

Effects of long-term drought on the hydrology and growth of a white pine plantation in the southern Appalachians

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Abstract

The southern Appalachians experienced record precipitation deficits for 4 consecutive years in the mid-1980s. We analyzed the impacts of the drought on the hydrology and stemwood growth of a 33-year-old white pine plantation. Increment cores and dendrometer bands indicated a significant reduction in basal area growth during the drought for all tree classes (dominant, codominant, and intermediate) and shifts in patterns of seasonal growth. There was little variation in pine foliage litterfall over the drought period, but substantial variation in other litterfall components (e.g. wood, cones, seeds, etc.). Precipitation-runoff (*P-RO*) relationships indicated less variation in evapotranspiration (*ET*) over the drought period than predicted by simulation modeling. The discrepancy between measured and modeled *ET* may be related to the importance of stored soil water to streamflow which dampens *P-RO ET* estimates. Regression analyses showed that growing season water potential explained as much as 61% of the variation in annual basal area growth. No significant relationships were established with climatic variables alone.

Keywords: Drought; Hydrology; Growth; *Pinus*

1. Introduction

Precipitation is usually plentiful in the southern Appalachians (mean 1800 mm year⁻¹ at the Coweeta Hydrologic Laboratory) because humid air masses from the Gulf of Mexico rise, cool, and deposit moisture over the mountains. The regional climate is characterized as marine and, for the most part, water availability is not a major factor limiting plant growth. However, during the mid 1980s the region experienced record precipitation deficits. At Coweeta, mean annual precipitation ranged from 18 to 31% below av-

erage during calendar years 1985-1988 (Fig. 1(a)). During 3 of the 4 drought years, the driest period was during the plant growing season (Fig. 1(b)). Swift et al. (1989) analyzed the significance of the 1986 drought using long-term streamflow records and predicted a recurrence interval of 277 years for drought duration and 233 years for drought deficit of this magnitude. Studies at Coweeta during the drought documented increased overstory tree mortality in oak stands (Clinton, 1989) and changes in physiological processes, such as decreased photosynthesis and stomatal conductance in white pine (*Pinus strobus* L.) trees (Maier and Teskey, 1992). We analyzed drought related changes in

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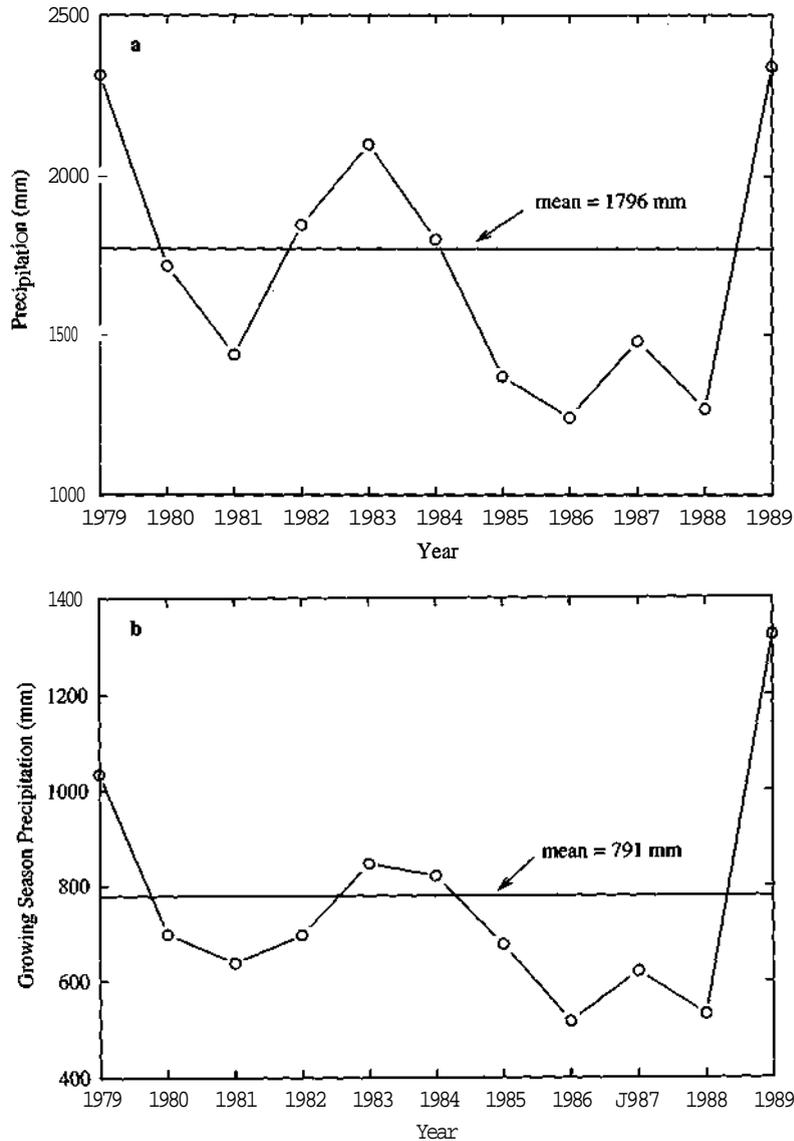


Fig. 1. (a) Annual and (b) April-September growing season precipitation at the Coweeta Hydrologic Laboratory in Otto, NC, 1979-1989.

tree growth and hydrologic budgets on a small watershed at annual and seasonal time scales.

