood intensity gradient. Generally, more extensive flooding results in less production allocation belowground. Erroneous conclusions regarding wetland production are reached if aboveground parameters alone are considered. Root decomposition rates are slowest where the duration of soil saturation is the longest. Organic accumulation rates in wetlands are determined by the amount of production of particular biomass types (eg., leaves vs. roots) and the rate at which they decompose. Biomass allocation patterns seem to change in response to a flooding gradient. This represents a major implication for wetland ecosystem functions, as carbon allocation patterns determine the array of litter types that affect decomposition rates and thus nutrient availability. The hydroperiod data from the Dismal Swamp demonstrate the highly variable nature of flooding in forested wetlands, especially during the growing season. The data suggest that it is unwise to rely on hydroperiod as a direct criterion for identifying a jurisdictional wetland.

Key Words: allocation, belowground, forested wetland, hydrology, hydroperiod, production

INTRODUCTION

Hydrology is the dominant controlling influence on ecosystem dynamics in forested wetlands (Conner et al. 1981, Brinson et al. 1981, Brown 1981, Wharton et al. 1982, Brinson et al. 1984, Day et al. 1988). However, surface flooding seems to receive an inordinate amount of attention in spite of the knowledge that the hydroperiod in most forested wetlands is extremely variable and the hydrodynamics of these systems primarily occur below the soil surface (Day et al. 1988). The overemphasis on aboveground features of forested wetlands also extends to estimates of primary production and organic turnover, even though belowground contributions often differ dramatically from aboveground contributions (McClougherty et al. 1982, Vogt et al. 1986, Megonigal and Day 1988, Powell and Day 1991, Megonigal and Day 1992). For instance, roots can represent a highly significant contribution to system productivity. In the Dismal Swamp, roots con-

tribute as much as 60% of the annual increment to soil organic matter (Megonigal and Day 1988). There is a lot of activity below the soil surface in terms of biological processes and hydrological control; consequently, ecosystem-level patterns and relationships cannot be inferred from aboveground data alone.

A stress-subsidy gradient has been proposed, which suggests that too little or too much water reduces primary productivity and organic turnover rates (Mitsch and Ewel 1979) (Figure 1). Our primary objective in this paper was to review some of our previous work in relation to such a stress-subsidy gradient and particularly to emphasize the significance of belowground data in the evaluation of these relationships. We have used results from field studies in the Great Dismal Swamp in Virginia, a greenhouse experiment on red maple (*Acer rubrum* L.) seedlings, and a mesocosm-scale experiment with bald cypress (*Taxodium distichum* (L.) Richard).

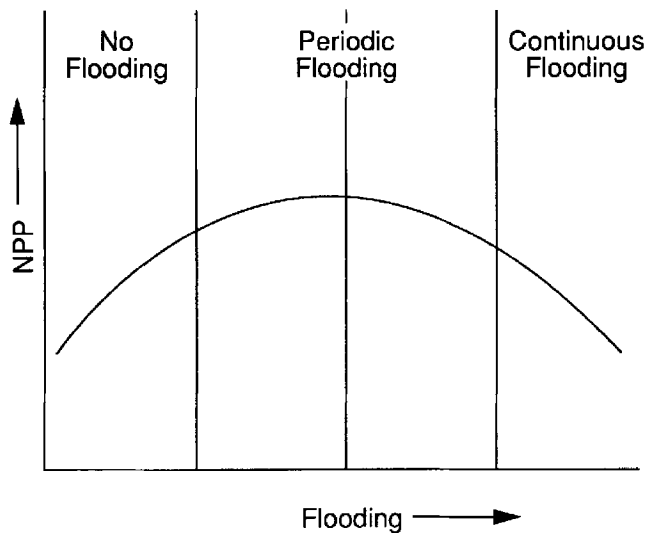


Figure 1. Hypothetical stress-subsidy relationship that suggests too little or too much water inhibits net primary production in forested wetlands.

METHODS

Field Studies

Study Area. The Great Dismal Swamp is located on the coastal plain in southeastern Virginia and northeastern North Carolina. The soils are highly acidic (pH 3.2–5.6), relatively low in nutrients, and high in organics. Flooding occurs during the winter and spring months and following periods of abundant rain. Flood depth and frequency vary throughout the swamp.

