THE RELATIVE EFFECT OF SOIL CHANGES ASSOCIATED WITH OLD-FIELD SUCCESSION AND AVAILABLE MOISTURE UPON THE GROWTH OF THREE UPLAND TREE SPECIES

by

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INTRODUCTION

A detailed knowledge of successional trends and the ecological structure of natural plant communities contributes materially to successful silvicultural practice and forest management. This is especially true in the south because of the rapid growth rates and high commercial value of the yellow pines that are associated with the successional pattern. Under intensive management Loblolly pine will attain growth rates of nearly 2.5 cords per acre per year and Shortleaf and Virginia pine 1.5 cords per acre per year (Korstian, 1962). This along with potential rotations of 30-50 years have made the yellow pines the leading species in the Southern pulp industry.

The general successional pattern of the upland Piedmont region has been described by Oosting (1942). Various early herbaceous plants are replaced by pine which eventually gives way to the climax oak-hickory type. The pioneer pine species are fast growing valuable commercial species but under natural conditions they are replaced by the lower-valued hardwoods of the oak-hickory type.

The intensive management of a forest area requires a knowledge of the factors that affect the establishment of the species concerned; also, the possible effect of changes in soil characteristics that would influence the growth of the species of the successional pattern.

Secondary succession results from a complex series of environmental changes and interactions that separately cannot be evaluated. The difficulties in measuring these effects can be seen in the conflicting results of many experiments. Coile (1940) and others contend that factors other than soil changes are of primary importance in the establishment and development of the secondary successional pattern. On the other hand, Billings (1938), Auten (1939), and Minckler (1946) have suggested that changes in soil characteristics play a primary role in the development of each successional stage. This experiment will attempt to determine the relative importance of changes in soil characteristics by measuring (1) the relative effects of soil changes associated with old-field successional stages upon the growth of three upland tree species, and (2) the relative effects of varying moisture levels upon the growth of the same three tree species.

LITERATURE REVIEW

Plant succession is the replacement of one plant community by another until the climax association is reached. In some cases, observation has given rise to the idea that succession is caused by environmental changes that favor invasion and development of new plant communities in place of those already present.

Although the environmental factors associated with plant development are numerous, some writers have suggested that changes in various soil characteristics are of prominent importance in the development of communities toward the climax association. Clements (1931), discussing the influence of climate on climax community development, wrote: "The primary control of climate is expressed not only in the corresponding climax, and its shifts in the concomitant movement of climaxes, but it likewise initiates and sets a term to physiographic and soil changes that direct succession and bring it to a close in the climax organism." Likewise, Billings (1938) referring to physical soil changes associated with old-field succession, stated: "These causal factors in soil change are conditioned by the presence of pine vegetation which in turn is changed and eventually disappears because of its effect on its own environment."

Pine will not reproduce itself under the low light conditions present under mature pine stands, and it is eventually succeeded by the slower growing, lower valued hardwoods. Consequently, many of the earlier studies have concentrated on the effect of light and moisture upon pine and hardwood regeneration.

Kramer and Decker (1944) and Kozlowski (1949) compared the effects of various light intensities and moisture levels upon the growth of loblolly pine and oak seedlings. They found that loblolly pine seedlings with secondary needles did not reach maximum photosynthetic rates until they were exposed to full sunlight. On the other hand, the oak seedlings reached maximum photosynthetic rates at about one-third full sunlight. They concluded that under low light intensities pine seedlings did not produce enough photosynthate to promote adequate root growth. This, in turn, lessened the pine seedlings' ability to compete with the more vigorous hardwoods for the available soil moisture.

Bourdeau (1954), experimenting with loblolly pine and oak seedlings on good and poor forest sites, found that the pine could not produce adequate root growth under low light intensities to effectively compete for soil moisture during periods of dryness. Oosting and Kramer (1946) compared loblolly, shortleaf and Virginia pine growth under the forest canopy, at the stand margin and in the open. They found that the pines in the open and at the stand margin could successfully compete for soil moisture, even during dry periods, while the seedlings under the forest canopy could not.

Kramer, Oosting, and Korstian (1952) compared the relative survival of pine and hardwood seedlings under forest and open conditions. They found the survival of pine to be best in the open and at the stand margin but the oak survived best under the forest canopy and poorest in the open. Wenger and Trousdell (1957) stated that: "Hardwoods thus are distinctly superior to pine in photosynthesis under all conditions of light and moisture." Relative photosynthetic differences of pine and most hardwoods could be a major factor in this stage of the successional pattern. However, this does not explain the relative inability of hardwoods to grow well on old fields.

Minckler (1946) and Minckler and Chapman (1948) recommended pines over hardwoods for typical old-field planting sites in the Central, Piedmont and southern Appalachian regions because of the inability of the hardwoods to survive and grow under old-field conditions. Minckler (1952) and Ryker (1958) compared growth and survival of planted pines and hardwoods on abandoned fields in Southern Illinois. After five years on poor sites, loblolly and shortleaf pine obtained average heights of 9 feet and 7 feet respectively, while yellow poplar and white ash averaged 4 feet and 3 feet. At the end of 11 years, average heights were 24 and 18 feet for loblolly and shortleaf pine and 6 and 4 feet for yellow poplar and white ash. Although hardwood survival averaged 90% after five years, it dropped to 47% 11 years later and was expected to fall even lower as time progressed.