Drought, when manifested as plant water stress, can affect aboveground forest productivity through loss of turgor, reduced carbon gain, and/or shifts in the allocation of carbon between roots and shoots (Teskey and Hinckley, 1986). Loss of turgor, through its effect on cell expansion, has been directly related to decreased tree

growth (Sands and Correll, 1976). Water stress related decreases in canopy carbon gain can result from reduced foliage biomass due to accelerated needlefall and reduced production (Linder et al., 1987) and/or reductions in net photosynthesis (Teskey et al., 1987; Maier and Teskey, 1992). Reduced canopy carbon may result in reduced biomass or size increment for all components, or, only tissues with low priority for

assimilates may be affected. Mechanisms regulating shifts in stand-level carbon allocation between above- and **belowground** components as a result of water stress are not well understood, but field studies indicate an increased proportion of carbon allocated belowground under dry conditions (Keyes and Grier, 1981; Comeau and Kimmins, 1989). If stemwood has lower priority than roots and foliage in carbon allocation (Waring and Schlesinger, 1985), an increased proportion of carbon allocated belowground will thus reduce carbon allocation to stemwood, as found by Bongarten and Teskey (1987) in drought-stressed loblolly pine (*Pinus taeda* L.) seedlings.

Translating precipitation deficits into plant moisture stress can be difficult because of the lag between precipitation deficit and depletion of available soil water by plants. The problem has been simplified by measuring soil water content (Cregg et al., 1988) or plant water status has been assessed directly using xylem pressure potential (Hinckley et al., 1978). However, neither of these approaches are applicable at the watershed scale. There, soil water status has been assessed from gross measures of plant water demand (e.g. potential evapotranspiration estimates; Thornthwaite, 1948; Mongaran, 1973), from water budgets developed on gauged watersheds, or from hydrologic models (Huff and Swank, 1985).

The objectives of our study were: (1) to assess the impacts of drought on stemwood growth in a 33-year-old white pine (*Pinus strobus* L.) plantation; (2) to quantify changes in seasonal basal area increment and litterfall during drought; (3) to characterize the hydrology of the stand during the drought and non-drought periods using (a) water budgets and (b) a hydrologic simulation model. Analyses included both extensive measurements (e.g. individual tree basal area increment) over an 11 year period encompassing average precipitation (1979-1984), record precipitation deficits (1985-1988), and a record precipitation amount (1989), and intensive measurements (e.g. litterfall, radial increment) during the precipitation deficit period.

2. Materials and methods

2.1. Site and stand description

The study area is in a 36-year-old white pine plantation (WS1) at the Coweeta Hydrologic Laboratory in the southern Appalachian Mountains of western North Carolina, USA. The watershed is 16.1 ha, has a southerly aspect, and spans a elevation range of 705-988 m. Soils are mesic Typic Hapludults of the Fannin soil series. Soil texture is fine sandy loam derived from mica schist and gneiss. Mean annual precipitation is 1786 mm and is evenly distributed throughout the year (Swift et al., 1988). Mean annual temperature is 12.6°C and temperatures average 6.7°C in the dormant season and 18.5°C in the growing season (Swift et al., 1988). The first-order stream draining WS1 has a 90° V-notch weir that has been in operation since 1934. The white pine stand was planted in 1957 at a spacing of 1.8 m x 1.8 m. In subsequent years, pines were released from hardwood competition with cutting and herbicides as necessary. No thinning has been conducted in the stand. In 1990, stand basal area was 53.2 m² ha⁻¹ and density was 1015 stems ha⁻¹.

2.2. Extensive measurements

Annual basal area increment of individual trees was determined from increment cores. In winter 1990, 40 trees were randomly selected over the entire watershed. Sampling was proportional to crown-class occurrence in the stand; 24 dominant, 10 codominant, and six intermediate trees were selected. Two cores from each tree were extracted at 1.4 m **aboveground** from opposite sides of the tree and parallel to the slope. Extracted cores were stored in drinking straws, transported to the laboratory, mounted in a jig, and shaved to provide a clean, flat surface for measurement. Annual ring widths for an 11 year period (i.e. 1979-1989) were measured to 0.01 mm under a 375 X microscope using a incremental measuring device coupled to a microcomputer. Measurements from the two cores were averaged. No

distinction was made between **earlywood** and latewood.

2.3. Intensive measurements

Intensive measurements (i.e. less than 1 year **resolution**) were taken on a 0.20 ha plot located midslope in the lower portion of **WS1**. Measurements began in June 1985 and continued through January 1989. Because intensive measurements were taken on a single plot, it is not possible to extrapolate the absolute responses observed to the entire watershed. However, the midslope location does allow for an assessment of the relative responses observed under 'average' conditions.

2.4. Radial increment

Monthly or biweekly radial increment (at 1.8 m) was determined using dendrometer bands (Liming, 1957). Fifteen bands were installed, one on each of five trees in the diameter classes of 17-24 cm, 25-29 cm, and 30-40 cm. These diameter classes corresponded to trees in intermediate, codominant, and dominant canopy positions, respectively. Bands were read to the nearest 0.01 cm at approximately 2 week intervals (summarized on a **monthly** basis) in the growing season (**April-October**) and monthly in the dormant season from June 1985 until January 1989. Data were standardized by expressing growth per day as a percentage of annual increment. Thus, growth over a given time interval was divided by the total annual growth and the number of days in the time interval.

2.5. Litterfall

Litterfall was collected from four 0.5 m² fiberglass screen traps. In 1985, litter traps were installed in early June and litter was collected in late December. Litterfall was collected two times per year (late summer and early winter) from 1986 through 1989. It was divided into needles, wood, and other material (e.g. fruits, bud **scales**), dried, and weighed. Variations in annual litterfall biomass were analyzed for statistically sig-

nificant differences using repeated measures analysis of variance (Statistical Analysis Systems Institute, 1982).

