EFFECTS OF SUBSURFACE DRAINAGE ON TREE GROWTH AND FOREST SUCCESSION

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In 1969, subsurface drains were installed in one half of an oak forest to permit development of an industrial park. Subsequent abandonment of the project permitted comparisons of growth rates of dominant trees and shrubs on drained and undrained plots, correlation of those growth rates with soil moisture fluctuations, and some insights to the possible long-term effects of drainage on forest succession.

Where differences in growth were statistically significant, species on the drained site grew less. Drainage did not affect leaf production, but did cause early loss of foliage. Generally, it appears that the typical response to moisture stress is an increase in terminal stem growth at the expense of lateral stem growth. The present structure of the forest will remain the same, although white oak's (Quercus alba L.) relative abundance in the canopy may decline and the shrub, blueberry (Vaccinium vacillans Torr.), may eventually be replaced as a result of its poor growth.

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INTRODUCTION

Drought has been defined as a period when soil moisture is insufficient to allow a plant to absorb enough water to offset transpiration losses (Reisch 1958). Biochemical and physiological characteristics of moisture stress have been well documented (Brix 1961, Jarvis and Jarvis 1963, Kozlowski 1968, Quaraishi and Kramer 1970, Treshow 1970, Borger and Kozlowski 1970, and Levitt 1972). Moisture stress is characterized by numerous changes in external growth and appearance. Bonner (1965) and Hinckley (1974) found reductions in stem growth during moisture stress. Stem circumference may decrease as transpirational losses are replaced by internal water (Holmes and Shim 1968, Hinckley and Bruckerhoff 1975). One of the earliest external signs of moisture stress is wilting, as the plant attempts to lower surface temperatures by orienting leaf blades parallel to incoming radiation (Treshow 1970). Dogwoods (Cornus florida L.) were visibly wilted even before sunrise during a drought in Missouri (Hinckley and Bruckerhoff 1975). Pool (1913) and Shirley (1934) reported premature leaf loss in deciduous trees in response to drought.

In severe or prolonged drought, mortality rates may increase. Shirley (1934) stated that forest plantations in Minnesota sustained losses of 30 to 50 percent during a drought in 1930, and even swamps suffered a 25 percent mortality among trees under one inch dbh. Karnig and Lyford (1968) also reported high mortality in scarlet oak (Quercus coccinea Muenchh.) during a 5-year period of drought.

Depth to water table has been shown to be an important edaphic factor influencing the distribution and growth of a variety of trees (e.g., see Bassett 1964, Mueller-Dombois 1964). Prolonged summer drought may lead to the depletion of deep-soil water reserves, and subsequent growth must depend wholly on precipitation. Drainage could eliminate this deep source of summer transpirational water; and may produce a drought condition much earlier in the growing season during years of below normal rainfall. Conversely, growth of pin oak (Quercus palustris Muenchh.) and silver maple (Acer saccharinum L.) was impaired by an increase in the water table (Yeager 1949). Thus, a lowered water table may influence tree growth positively or negatively and could, in the long run, change the forest composition by either elimination or enhancement of species.

In 1969, a 90-ha oak forest in Lucas County, Ohio, was bisected and subsurface drains were installed in one half of the forest to permit the development of an industrial park. This manipulation gave us the opportunity to determine the effects of drainage on forest growth and leaf production. Our purpose is twofold: (1) to elucidate the effects of subsurface drainage on stem elongation and leaf production and (2) to predict the effects of drainage on long-term forest succession. Fortuitously, in the first year of this study (1973) there was an excess of precipitation, while in the second year (1974) near-record drought conditions prevailed during much of the summer.

STUDY AREA AND PROCEDURES

The study area is located at approximately 41° 36′ N latitude and 83° 48′ W longitude in the Ottokee soil series, a fine sand of the Oak Openings region of western Lucas County, Ohio. During the late winter-early spring period, the water table at the site naturally lies at or very near the ground surface.

A preliminary survey was undertaken in early May 1973 to determine the tree species composition of the proposed industrial park. White oak (Quercus alba L.) and a red oak hybrid (Q. rubra x velutina) comprised almost 100 percent of the forest canopy, while black cherry (Prunus serotina Ehrh.) and red maple (Acer rubrum L.) made up approximately 95 percent of the understory species. Blueberry (Vaccinium vacillans Torr.) constituted 80 percent of the shrubs.

The study sites consisted of two 0.5-ha plots, one located in the drained area and one in the undrained (natural) area. Depth to the water

table was monitored by continuous recording instruments installed in the center of both plots and maintained by the University of Toledo Geology Department. Soil moisture was measured weekly at 0.3 m intervals down to a depth of 3 m with a soil moisture meter (model MC-300a and soil cells, Soiltest, Inc., Evanston, Illinois). Field capacity was estimated by arbitrarily considering resistance 0.3 m above the water table as 100 percent field capacity, while the resistance value noted when wilting was first observed was considered to be the wilting point, or 50 percent field capacity.