The research was conducted on four sites that have been extensively studied (Dabel and Day 1977, Day 1982, Megonigal and Day 1988). The cypress site is dominated by bald cypress, red maple, and black gum (*Nyssa sylvatica* var. *biflora* (Walter) Sargent). The maple-gum site is characterized by water gum (*Nyssa aquatica* L.), red maple, and black gum. Dominant tree species on the cedar site include Atlantic white cedar (*Chamaecyparis thuyoides* (L.) BSP.), black gum, and red maple. The mixed hardwood community is dominated by laurel oak (*Quercus laurifolia* Michaux), white oak (*Quercus alba* L.), and sweet gum (*Liquidambar styraciflua* L.). More detailed site descriptions can be found in Dabel and Day (1977) and Day (1982).

Hydrology. Water levels were continuously recorded by Stevens model F water-level recorders installed on a shallow ground-water well on each site (Day et al. 1988). The depth of the wells was 1.3 m. Water levels were recorded from December, 1984 to July, 1986, and the data were digitized daily. A non-recording deep well was also installed to a depth of 3.3 m, and water levels were determined with a chalked tape.

Biomass and Production. Aboveground biomass and

production were estimated from diameter-mass regressions (Day and Dabel 1978) and biomass increments based on diameter growth (Megonigal and Day 1988). On each site, the diameter of all trees in ten 10 × 10 m plots was recorded during the summer of 1975. Leaf and wood biomass were estimated from regression equations of the form $\log_{10} \text{dry mass} = A + B \log_{10} \text{diameter}$. Separate equations were used for leaves, boles, and branches and for hardwoods, cedar, and cypress. Aboveground woody production was determined by increasing the original diameters by annual increments measured with vernier tree bands (Day 1985) and then estimating the increase in biomass. Leaf production was assumed to equal leaf biomass for deciduous species and leaf litter production for evergreen species.

Belowground biomass and production were determined by the sequential coring technique (Powell and Day 1991). Ten soil cores were extracted each month from each of the four sites from March 1985 through February 1986. Cores were obtained with a 7-cm diameter bucket auger to a depth of 40 cm. The roots were washed in nested sieves, sorted by size category and dead or alive, oven dried at 70 C for 48 hr, and weighed. An estimate of belowground production was obtained by summing significant increases in biomass throughout the year. Even though the aboveground and belowground data were not determined in the same year, we feel the patterns are valid.

Decomposition. Root decomposition rates were quantified by a modified litter bag method that involved recovery of 40-cm-long mesh bags of pre-weighed roots inserted vertically into the soil (Tupacz and Day 1990). Roots used in the bags were collected from the maple-gum site. Most of the roots were 2 to 5 mm in diameter and about 10–20% by volume were less than 2 mm in diameter. All bags were implanted during the first 2 weeks of January 1985. The first nine sets of samples were taken approximately every 4 weeks. The remaining three sets were spaced approximately 7, 6, and 8 weeks apart. Five replicates were removed from each site on each sample date. After retrieval, litter bags were washed, opened, and ingrown roots removed. The samples were oven dried and weighed. Rates of decomposition for the entire study period were calculated with a simple linear model ($y = mx + b$) where the slope (m) represents the instantaneous decay rate in $\text{mg g}^{-1} \text{day}^{-1}$.

Greenhouse Studies

Conditions of the experiment included potted first year red maple seedlings exposed to three different flooding regimes in a greenhouse (no flooding, periodic

flooding, and continuous flooding). Seedlings were transplanted into 15-cm clay pots filled with soil from the maple-gum site. At the start of the 1985 growing season, the potted seedlings were placed into 33 cm × 33 cm × 20.5 cm deep, water-tight, plastic boxes (4 pots per box). Flooded plants were inundated to 5 cm above the soil surface throughout the 7 month experiment. The periodically flooded plants were alternately drained and reflooded every two weeks. The unflooded plants were watered two to three times a week with constant volumes of water.