2.6. Hydrology

We used precipitation (*P*) and **streamflow** (*RO*) data from 1979 through 1989 to characterize the hydrology of the watershed. From these data we calculated monthly evapotranspiration (*ET*) from the relationship $ET = P - RO$. In addition, we used the **hydrologic** simulation model PROSPER (Goldstein et al., 1974) to provide an independent *ET* estimate and to provide an estimate of site water status. **PROSPER-derived** estimates of *ET*, outflow (i.e. drainage from the deepest soil layer), and soil water potential were used to characterize the hydrologic response and to link that response with **stemwood** growth. PROSPER has been described in detail elsewhere (Goldstein et al., 1974; Huff and Swank, 1985), so only a general description is presented here. PROSPER is a **phenomenological**, one-dimensional model that links the atmosphere, vegetation, and soils. Plant and soil characteristics are combined in an *ET* surface that is characterized by a 'surface resistance' to water vapor loss. This resistance, which is analogous to the relationship between stomatal resistance and leaf water potential, is a function of the water potential of the *ET* surface. *ET* is predicted by a combined energy balance-aerodynamic method (Penman-Monteith equation modified as described in Swift et al., 1975), which is a function of the surface resistance to vapor loss described above. PROSPER uses electrical network equations to balance water allocation among vegetation and the three soil layers. The flow of water within and between soil and plant is a function of soil hydraulic conductivity, soil water potential, root characteristics in each soil layer, and surface water potential. Water flux in unsaturated soil is governed by hydraulic conductivity, where hydraulic conductivity is estimated from the relationship between soil **matric** potential and moisture content by the procedure described in Luxmoore (1973). PROSPER simulates *ET* and

Table 1
PROSPER input parameters

Climate	Vegetation	Soils
<i>Measured</i>		
Air temperature	Canopy: Interception capacity	Initial H ₂ O content
Wind speed	Leaf area index	Release curves
Precipitation	Mean leaf length	Porosity
Short-wave radiation	Ratio of latent to sensible heat loss	Saturated hydraulic conductivity
Vapor pressure	surface area	
	Albedo	
	Resistance to vapor loss	
	Energy exchange with ground	
	Belowground:	
	Root cross-sectional area	
	Root distribution	
<i>Computed</i>		
Saturation vapor pressure	Leaf area index dynamics	Unsaturated hydraulic conductivity

soil water redistribution between soil layers daily. PROSPER requires climatic inputs of solar radiation, precipitation, windspeed, air temperature, and vapor pressure. With the exception of solar radiation, data were collected from a climatic station bordering WS1. Solar radiation was measured at the main climatic station at valley bottom and extrapolated to WS1 using the algorithm of Swift (1976). Vegetation and soil parameters (see Goldstein et al., 1974 for a complete list of model parameters) required for PROSPER were determined from recent site measurements (e.g. leaf area index and soil moisture release characteristics) and from hydrologic simulations on a similar white pine watershed (WS17) in a previous study (Swift et al., 1975). Important input parameters are listed in Table 1. These parameters were kept constant for all simulations. Climatic input variables for each simulation period were based on actual measurements.

3. Results and discussion

3.1. Growth response

Analyses of increment cores revealed substantial reductions in basal area increment of domi-

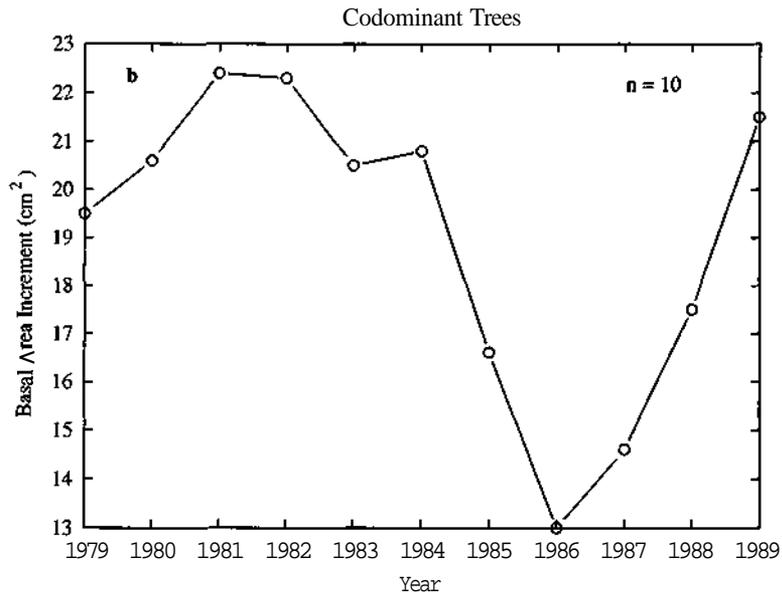
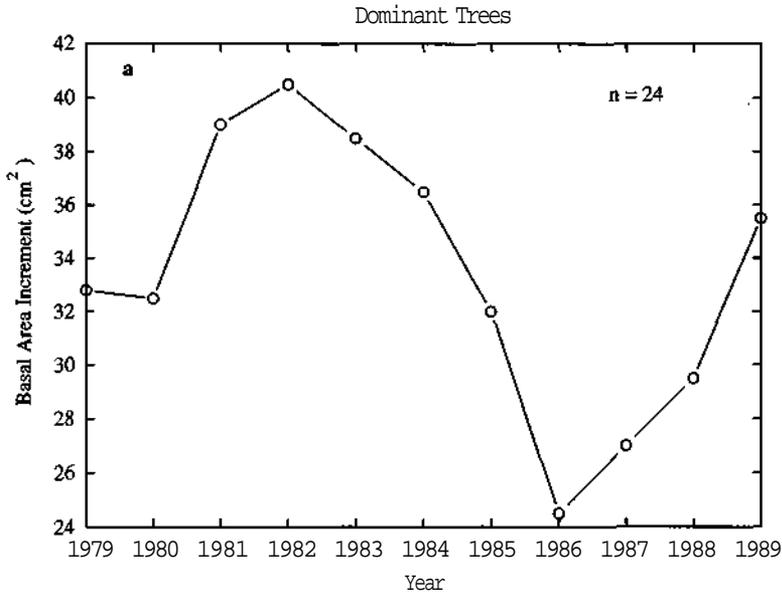
nant, codominant, and intermediate trees in 1985-1988 (Figs. 2(a)-2(c)). The average percent growth decline increased from upper to lower position canopy positions—22% for dominant, 28% for codominant, and 38% for intermediate. Statistical comparisons of average annual basal area increment (BAI) during the non-drought periods (1979-1984, 1989) with BAI during drought periods (1985-1988), showed significantly greater BAI during the non-drought periods (Table 2).