Eight trees of each species were selected at random on both sites. On each tree, 5 stems were tagged for periodic measurements of shoot elongation and number of leaves present on new growth. Stems forming the distal end of a branch were designated as terminal, while all others were designated as lateral. Stem elongation was measured in mm from the base of the previous year's bundle scar to the tip of the shoot. The stems were straightened in order to avoid errors caused by bending.

Measurements began in mid-May and ended 30 September in 1973 and 26 October in 1974. Growth measurements and leaf counts were taken every 7 to 14 days. Each year's data were arbitrarily divided into three intervals referred to for convenience as spring (13 May to 15 June in 1973, and 17 May to 27 June in 1974), summer (16 June to 13 August in 1973, and 28 June to 17 August in 1974), and fall (14 August to 30 September in 1973, and 18 August to 26 October in 1974).

Mean shoot elongation or leaf production for each species was determined by finding the mean of the eight individual tree means. The Mann-Whitney U-test was used to determine significant differences between sites and years for both stem elongation and leaf production, and to make interspecies comparisons. The field data are too detailed to be presented in this paper, therefore in most cases only statistically significant results will be given. Copies of the field data may be obtained by writing the authors.

Predictions on forest succession were generated as follows: First we estimated the amount of growth to be expected in a summer of normal rainfall. Mean shoot elongation values for each year were plotted against actual precipitation (Figures 1a, 1b and 1c). Terminal and lateral shoot means were plotted separately. Lines were drawn connecting the mean shoot elongation values for the wet year (1973) and the dry year (1974) on both natural and drained sites. This assumes a linear relationship between precipitation and shoot elongation. Finally, a vertical line was drawn corresponding to the mean rainfall for the period May through August. The average amount of growth expected in a normal season of rainfall for each site was then estimated by the intercepts of the shoot elongation curves with the vertical mean rainfall line.