The experiment was completed over one growing season, at which time the plants were beginning to show a root-bound condition in the pots. After 7 months, 20 plants from each treatment were harvested, and aboveground and belowground biomass were determined (Day 1987). Preweighed unconfined bundles of maple-gum roots were also inserted into the pots, and 20 bundles were retrieved at the end of the study to determine mass loss rates (Day et al. 1989).

Mesocosm Studies

Twenty-five cypress seedlings were planted at regular spacing into two large (8.0 m² × 1.5 m deep) wetland rhizotron cells in the Savannah River Ecology Laboratory rhizotron. One cell was continuously flooded, and a seasonal flooding regime was simulated in the other (Day et al. 1989, Megonigal and Day 1992). The reconstructed soil profiles consisted of 100 cm of a sapric Histosol underlain with 10 cm of sand and 10 cm of gravel. A pipe in the bottom of each cell allowed soil-water to drain at a controlled rate; the soil-water pool turned over about every 9 mo. Creek water was pumped from a polyethylene storage tank and sprinkled onto the soil surface to replace drained water. A system of wells, floats, solenoid switches, and pumps prevented the water table from falling below a prescribed depth. The prescribed depth was +20 cm above the soil surface in the continuously flooded cell and varied in the periodically flooded cell according to the following schedule: -20 cm from March to May and October to December, -50 cm from June to September, and +20 cm from January to February.

The experiment was conducted over a three-year period (May 1986 to October 1988), and thus, some of the deficiencies of potted plant studies were remedied. A sample of plants (N = 8 in 1986 and 1988; N = 9 in 1987) was harvested each October prior to leaf abscission, and aboveground biomass was determined. Plants were harvested in a pattern designed to maximize interplant distances among remaining plants. Root biomass was quantified by pit excavations centered on each plant (30 × 30 cm to 30-cm depth) and, in the final year, complete excavation of the root systems.

Root decomposition rates were measured by the same vertical litter bag technique used in the Dismal Swamp (Day et al. 1989). Five bags of cypress roots were recovered from each treatment after 17 months and percent mass loss was determined. Vertical patterns of redox potential and oxygen levels were simultaneously determined with three fused platinum/copper redox probes and two oxygen chambers buried at 20-cm depth intervals.

RESULTS AND DISCUSSION

Hydrology

Large fluctuations in water levels occur in the Dismal Swamp (Figure 2). Very little surface flooding occurs; only the cypress site showed surface flooding during the growing season in this study. On all sites, the duration of soil saturation in the root zone is relatively short during the growing season. All but the mixed hardwood site experienced extensive saturation in the root zone throughout the winter months. The water level at the cypress site dropped precipitously in the summer (3.25 m below the soil surface). The ranking of sites based on mean annual water levels in 1985 was cedar > maple-gum > cypress > mixed hardwood. Our data demonstrate the highly variable nature of flooding in forested wetlands, especially during the growing season.

Biomass and Production Allocation

Our data suggest that attempts to fit forested wetlands to a stress-subsidy curve (Figure 1) may be inaccurate if belowground production is not included. Biomass data show no trend aboveground (Figure 3), although there were no continuously flooded sites representing the wet extreme of the stress-subsidy gradient. The flooded sites in the Dismal Swamp had significantly less belowground biomass than the unflooded mixed hardwood site (Figure 3), but the lack of pattern aboveground is not altered by adding the belowground data. The production data present a different story. The flooded sites had significantly greater aboveground production, but less belowground, than the unflooded site (Figure 4). Production allocation patterns are different under different flooding regimes. Aboveground production data suggest that the unflooded site is the least productive, but the addition of the belowground data demonstrates that the site is actually the most productive. The possible interpretations of aboveground values can be considerably different with the addition of belowground data.