3.2. Radial increment

Monthly radial growth patterns varied among canopy classes and years (Figs. 3(a)-3(d)). For example, in all years, the growth rate of the intermediate trees was generally greatest in the early growing season and lowest later in the growing season. This response pattern in intermediate trees may be related to changes in light availability in lower canopy positions through the growing season. In the early growing season (April-June), leaf area index in WS1 is 3.5-4.0, which equates to 20-30% light penetration in lower canopy positions (Vose and Swank, 1990). In contrast, in July, August, and September, leaf area index is 5-5.5, which equates to 5-10% light

penetration. Growth patterns in dominant and codominant trees were similar to each other. While growth rate patterns varied among years, relationships between these patterns and drought were difficult to discern. The most obvious differences were between 1986 when growing sea-

son precipitation was 54% below average and 1989, when growing season precipitation was 63% above average. Peak growth rate of dominant trees (percentage of annual increment per day) occurred between May (Julian day 120) and June (Julian day 154) in 1986 (Fig. 3(a)).



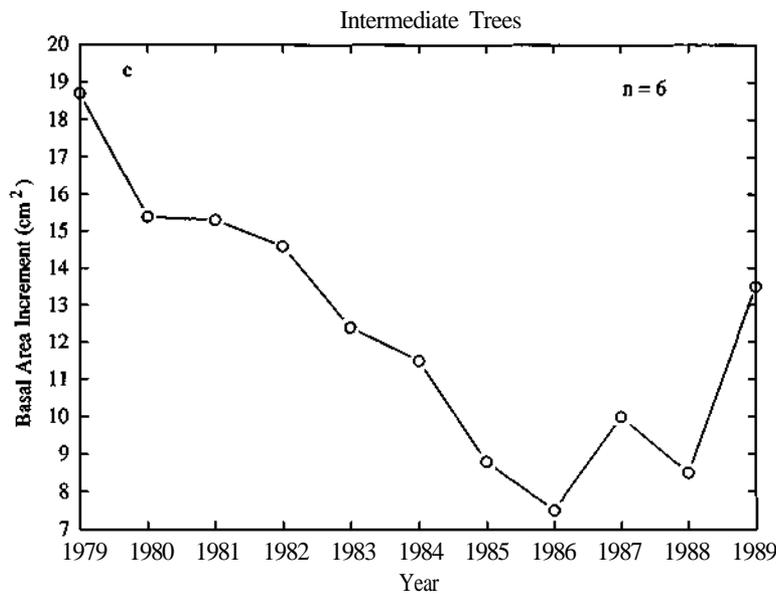


Fig. 2. Annual basal area increment, 1979-1989: (a) dominant; (b) codominant; (c) intermediate.

Table 2

Mean (\pm SE) annual basal area increment ($\text{cm}^2 \text{year}^{-1}$) during drought (1985-1988) and non-drought (1979-1984, 1989) periods

Canopy class	<i>n</i>	Non-drought	Drought	<i>P</i> > <i>F</i> ^a
Dominant	24	36.5(1.1)	28.6(1.6)	0.003
Codominant	10	21.1(0.4)	15.4(1.0)	0.0001
Intermediate	6	14.0(1.0)	8.5(0.5)	0.001

^aData analyzed by *t*-tests, where *n* = 4 for drought period and *n* = 7 for non-drought period.

It declined substantially thereafter, when monthly precipitation ranged from 30 to 80% below average. In contrast, while growth rates in 1989 showed a similar peak in the spring, substantial growth continued later in the summer (Fig. 3(d)). Similar but less distinct patterns were evident for the other dry years and canopy classes.