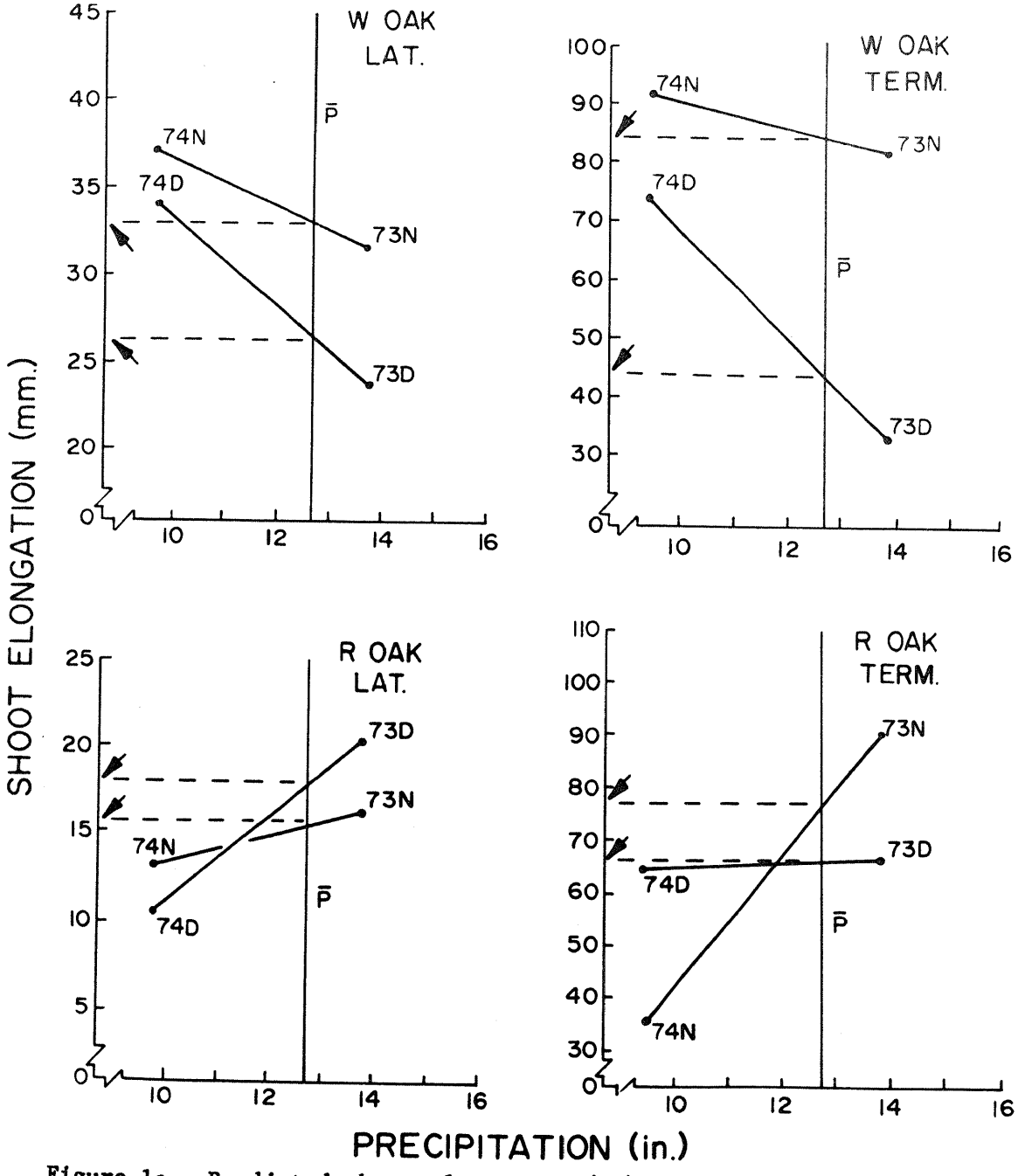

Figure 1a. Predicted shoot elongation (mm) in white and red oaks as a function of precipitation (in) for the period May through August. 73N, 73D, 74N and 74D represent mean total growth for each species on the natural (N) or drained (D) sites for 1973 and 1974 respectively. $\bar{P}$ is the mean precipitation for May through August. Each intersection of the dotted lines with the vertical axis (arrows) represents the estimated mean shoot growth during a normal year of rainfall.

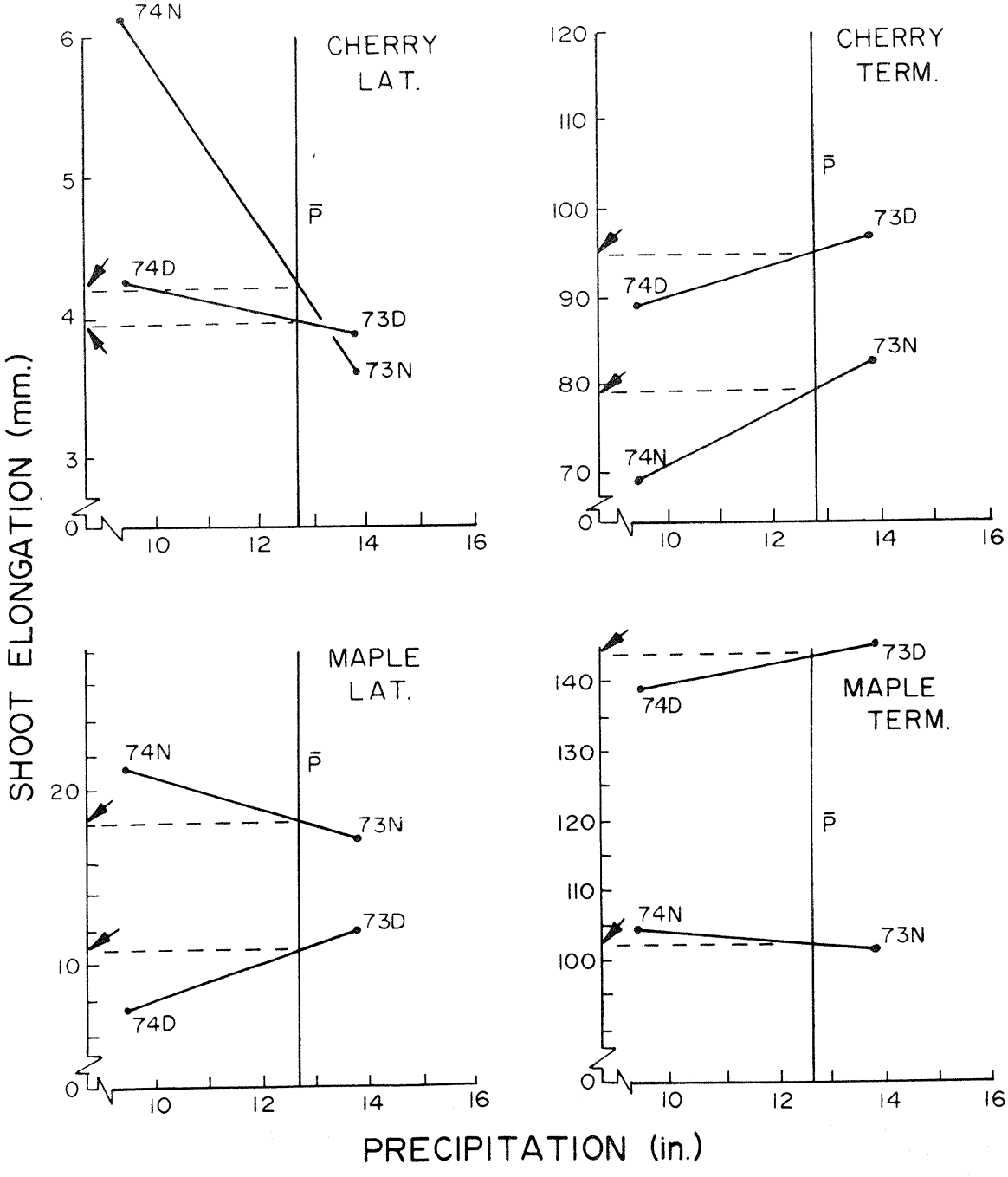

Figure 1b. Predicted shoot elongation in black cherry and red maple as a function of precipitation. For explanation of symbols see legend, Figure 1a.