In the mesocosm study, the results from the first two growing seasons were similar to the findings of many

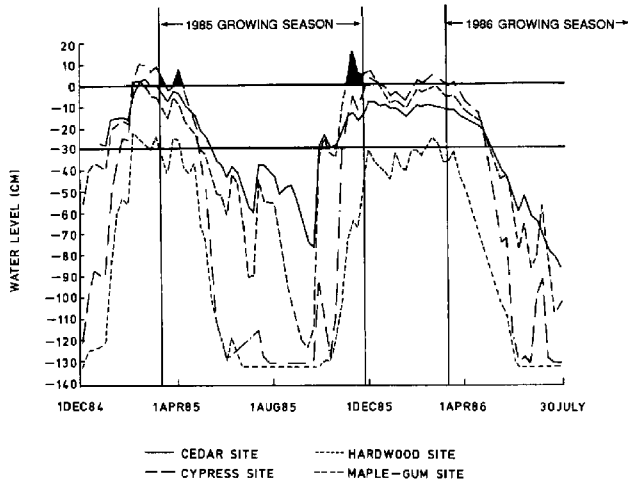


Figure 2. Water levels generated from weekly means. Top horizontal line indicates soil surface; lower horizontal line indicates approximate bottom of root zone. Vertical lines approximate limits of growing season. Surface flooding during growing season is shaded black. The deepest levels recorded represent the bottom of the wells. (modified from Day et al. 1988)

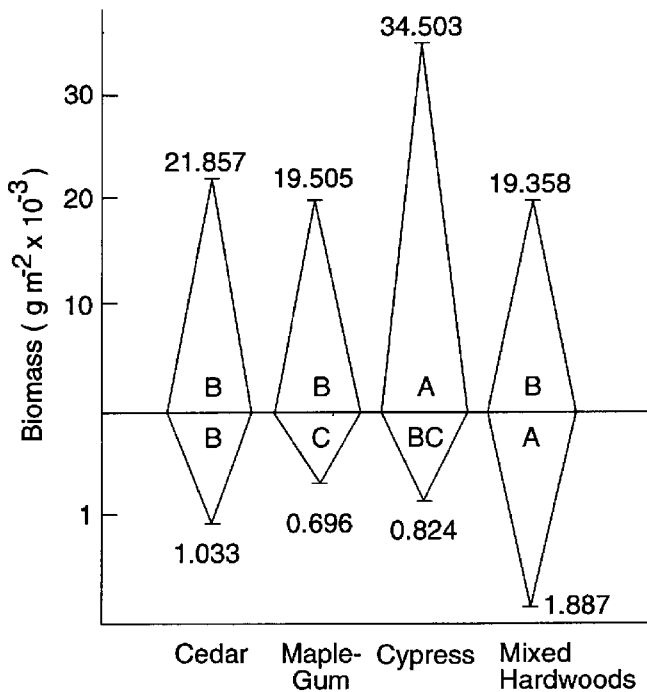


Figure 3. Aboveground and belowground biomass allocations on each of the Dismal Swamp study sites. Sites with different letters are significantly different (ANOVA and Duncan's Range Test, $P \leq 0.05$). $N=10$ for aboveground data and $N=110$ for belowground data (106 for mixed hardwood site). Note that the aboveground and belowground scales differ.