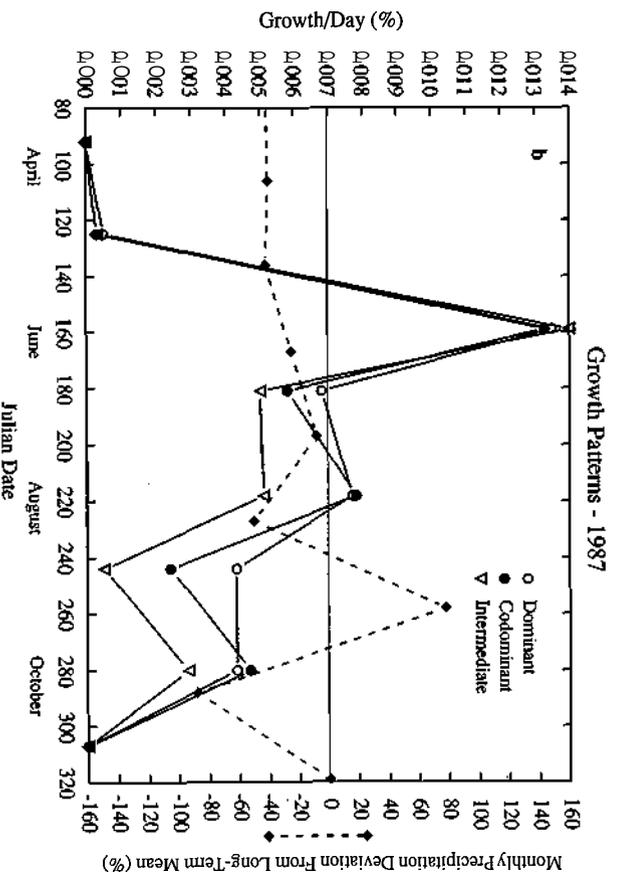
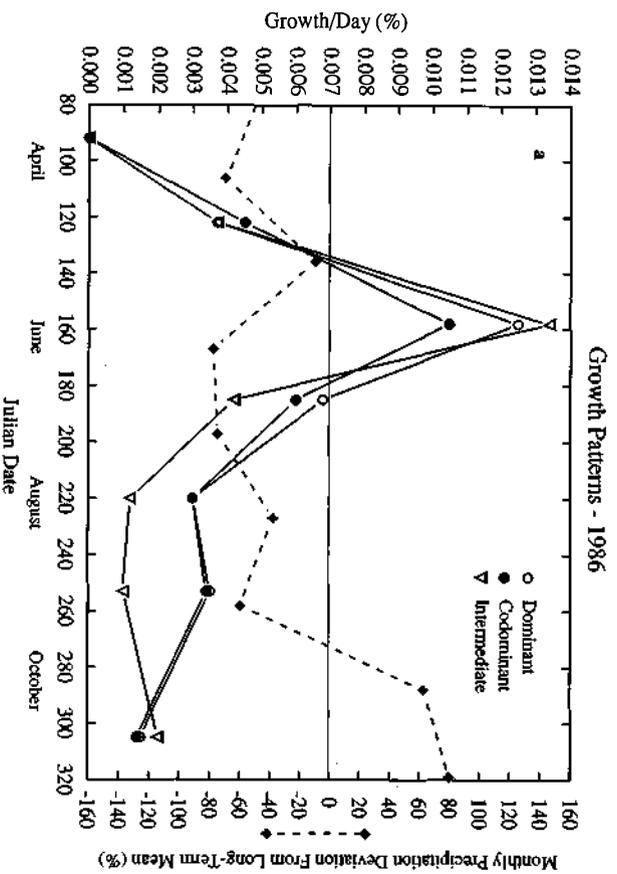
Although **earlywood** and **latewood** were not distinguished in the increment core analyses, the pattern of peak growth rate in the early growing season (regardless of precipitation amount) indicates **consistency** in the allocation of carbon to stemwood early in the growing season. This response is comparable to that in southern pines, which have generally uniform earlywood growth

(Zahner, 1968). A primary carbon source for this early pulse in stemwood growth is stored reserves; hence, one might expect a correlation between climatic conditions of the previous year and early season growth. However, fall and winter photosynthesis in warmer climates has been postulated as a mechanism that replenishes carbon storage pools that have been reduced during stressed conditions (Zahner and Grier, 1990). If so, then the linkage between current climatic condition and early-season stemwood growth should not be strong. Consistent with responses observed in southern pines (Zahner, 1968; Zahner and Grier, 1990), stemwood growth in the latter growing season varied in ways that appeared related to variation in precipitation.

3.3. Litterfall

Total annual litterfall varied up to 40% from 1986 to 1990 (Table 3). Most of this variation was due to differences in the amounts of wood and 'other' materials in the litter. Annual varia-

tions in woody inputs may be related to variable wind conditions. Substantial quantities of older dead branches can occur during high winds (W.T. Swank, personal observation). In addition, drought may cause branch mortality, increasing woody litterfall. Under these circum-



Monthly Precipitation Deviation From Long-Term Mean (%)

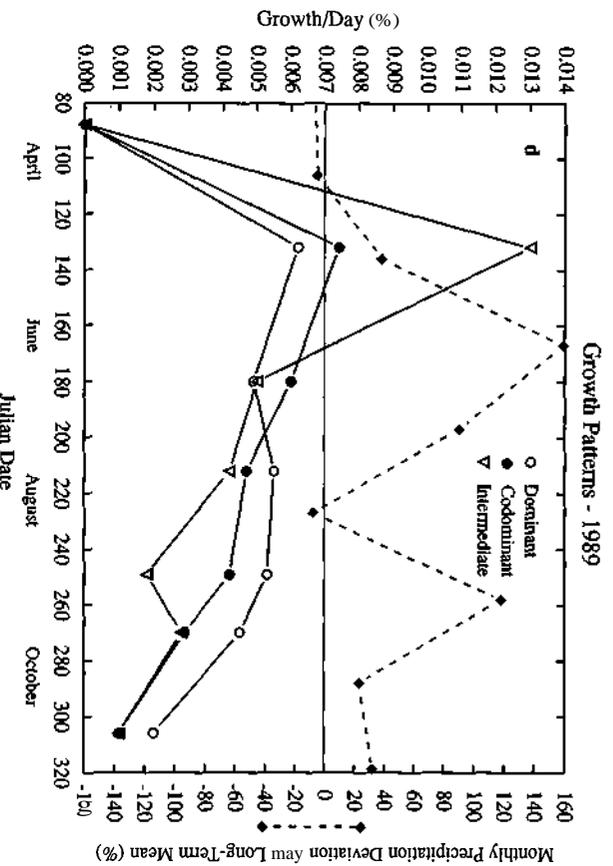
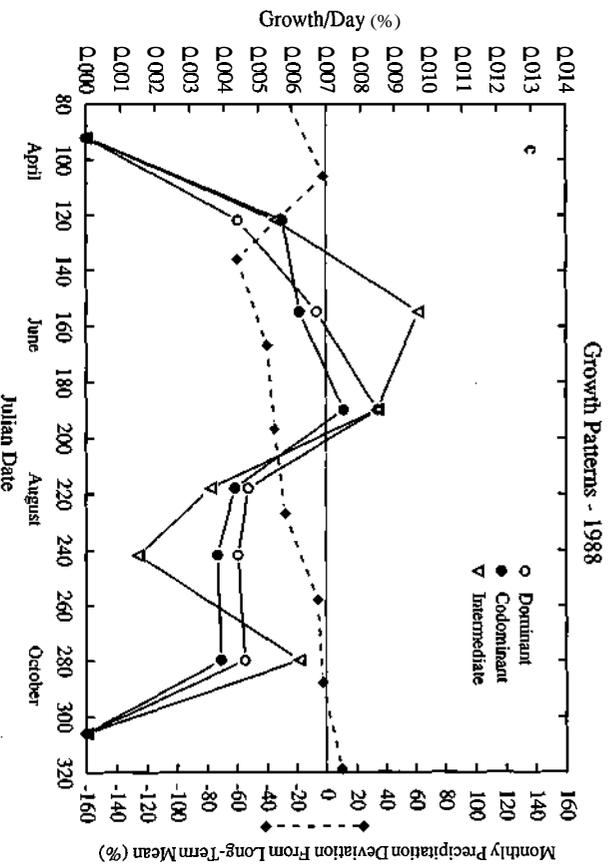