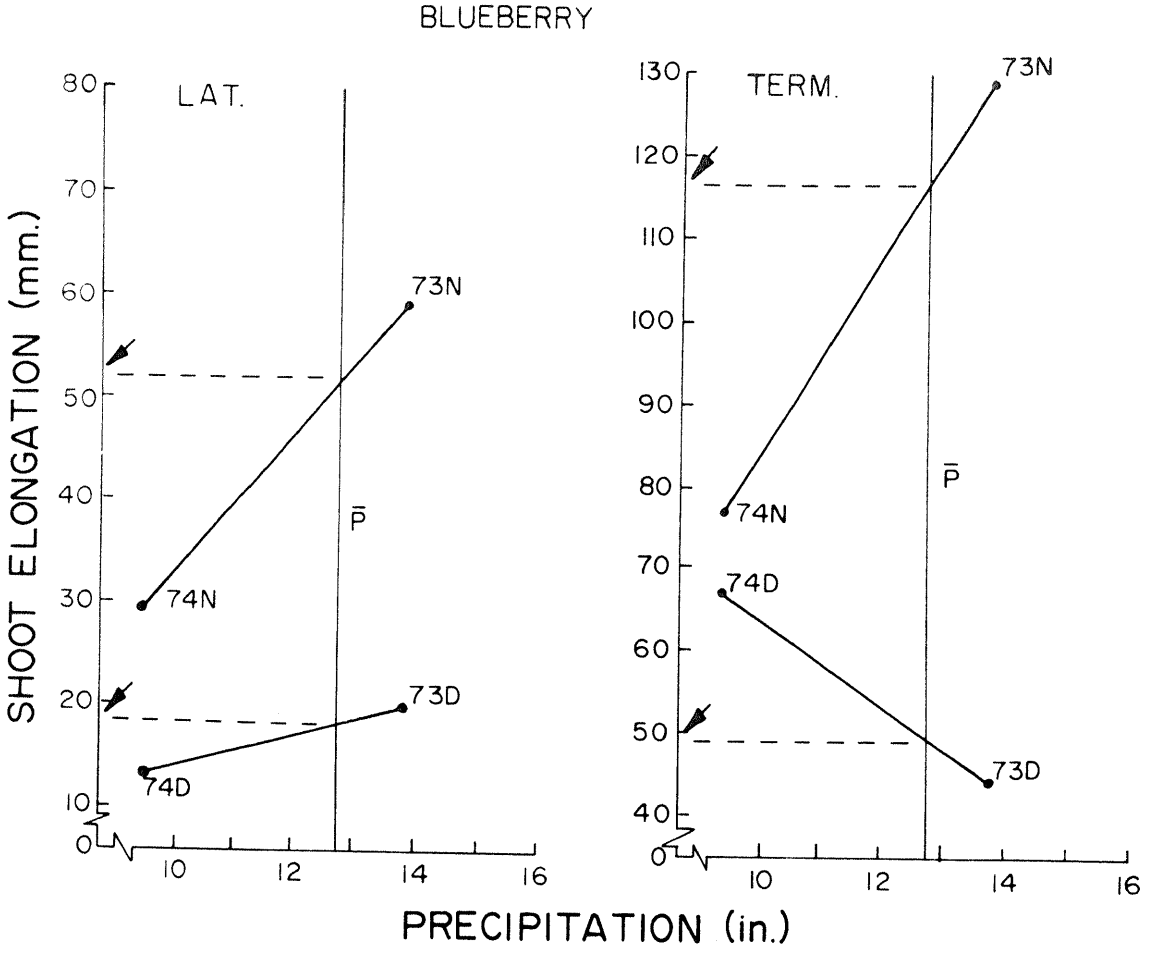

Figure 1c. Predicted shoot elongation in blueberry as a function of precipitation. For explanation of symbols see legend, Figure 1a.

Second, a histogram (Figure 2) was drawn comparing the estimated average growth increments on the natural site with those on the drained site. On each site differences in estimated average shoot growth between all pairs of species were determined. These differences between species on the natural site were subtracted from the same differences on the drained site to determine the magnitude of the change in relative growth among species due to drainage. This average annual difference in growth between species due to drainage was multiplied by 100 to compare the long term (100 year) effects on the relative growth rates between species.