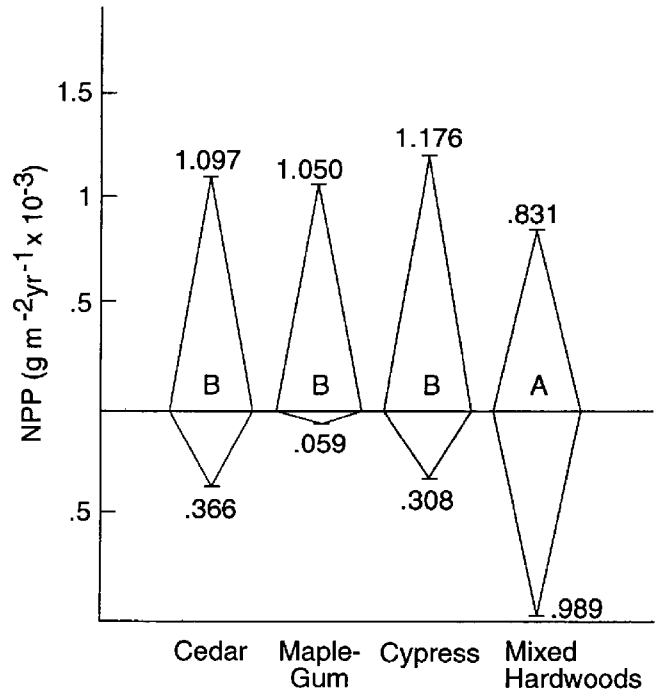


Figure 4. Aboveground and belowground net primary production allocations on each of the Dismal Swamp study sites. $N = 10$ for aboveground data. Sites with different letters are significantly different (ANOVA and Duncan's Range Test, $P \leq 0.01$). The method of estimating root production did not allow statistical testing since those values are the sum of differences between sample data means. However, other techniques used on these same sites demonstrate the same statistically significant trends (Powell and Day 1991).

1-year studies of potted plants (Keeley 1979, Sena Gomes and Kozlowski 1980, Norby and Kozlowski 1983, Kozlowski 1984, Peterson and Bazzaz 1984, Donovan et al. 1988). There was significantly less aboveground and belowground biomass in the continuously flooded treatment compared to the periodically flooded treatment (Table 1). However, by the end of the third growing season, the aboveground biomass of the continuously flooded plants was not statistically different from the periodically flooded plants, although belowground production was still significantly greater in the periodically flooded treatment. Total production was about equal in the two treatments by the third growing season. The first year response was possibly due to inhibition by the flooding in the continuously flooded seedlings, and acclimation subsequently took place (Magonigal and Day 1992). A greater proportion of the stems of the first year plants were under water. A conclusion of reduced production in more extensively flooded conditions is reached if the study duration is short, but different conclusions are reached if the study is of longer duration. Allocation ratios of aboveground and belowground production vary in re-

Table 1. Annual biomass increment ($\text{g plant}^{-1} \text{yr}^{-1}$) for red maple seedlings in the greenhouse and bald cypress seedlings in the mesocosms. Treatments with different letters are significantly different (ANOVA and Duncan's Range Test, $P \leq 0.05$). $N = 20$ for greenhouse study; $N = 8$ in mesocosms in 1986 and 1987 and $N = 9$ in 1988.

Study	Year	Treatment	Aboveground Production	Belowground Production	Total Production
Greenhouse	1985	no flooding	8.5 A	7.2 A	15.7 A
		periodic flooding	6.4 B	3.5 B	9.9 B
		continuous flooding	4.5 C	2.1 C	6.6 C
Mesocosm	1986	periodic flooding	64.7 A	31.7 A	96.4 A
		continuous flooding	22.0 B	11.4 B	33.4 B
	1987	periodic flooding	420.9 A	179.0 A	599.9 A
		continuous flooding	308.4 B	129.6 B	438.0 B
	1988	periodic flooding	718.7 A	739.8 A	1,458.5 A
		continuous flooding	1,026.8 A	448.8 B	1,475.6 A

sponse to hydroperiod and duration of exposure to a given hydroperiod.

In the greenhouse study, there was a significant gradient of decreasing production (aboveground and belowground) from the unflooded treatment to the continuously flooded treatment (Table 1). The more extensively flooded plants also showed a lower percent allocation of production belowground. A study of longer duration may have produced different results. The continuously flooded maple seedlings showed signs of compensatory activity and acclimation by producing extensive adventitious water roots (Day 1987).

Decomposition

Root decomposition rates were consistently lower on the sites with the longest duration of soil saturation in the Dismal Swamp and in the more extensively flooded experimental treatments in the greenhouse and mesocosm studies (Table 2). The flooding extremes in

all three studies were significantly different. Inhibition of root decomposition rates was at least partly due to more anaerobic conditions in the more extensively flooded treatments (Day et al. 1989). Thus, sites or conditions that favor the greatest belowground production also show the highest organic turnover rates. However, sites or conditions that result in a higher proportion of production allocated belowground may be putting more into more recalcitrant tissues (roots).