Fig. 3. Growth patterns for Watershed 1 (% growth day⁻¹) for dominant, codominant, and intermediate trees, 1986-1989: (a) 1986; (b) 1987 (c) 1988; (d) 1989.

stances, however, additional foliage litter will be expected in association with high canopy and this response was not observed. Variation in the 'other' category may be related

to differences in carbon allocation to secondary producers. Cones and seeds are the primary components of this category. Thus, the substantial biomass in the 'other' category in the 1990 col-

Table 3
Annual litterfall (kg ha^{-1}) by component. Data are means ($n=4$) and standard errors

Litterfall component	1985 ^a	1986	1987	1988	1989	1990
Pine foliage	3048(200)	4032(221)	3953(165)	3763(86)	4356(275)	3942(127) n.s.
Wood ^b	468(76)	1999(867)	1373(168)	1286(105)	1068(176)	1778(472)
Other ^c	129(53)	776(165)	811(95)	1217(375)	999(230)	1888(421)
Total	3645(328)	6031(422)	5326(426)	6265(547)	6424(432)	7608(894)

^aPartial collection year: June-December 1985.

^bIncludes woody tissue and bark.

^cIncludes hardwood foliage, cones, seeds, male flowers, bundle sheaths, insect frass, lichen.

lections may reflect a cone and seed production response to the favorable growing conditions. The lack of variation in the foliage litterfall component was somewhat surprising. In general, needles that naturally senesce and abscise in white pine were produced the previous year. Hence, the foliage component of litterfall biomass reflects canopy biomass of the previous growing season. If reduced foliage production had occurred, then lower foliage litterfall would have been measured for 1986–1989 relative to 1990. Other studies have documented decreased foliage production in response to drought (Linder et al., 1987), as well as lower foliar biomass on xeric sites (Keyes and Grier, 1981; Comeau and Kimmins, 1989).

3.4. Hydrology

3.4.1. Water budgets

In stand-level water budgets over the 11 year period, streamflow corresponded closely to precipitation (Fig. 4). A regression predicting streamflow from precipitation was highly significant and explanatory ($r^2=0.86$; $P>F=0.0001$; $MSE=110.73$; $n=11$). Other environmental variables (solar radiation, temperature, and vapor pressure) did not significantly ($\alpha=0.05$) improve predictions of annual *ET*.

The highly significant relationship between *P* and *RO* indicates little year-to-year variation in *P-RO* relative to *RO*. As an illustration of this point, coefficients of variation (CV) were 17.6% and 56.5% for *P-RO* and *RO* means, respectively. Thus, *P-RO* relationships were relatively

consistent, even under highly variable climatic conditions. This was further evidenced by the lack of significant difference in the *P-RO* mean (1139 mm) for the drought period (May–April water year 1985–1988) compared with the mean (1262 mm) of the other years (May–April water year 1979–1984, 1989). The narrow range in *P-RO* does not necessarily imply consistency in *ET*, because the influence (\pm) of stored soil water on streamflow is not accounted for in the $ET=P-RO$ model. Depending on soil and site characteristics, soil water storage can be a major component of the site water balance (i.e. $ET=P-RO+\text{soil water storage}$). At annual time scales, the soil water storage term is often ignored because, in most instances, it can be assumed that additions and losses from soil water storage are balanced. When significant increases or decreases in soil water storage occur, *ET* estimates based solely on *P-RO* will be less accurate.