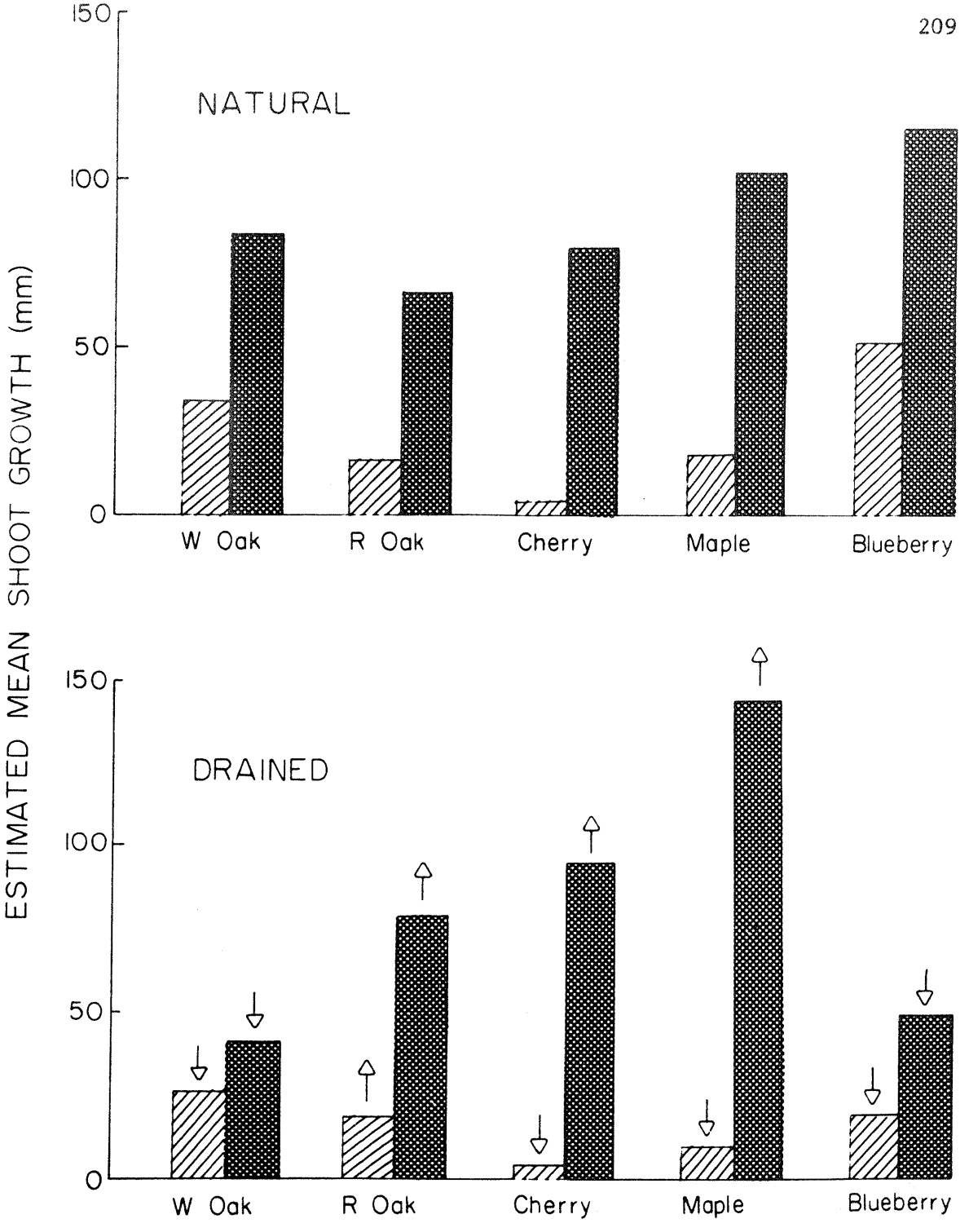

Figure 2. Estimated mean shoot growth (mm) on both sites during a normal year of precipitation. Patterned bars represent terminal stems, while cross-hatched bars represent lateral stems. Arrows indicate an increase (↑) or decrease (↓) in growth as a result of drainage.

RESULTS

Precipitation, Water Table, and Soil Moisture

Precipitation data were obtained from the U.S. Weather Service station at Toledo Express Airport located 2.0 km southwest of the study area. Mean rainfall for the period May through August was 32.4 cm. In 1973 there was a slight excess for the period with 34.8 cm, although August precipitation was well below the monthly mean. In May-August 1974, rainfall totalled only 23.7 cm, and the total for July and August was 10.4 cm below normal.

The depth to the water table increased throughout the summer on both sites. In May the water table on the drained site was 1.28 m lower in 1973 and 1.21 m lower in 1974 than on the natural site. By October this difference decreased to 0.88 m in 1973 and 0.67 m in 1974. There was a greater fall in the water table on both sites in the dry year (1974), and the water table on the drained site did not fluctuate as much as the natural site in either year.

Mean monthly soil moisture (Table 1) decreased from May to September on both sites. Generally, the drained site had less soil moisture than the natural site. There was less soil moisture on both sites during the dry year (1974) than in 1973.

Table 1. Mean monthly soil moisture measured as percent of field capacity. Field capacity is defined as the water content of the soil after gravitational water has been removed.

		May	June	July	August	September
NATURAL	1973	79.5	66.7	76.6	57.9	55.1
	1974		75.3	58.2	52.7	59.3
DRAINED	1973	75.0	75.0	61.3	48.0	53.8
	1974		74.3	61.8	42.9	48.6

Stem Elongation

Drained versus Natural: In all cases of a significant difference in stem elongation for the year or for seasonal intervals, species on the drained site grew less than on the natural site. Black cherry was the only species showing no significant differences in growth. Leaf emergence and the onset of stem growth in black cherry occurred at least 2-3 weeks before any other tree and ended sooner. As a result, most of this species' growth took place before signs of moisture stress were apparent.