CONCLUSIONS

Production allocation patterns (ratios) seem to vary in response to a flooding gradient. The major implication with regard to ecosystem function and process rates is that carbon allocation patterns determine the array of litter types (aboveground versus belowground or leaf versus root) produced, which in turn affects decomposition rates and thus nutrient availability (Aber et al. 1985, Powell and Day 1991). Because of the

Table 2. Decomposition rates of maple-gum roots in the field and greenhouse and cypress roots in the mesocosms. All data are from the top 20 cm of soil. Treatments or sites with different letters are significantly different (ANOVA and Duncan's Range Test, $P \leq 0.05$). N for each study was field = 58–60, greenhouse = 20, mesocosm = 5.

Study	Period (months)	Site	Treatment	Decomposition Rate ($\text{mg g}^{-1} \text{day}^{-1}$)	Percent Mass Remaining
Dismal Swamp (field)	12	cedar		-0.92 B	
		maple-gum		-0.83 B	
		cypress		-1.15 AB	
		mixed hardwood		-1.36 A	
Greenhouse	7		no flooding		54 A
			periodic flooding		68 B
			continuous flooding		70 B
Mesocosm	17		periodic flooding		67 A
			continuous flooding		77 B

variability in production allocation patterns, studies that neglect to quantify the belowground portion of the system are missing a substantial component of the system's response. Many ecological evaluations of forested wetland ecosystems with regard to flooding gradients (Figure 1) or other parameters should be viewed with caution if belowground data are absent. Aboveground data alone can generate inaccurate conclusions.

The results of the mesocosm study suggest that the stress-subsidy curve for flooding influence on production in wetlands may need some revision. Total production levels were about the same after three years in continuously flooded and periodically flooded treatments. The effects of the conditions of an experiment should be carefully considered before generalizing the results. Short-term studies of flooding effects on potted plants may yield results that do not represent plant responses to longer durations of flooding. One growing season in a pot represents a limited view of the effects of flooding on plant growth and production.

Finally, the hydroperiod data from the Dismal Swamp provide a basis for evaluation of the regulatory significance of hydrology. The highly variable nature of flooding and soil saturation during the year, from year to year, and from one location to another suggests that it is unjustified and impractical to use hydrology as a criterion for identifying jurisdictional wetlands. Delineation methods for jurisdictional wetlands requiring use of three criteria (hydrology, soils, vegetation), rather than two of these three criteria, are thus not practical. Soils and vegetation are products of their hydrological regimes and are persistent features of the system. The absence of flooded or saturated soils during a specific period does not indicate the area is a non-wetland.

ACKNOWLEDGMENTS

We thank Susan Powell, Jerry Tupacz, and Lyndon Lee for contributing portions of the work upon which this paper is based. Funding for the research has come from a variety of sources but principally the NERP program of the Savannah River Ecology Laboratory and the Division of Wetlands (contract DE-AC09-76SR00-819 between the U.S. Department of Energy and the University of Georgia), the Oak Ridge Associated Universities Faculty Research Participation program (contract S-3221), and the National Science Foundation (DEB-7708609, DEB-7708609-A01, and BSR-8405222).

LITERATURE CITED

Aber, J.D., J.M. Melillo, K.J. Nadelhoffer, C.A. McClaugherty, and J. Pastor. 1985. Fine root turnover in forest ecosystems in re-