3.4.2. Simulation modeling: *ET* and runoff

PROSPER predictions of outflow (i.e. the drainage component of PROSPER) and measured streamflow over the 11 year period were highly correlated ($r^2=0.81$, root $MSE=18.13$; $P<0.0001$) (Fig. 5), but PROSPER generally over-estimated streamflow, particularly at the higher flows. Good correlations between streamflow and PROSPER outflow have been demonstrated previously in many different ecosystems and climatic conditions (Swift et al., 1975; Vose and Swank, 1992). Because there is no reliable method for directly determining *ET* at wa-

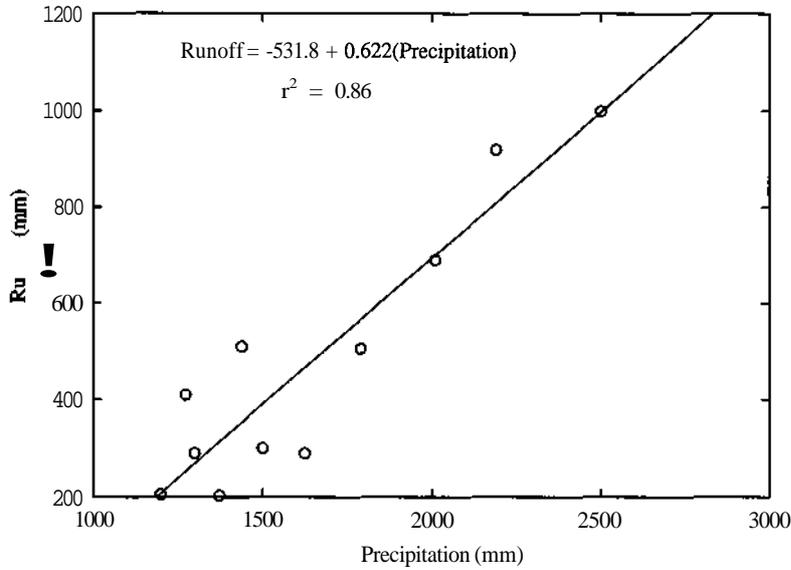


Fig. 4. Relationship between precipitation and measured runoff, 1979-1989.

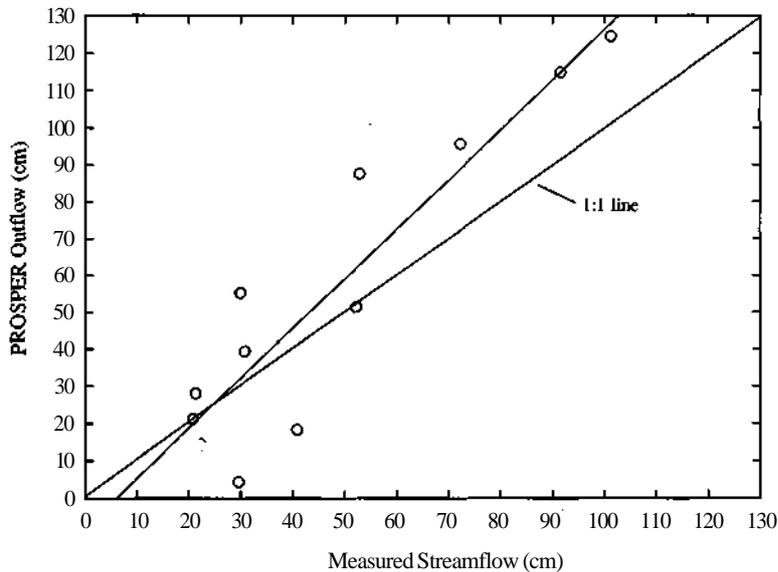


Fig. 5. Relationship between PROSPER outflow and measured streamflow, 1979-1989.

tershed scales, correspondence between PROSPER outflow and measured streamflow has been used as validation of the *ET* predictions from PROSPER.

Across the entire 11 year simulation period (i.e. 1979-1989), annual *ET* estimates from PROSPER averaged 1130 mm and ranged from 957 to 1431 mm. By comparison, the *P-RO* es-

timate of *ET* averaged over the same time period was 1217 mm and ranged from 911 to 1588 mm. While the means and ranges of the two *ET* estimates were comparable across the 11 year period, there was no correlation between annual PROSPER and *P-RO ET* estimates. During the drought (1985-1988), PROSPER *ET* averaged 1165 mm and ranged from 957 to 1431 mm. By

comparison, *P-RO ET* during the drought averaged 1139 and ranged from 974 to 1237 mm. Like the results from correlation analyses across the 11 year period, the drought period annual *ET* values predicted by the two methods were not correlated. One potential reason for the lack of correlation between these two approaches during both drought and non-drought periods is that *P-RO ET* estimates do not account for the effects of belowground water storage and flow pathways to the stream. One of the effects of these belowground processes is to buffer **streamflow** response to variation in *ET*. The correspondence between mean values derived by the two approaches is indicative of the fact that averaging over multiple years reduces the influence of lags between precipitation input (*P*) and streamflow output (*RO*). In contrast, PROSPER provides *ET* estimates **which** are independent of these processes.

3.5. Linkages between site water status and growth

Basal area increment of trees in all canopy classes was significantly ($P < 0.05$) related to soil water potential predicted by PROSPER ($r^2 = 0.61, 0.48, \text{ and } 0.37$ for dominant, codominant, and intermediate trees, **respectively**). As indicated for dominant trees (Fig. 6), soil water potential is an excellent measure of site water availability because it integrates multiple factors determining soil water available to roots; i.e. the net effect of input, uptake and drainage, and storage. Adding additional parameters such as total or growing season precipitation and mean annual or growing season temperature did not significantly improve the **univariate** regression. Other researchers using different methods have found close agreement between site water status and tree growth for a variety of species (Spittlehouse, 1985; McLeod and Running, 1988; Zahner and Grier, 1990; Robertson et al., 1990). A probable explanation for the strength and consistency of the relationship is that the combination of supply (**precipitation**), use (transpiration), drainage, and storage integrates the important components determining plant water

stress and, hence, expresses the relationship between available water and growth. Plant water stress (i.e. negative plant water potential) occurs when soil water is depleted through the combined effects of plant uptake and insufficient precipitation input. Short-term water stress due to daily relationships between stomatal conductance and vapor pressure gradients (e.g. mid-day stomatal closure) are not simulated by PROSPER. Hence, some of the residual variation in the soil water potential vs. growth relationships may be attributable to the cumulative impacts of short-term water stress on carbon gain.