Most significant differences in growth developed during the summer or fall intervals, the only exception being white oak terminal stems in the spring interval of 1973. Blueberry showed significant decreases in lateral stem growth on the drained site for total season and summer interval periods in both years, while terminal growth was only affected in 1973 (total and summer interval). During the summer interval of the dry year (1974), growth of red oak and red maple lateral stems decreased significantly on the drained site.

Comparisons between years: Significant within-site differences in growth appeared during the summer interval of the growing season. More growth always occurred in the wet year, except for white oak terminal stems which grew significantly more in the spring interval of the dry year than in the spring interval of the wet year.

Interspecies comparisons: Growth responses of terminal and lateral stems were different. First, we will consider terminal stems. On the natural site in 1973, there were no significant interspecies differences in mean terminal stem growth (Table 2). During the dry year, however, the red oak hybrid on the natural site grew significantly less than red maple, white oak and black cherry. On the drained site in 1973, white oak grew significantly less than red maple and the red oak hybrid, but not less than black cherry whose mean was statistically indistinguishable from red maple and the red oak hybrid. Red oak differed significantly from white oak because both species had clumped data points with little overlap. However, the white oak mean was indistinguishable from that of black cherry because the black cherry data were distributed in a bimodal fashion with the lower curve overlapping much of the white oak data. All four species had similar means in 1974.

Lateral stem growth is illustrated in table 3. On the natural site in 1973, red oak, white oak and red maple had a significantly greater lateral stem elongation than black cherry. White oak grew more than red oak, but not more than red maple. In 1974, white oak significantly outgrew the other three species on the natural site. Red maple and red oak had similar means, but were significantly different from black cherry. On the drained site in 1973, white oak, red maple, and red oak had like means, and all were significantly greater than black cherry. White oak grew significantly more than the other three trees during the dry year (1974).

Table 2. Mean shoot elongation (mm) for terminal stems. Underlined means are not significantly different ($p<0.05$). RM - red maple, WO - white oak, RO - red x black oak hybrid, and BC - black cherry.

Condition and year	Mean shoot elongation (mm)			
	RM	RO	BC	WO
Natural 1973	102.2	90.4	82.7	82.6
	RM	WO	BC	RO
Natural 1974	104.2	91.9	68.8	35.1
	RM	BC	RO	WO
Drained 1973	146	96.4	66.6	33.9
	RM	BC	WO	RO
Drained 1974	139.2	88.8	74.1	64.4

Table 3. Mean shoot elongation (mm) for lateral stems. Underlined means are not significantly different ($p<0.05$). RM - red maple, WO - white oak, RO - red x black oak hybrid, and BC - black cherry.

Condition and year	Means			
	WO	RM	RO	BC
Natural 1973	31.5	17.3	16.8	3.6
	WO	RM	RO	BC
Natural 1974	37.1	21.0	13.4	6.2
	WO	RO	RM	BC
Drained 1973	23.9	21.1	11.9	3.9
	WO	RO	RM	BC
Drained 1974	34.1	10.6	7.6	4.3

Leaf Production and Phenology

Drained-site red oaks produced fewer lateral-stem leaves than red oaks on the natural site in 1974. There were no other significant differences in leaf production.

Drainage influenced the time of leaf fall for all species. Red oaks on the drained site lost significantly more lateral leaves in the summer and fall intervals of 1973 when compared to the natural site. Drained site black cherry lost significantly more lateral leaves in the fall interval of 1973. During 1974, earlier leaf loss on the drained site was even more obvious. Red oak, black cherry and blueberry lateral leaves fell in significantly greater quantities in the summer interval than their counterparts in the natural site. All five species lost significantly more lateral leaves on the drained site in the fall interval. White oak was the only species on the drained site that did not lose significantly more terminal leaves during the third interval of the dry year.

Effects of Drainage on Relative Growth Rates

Table 4 shows the predicted effects of drainage on the relative gain or loss in stem elongation for the four tree species over a 100 year period. On the natural site, red maple terminal stems will outgrow white oak by about 1.8 m/100 yr., black cherry by about 2.2 m/100 yr., and red oak by about 2.4 m/100 yr. On the drained site red maple will outgrow black cherry by about 4.7 m/100 yr., red oak by about 7.6 m/100 yr., and white oak by about 10.0 m/100 yr. Thus, as a result of drainage, red maple terminal stems will gain a competitive advantage of approximately 2.5 m/100 yr. over black cherry, 5.2 m/100 yr. over red oak and 8.2 m/100 yr. over white oak. Black cherry will gain a competitive advantage of 2.8 m/100 yr. over red oak and 5.7 m/100 yr. over white oak. Red oak will gain 3.0 m/100 yr. over white oak.

There was a change in the rank order of terminal stem growth as a result of drainage. The growth rate of white oak terminal stems dropped from the second highest to the lowest. Red maple remained the highest, while black cherry and red oak each moved up one position.