- lation to quantity and form of nitrogen availability: a comparison of two methods. *Oecologia* 66: 317-321.
- Brinson, M.M., A.E. Lugo, and S. Brown. 1981. Primary productivity, decomposition and consumer activity in freshwater wetlands. *Annual Review of Ecology and Systematics* 12: 123-161.
- Brinson, M.M., H.D. Bradshaw, and E.S. Kane. 1984. Nutrient assimilative capacity of an alluvial floodplain swamp. *Journal of Applied Ecology* 21: 1041-1057.
- Brown, S. 1981. A comparison of the structure, primary productivity, and transpiration of cypress ecosystems in Florida. *Ecological Monographs* 51: 403-427.
- Conner, W.H., J.G. Gosselink, and R.T. Parrondo. 1981. Comparison of the vegetation of three Louisiana swamp sites with different flooding regimes. *American Journal of Botany* 68: 320-331.
- Dabel, C.V. and F.P. Day. 1977. Structural comparisons of four plant communities in the Great Dismal Swamp, Virginia. *Bulletin of the Torrey Botanical Club* 104: 352-360.
- Day, F.P. 1982. Litter decomposition rates in the seasonally flooded Great Dismal Swamp. *Ecology* 63: 670-678.
- Day, F.P. 1985. Tree growth rates in the periodically flooded Great Dismal Swamp. *Castanea* 50: 89-95.
- Day, F.P. 1987. Effects of flooding and nutrient enrichment on biomass allocation in *Acer rubrum* seedlings. *American Journal of Botany* 74: 1541-1554.
- Day, F.P. and C.V. Dabel. 1978. Phytomass budgets for the Great Dismal Swamp ecosystem. *Virginia Journal of Science* 29: 220-224.
- Day, F.P., J.P. Megonigal, and L.C. Lee. 1989. Cypress root decomposition in experimental wetland mesocosms. *Wetlands* 9: 263-282.
- Day, F.P., S.K. West, and E.G. Tupacz. 1988. The influence of ground-water dynamics in a periodically flooded ecosystem, the Great Dismal Swamp. *Wetlands* 8: 1-13.
- Donovan, L.A., K.W. McLeod, K.C. Sherrod, and N.J. Stumpff. 1988. Response of woody swamp seedlings to flooding and increased water temperatures. I. Growth, biomass, and survivorship. *American Journal of Botany* 75: 1181-1190.
- Keeley, J.E. 1979. Population differentiation along a flood frequency gradient: physiological adaptations to flooding in *Nyssa sylvatica*. *Ecological Monographs* 49: 89-108.
- Kozlowski, T.T. 1984. Responses of woody plants to flooding. p. 129-162. In T.T. Kozlowski (ed.) *Flooding and Plant Growth*. Academic Press, New York, NY, USA.
- McClougherty, C.A., J.D. Aber, and J.M. Melillo. 1982. The role of fine roots in the organic matter and nitrogen budgets of two forested ecosystems. *Ecology* 63: 1481-1490.
- Megonigal, J.P. and F.P. Day. 1988. Organic matter dynamics in four seasonally flooded forest communities of the Dismal Swamp. *American Journal of Botany* 75: 1334-1343.
- Megonigal, J.P. and F.P. Day. 1992. Effects of flooding on root and shoot production of bald cypress in large experimental enclosures. *Ecology* 73: 1182-1193.
- Mitsch, W.J. and K.C. Ewel. 1979. Comparative biomass and growth of cypress in Florida wetlands. *The American Midland Naturalist* 101: 417-426.
- Norby, R.J. and T.T. Kozlowski. 1983. Flooding and SO₂ stress interaction in *Betula papyrifera* and *B. nigra* seedlings. *Forest Science* 29: 739-750.
- Peterson, D.L. and F.A. Bazzaz. 1984. Photosynthetic and growth responses of silver maple (*Acer saccharinum* L.) to flooding. *The American Midland Naturalist* 112: 262-272.
- Powell, S.W. and F.P. Day. 1991. Root production in four communities in the Great Dismal Swamp. *American Journal of Botany* 78: 288-297.
- Sena Gomes, A.R. and T.T. Kozlowski. 1980. Growth responses and adaptation of *Fraxinus pennsylvanica* seedlings to flooding. *Plant Physiology* 66: 267-271.
- Tupacz, E.G. and F.P. Day. 1990. Decomposition of roots in a seasonally flooded swamp ecosystem. *Aquatic Botany* 37: 199-214.
- Vogt, K.A., C.C. Grier, and D.J. Vogt. 1986. Production, turnover,

and nutrient dynamics of aboveground and belowground detritus of world forests. *Advances in Ecological Research* 15: 303-377.

Wharton, C.H., W.M. Kitchens, E.C. Pendleton, and T.W. Sipe. 1982. The ecology of bottomland hardwood swamps of the southeast: a community profile. U.S. Fish and Wildlife Service, Bio-

logical Services Program, Washington, DC, USA. FWS/OBS-81/37.

Manuscript received 27 February 1992; revision received 10 July 1992; accepted 25 September 1992.