Growth should be more highly correlated with soil water potential than with precipitation quantities because transpiration rates can be very different under similar precipitation input regimes. For example, plant transpiration was 960 mm during the 1987–1988 simulation period vs. 620 mm during the 1984–1985 simulation period, while precipitation was essentially the same (1446 mm and 1434 mm, respectively). Typically, studies that have only considered simple climatic variables have found weak relationships for pine species of the southeastern United States (McClurkin, 1958; Chang and Aguilar, 1980). Other climatic factors may be important determinants of growth as well; however, they had little explanatory power in the present analysis.

What mechanisms explain the observed drought-related stem growth decline? Water stress directly affects cell turgor and cell expansion (Kozlowski et al., 1991). In addition, water stress indirectly affects photosynthesis, canopy leaf area, and shifts in carbon allocation. Maier and Teskey (1992) examined the impacts of drought on photosynthesis in a similar white pine stand at Coweeta and found a 10–75% reduction in net photosynthesis in 1986 (low spring and summer **precipitation**) relative to 1987 (low spring but above-average summer precipitation). Hence, some of the observed growth reduction may be due to drought impacts on net photosynthesis. Based on **litterfall** collections, there were no impacts of drought on canopy leaf area. Other studies have shown that both foliage **production** (Linder et al., 1987) and needlefall rates (Linder et al., 1987; Vose and Allen, 1991)

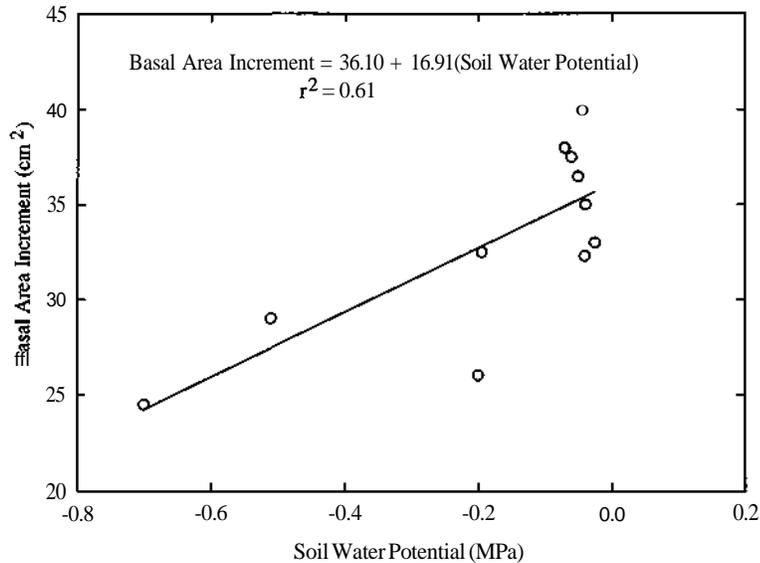


Fig. 6. Relationship between simulated soil water potential and measured basal increment, 1979-1989.

are affected by climatic conditions. The lack of canopy response in our white pine stand may be related to the age of the stand and the size of the trees. For example, **Gholz (1986)** reported that canopies of older (20+ years) slash pine stands were less responsive to fertilization input than younger stands. Although mechanisms regulating this response cannot be inferred from **Gholz's (1986)** study, older and larger trees may have sufficient carbohydrate reserves to maintain constant carbon allocation to high-priority tissues (e.g. foliage and roots) during stressed conditions. The allocation of carbon between foliage and stemwood shifted as a result of the drought (i.e. stemwood carbon/foliage carbon or growth efficiency; Waring and Schlesinger, 1986). This shift is indicated by the constant foliar biomass coupled with reduced stemwood increment. Some of this reduction in stemwood growth efficiency may be related to lower photosynthetic efficiency, but changes in carbon allocation may be equally important. In particular, more carbon may be allocated below ground during stressed conditions (Keyes and Grier, 1981; Bongarten and Teskey, 1987). If so, less carbon would be available for stemwood growth.

4. Summary and conclusions

We analyzed and documented the impacts of drought on white pine stand and individual-tree growth. Results indicate a significant drought effect on basal area increment of cored trees. Examination of growth patterns from dendrometer bands showed that most growth during the drought occurred in spring and early summer. In contrast, during a wet year (1989) growth was more uniform throughout the entire spring and summer. Amounts of pine foliage litterfall were similar over the dry and wet periods indicating constancy in both foliage production and senescence. In terms of canopy dynamics, the stand appeared well buffered against severe drought conditions. Rainfall-runoff relationships in wet and dry periods showed a close correspondence between precipitation input and streamflow. The residual variation in this relationship was not significantly related to climatic variables that regulate *ET* (i.e. solar radiation, temperature, vapor pressure) and probably represents unaccounted for interannual changes in moisture storage in the deep soils at Coweeta. Soil moisture storage also dampened the *P-RO ET* esti-

mates such that there was little variation ($CV=10\%$) over the drought period. In contrast, PROSPER ET estimates, which are not affected by interannual changes in soil moisture, were more variable ($CV=20\%$) over the drought period. Linkages between soil water potential and growth were strong. PROSPER estimates of soil water potential integrate supply, demand, and storage components at the stand level. Simulations indicated that trees continue to transpire even when precipitation inputs are low by utilizing stored soil water. Depletion of available soil water causes soil water potential to decline, with concomitant plant water stress and decline in plant growth.

5. Acknowledgments

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