On the natural site, white oak lateral stems will outgrow red maple lateral stems by 1.6 m/100 yr., red oak by 1.8 m/100 yr., and black cherry by 3.0 m/100 yr. (Table 5). On the drained site, white oak will outgrow red oak by 0.8 m/100 yr., red maple by 1.5 m/100 yr. and black cherry by 2.2 m/100 yr. White oak will still have the greatest stem elongation, but red oak will gain 1.0 m/100 yr. on white oak as a result of drainage. Red maple will gain 1.0 m/100 yr. and black cherry 0.8 m/100 yr. on white oak. Red oak gains 0.9 m/100 yr. on red maple and 0.3 m/100 yr. on black cherry. Black cherry will gain 0.7 m/100 yr. on red maple.

Red maple and red oak exchanged position in lateral stem growth as a result of drainage.

Table 4. Changes in relative growth of terminal stems due to drainage. Read across rows: e.g. - white oak outgrows red oak by 0.6 m/100 years on the Natural site (N), but loses 2.4 m/100 years on the Drained site (D). A positive sign (+) indicates a gain in competitive advantage, while a negative sign (-) indicates a loss of competitive advantage. All numbers are meters/100 years. The inequality expressions give the actual species rankings of terminal stem growth rates.

	RED OAK			MAPLE			CHERRY		
	Difference N	Difference D	Net Change	Difference N	Difference D	Net Change	Difference N	Difference D	Net Change
W. OAK	0.6	-2.4	-3.0	-1.8	-10.0	-8.2	0.4	-5.3	-5.7
R. OAK				-2.4	-7.6	-5.2	-0.1	-2.9	-2.8
MAPLE							2.2	4.7	-2.5

Natural site RM > WO > BC > RO

Drained site RM > BC > RO > WO

Table 5. Changes in relative growth of lateral stems due to drainage. Read across rows: e.g. - white oak outgrows red oak by 1.8 m/100 years on the Natural site (N) and by 0.8 m/100 years on the Drained site (D). A positive sign (+) indicates a gain in competitive advantage, while a negative sign (-) indicates a loss of competitive advantage. The inequality expressions give the actual species rankings of lateral stem growth rates.

	RED OAK			MAPLE			CHERRY		
	Difference N	Difference D	Net Change	Difference N	Difference D	Net Change	Difference N	Difference D	Net Change
W. OAK	1.8	0.8	-1.0	1.6	1.5	-0.1	3.0	2.2	-0.8
R. OAK				-0.2	0.7	0.9	1.1	1.4	0.3
MAPLE							1.4	0.7	-0.7

Natural Site WO > RM > RO > BC

Drained Site WO > RO > RM > BC

DISCUSSION

Stem Elongation

Drained versus Natural: In all cases of significant differences in growth between sites, stems on the drained site grew less. Nearly all of these differences occurred in either the summer or fall interval of the growing season, and are apparently attributable to a decrease in soil moisture resulting from drainage accompanied by insufficient precipitation. In the summer interval of 1973, growth differences appeared in red maple terminal stems apparently as a result of low August rainfall. Half of August lies in each interval, and during that month precipitation was 5.5 cm below the mean. Significant growth depression of several species occurred during the prolonged drought of 1974. No significant difference occurred in the fall interval of 1974 because, by then, both sites were adversely affected by the drought and accompanying low soil moisture. Reductions in stem growth occurred much sooner on the drained site during periods of insufficient precipitation.

Comparisons between years: The only significant differences in growth between years took place during the summer interval and can be attributed to the drought of summer 1974. More growth always occurred in the wet year (1973).

Terminal and lateral stems respond differently in their growth patterns. Terminal stems inhibit lateral stem growth through the influence of auxins, and should be given prime consideration when making predictions on the relative abilities of species to reach the canopy. However, lateral stems are also important in that they comprise the majority of the shoots and therefore bear the majority of the leaves. Wilson (1966) found that over 90 percent of the stems on red maple trees 30 years of age or older were lateral stems; thus lateral stem leaves are important in intercepting light. Any increase in lateral stem growth should confer a competitive advantage to a species by enabling it to utilize lighted areas not yet occupied by leaves, and to shade out seedlings (potential future competitors) underneath.

Terminal and lateral stems have different growth strategies which compete for a tree's resources. If the growth strategy in response to drought is to increase terminal stem elongation, perhaps this signifies that the tree is attempting to achieve exposure to full sun light so as to produce the same amount of photosynthate with fewer leaves. Thus, water loss is minimized. Our data (both significant differences and relative amounts) seem to reflect this strategy. Three out of four species responded to the combined stress of drainage and drought by increasing terminal stem growth. For example, black cherry terminal and lateral growth were greater on the drained site in the wet year, but during the dry year lateral growth was greatest on the natural site and terminal growth was greatest on the drained site. Red maple lateral stem growth was better on the natural site, while terminal stems grew better on the

drained site. It appears that red maple responds to drainage by shunting lateral growth to terminal stems regardless of precipitation conditions.

In the wet year, red oak terminal growth was better on the natural site, while lateral growth was better on the drained site. During the dry year, red oak terminal stems grew better on the drained site than on the natural site, while lateral stem growth was better on the natural site. Thus, red oak responds to both wet and dry conditions by increasing terminal stem elongation at the expense of lateral growth. White oak terminal and lateral stems grew less on the drained site in both years and may represent an alternate type of response; i.e., by a reduction in growth rather than a redistribution of it. White oak was affected the most by drainage, followed by red maple, red oak and black cherry.

Interspecies comparisons: We found that white oak terminal shoots grew less than red maple and red oak shoots on the drained site in the wet year (1973), while red oak grew less than the other three trees on the natural site in the dry year (1974). The relative soil moisture requirements of these trees are known: Fraser (1954) found that black cherry occupies driest soils, red oak ranges from dry to intermediate, and red maple is able to tolerate both the wetter soils and some of the drier ones. White oak is found in a variety of habitats from mesic woods, wet flats, and dry hillsides, while black oak is usually found on drier sites (Braun 1961). It is not clear why a species adapted to drier sites, such as the red oak hybrid, would grow less than other species on the natural site in the dry year. We can only suggest that factors other than moisture might be responsible for the unexpected growth differences found in white oak and red oak. Interpretation of these patterns in the light of the moisture preference literature is further complicated by the uncertain genetic background of the "red oaks" on our experimental site.

White oak is the only species to improve its rank in lateral stem growth. However, its advantage is probably due to drought rather than drainage, because its lateral growth is greater than all other species only during the dry year, and this pattern is evident on both sites. Black cherry lateral stems generally grow significantly less than all other species. Reduced lateral stem growth appears to be an inherent characteristic of this species, and not a response to any soil moisture variations. This tree characteristically bears small horizontal branches forming a narrow oblong head (Peattie 1966).

Leaf Production and Phenology

Subsurface drainage appears not to affect leaf production. Soil moisture remains high during the early part of the growing season and thus should not be a limiting factor in leaf production, except for affecting the few terminal stems still producing leaves in mid-summer.

The time of leaf fall is affected by drainage. Two species, red oak and black cherry, seem especially vulnerable to early ecdysis. This effect is compounded during a drought, since in 1974 blueberries, red maples, and white oaks also lost leaves prematurely on the drained site.

The Effects of Drainage on Succession

Using twig growth data for predicting future forest composition has limitations in that factors other than shoot elongation rates may play roles in directing forest succession. These include dispersability (Pijl 1972), allelopathy (Rice 1974), differential seed and seedling survival rates (Janzen 1970, Horn 1972), and other factors. The limitations are also compounded by the following built-in assumptions: (1) We have assumed a linear relationship between stem elongation and precipitation. (2) Species having the greatest growth rates may not, in the long run, be the best overall competitors. (3) The climax association for this region consists of a Beech-Maple forest (*Fagus grandifolia* Ehrh. and *Acer saccharum* Marsh), while for this local area the edaphic climax is a black oak-white oak association (Braun 1950). Oak forests are found in association with sandy areas throughout the eastern United States. These trees are well suited for growth on sand, and in the Oak Openings area of Ohio it may take thousands of years for the regional climax (Beech-Maple forest) to develop if they develop at all. Horn (1975) states that "multilayered" trees with leaves on the periphery only (red oaks, white oaks, red maples and black cherries) have a lower water loss per unit of photosynthate than "monolayered" trees which have leaves scattered throughout the crown (beeches and sugar maples), and should be dominant on well drained soil where water is scarce. This may explain the prolonged dominance of oaks on sandy soils in northwest Ohio. (4) It is not known how the roots are responding to the lowered water table.

From table 4, it can be seen that red maple, black cherry, and red oak will increase their terminal stem competitive advantage in the forest as a result of drainage, while white oak loses competitive advantage to all three species. Changes in stem growth relations between species may be used in combination with changes in species rank order to predict future forest composition. Red maple gains the most in terminal stem growth as a result of drainage, but its rank is not altered. Black cherry and red oak each move up one position, not because of their increase in stem elongation, but merely as a result of the decrease and resultant change in position of white oak. Factors presently unknown are preventing the understory red maples and black cherries from entering the canopy. We speculate that only the oaks are able to withstand the alternating extremes of hydric and xeric soil conditions characteristic of the oak openings, with its unusual combination of sand overlying a high, perched water table. Thus large maples and cherries may suffer heavy mortality during unusually dry or wet seasons, respectively, and only their superior dispersal mechanisms maintain them as dominants in the sapling layer. Furthermore, from table 5 it can be seen that red oak is the only species to increase lateral stem growth and also to

experience a positive change in position as a result of drainage. This should enhance red oak competitiveness as a canopy species. Assuming that oak will continue to dominate the canopy, we conclude that red oak should maintain its dominant position despite drainage, while white oak may become less competitive and eventually fall out. Blueberry will continue to grow poorly on the drained site, and may eventually be replaced.

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