Based upon a study of the comparative success of loblolly and sweetgum seedling on old-field sites, Bormann (1953) observed that the pine was better suited for the old-field site due to: (1) ability of the germinating pine seed to withstand drying (2) superior drought endurance of the pine seedlings, and (3) ability of the pine seedlings to tolerate the wide variety of old-field conditions.

Auten (1939, 1941, 1945) studied soil changes occurring under old-field stands of shortleaf pine, black locust, and sassafras. He mentioned that pioneer species could create a more favorable environment for the climax species. He also concluded that litter deposition, organic matter incorporation, and increases in porosity and infiltration rates were among the more prominent factors in the soil changing process.

It seems apparent that the large amounts of litter deposited annually plus the tremendous volume of root growth developed by the pine stand could have a significant effect upon the chemical, physical, and biotic properties of the soil.

Nutrient studies by Chandler (1941, 1944), Coile (1937), and Metz (1952a, 1952b) have shown that more than a ton of litter is deposited per acre per year under well-stocked stands. This would amount to more than 100 pounds of mineral nutrients and 20-30 pounds of nitrogen per acre per year. Lunt (1941) conducted lysimeter studies under northeastern hardwood and conifer stands. He observed that the bulk of the nutrient material (including nitrogen in various forms) leached out of the A_o horizon was either taken up by roots or fixed in the soil. Only a small portion leached deeper than four inches. In a comparison of nutrient contribution of overstory and understory vegetation, Scott (1955) found that litter of common understory species such as dogwood, red bud, and red maple contained more than twice as much nutrient material on a per pound basis as the pine overstory. Decomposition rates and incorporation of organic matter also increased with the increased density of these understory species.

Pearse (1946), while studying soil fauna populations under various forest types, found that the higher basic content of the understory hardwoods brought about a change in the fauna populations of the older pine stands, especially in the earthworm populations. Fenton (1947) found that higher calcium contents of hardwood litter increased its palatability to members of the fauna population and therefore increased its rate of decomposition. Increased decomposition and subsequent organic matter incorporation was found to result in a change from the mor to the mull humus type as described by Hoover and Lunt (1952).

The combination of organic matter incorporation, fauna activity, and root growth may significantly affect physical soil properties that could, in turn, affect tree growth.

Billings (1938) studied changes in physical properties of soil under shortleaf pine stands on the North Carolina Piedmont. He observed that only the upper six inches of soil was affected by the pine succession. He also found that the soil became lighter and held more water as the succession progressed due to addition of organic material, formation of root channels, and increased activities of soil fauna.

Coile (1940) and Hursh (1944) found macropore space under old pine and hardwood stands to be nearly three times as great, and infiltration rates ten to twenty times as great as that of the abandoned fields. Coile (1940) attributed the majority of the increased infiltration to the tremendous number of root channels left by the trees that had died during the development of the pine stand. Coile's conclusion is substantiated by Gaiser (1952) who, in a later study in Ohio, estimated the number of vertical root channels in an oak stand to be more than five thousand per acre and the total weight of all roots to be more than seven tons per acre.

Microclimate is another important factor that is altered by the closure of the canopy at the beginning of the pine stage.

Hursh (1947) and Greene (1953) observed that the 0-2 inch soil layer of abandoned fields were subjected to much greater extremes of temperature and moisture variation over a short period of time than were the comparable soil depths under pine and hardwood stands. Although best loblolly pine germination and seedling growth was found to occur at soil temperatures of 68-77°F (Barney, 1951), Borman (1952) has pointed out that pine seedlings are more tolerant to the high temperature-low moisture extremes of old-field sites than are hardwood seedlings.

Coile (1940) has conducted the most comprehensive study of soil changes associated with old-field succession. He found that, although measurable soil changes did occur during the succession, the changes occurring during the presence of a given stage in the succession did not bring about the development of a higher successional stage. Coile decided that seed dispersal and rooting characteristics of the particular species were of greater significance than soil changes during the successional pattern. Hardwood seeds were found to have a smaller dispersion radius and were more susceptible to dessication than were pine seeds. On the other hand, hardwood seedlings were found to have more vigorous root systems under shaded conditions than pine seedlings under similar conditions. The vigorous root system was thought to enable the hardwood seedlings to be a better competitor for soil moisture and nutrients than the less vigorous pine seedlings.

On the other hand, it has also been shown that hardwood seedlings do not grow well on typical old-field sites, and that they will grow adequately on soils that have not been depleted by agricultural use (Minckler and Chapman, 1948, Minckler, 1946, 1952). Therefore, these more recent experiments show the possibility of a more favorable environment, due to soil changes and interactions, for the growth of hardwood seedlings.

Although the presence of vegetative cover will have a beneficial effect on the moisture holding capacity of the soil (Metz, 1948; Southeastern Forest Experiment Station, 1949), the tremendous transpiration potential of a forest stand will tend to create a soil moisture deficit during periods of low precipitation. This moisture deficit, coupled with the high amount of water loss from the surface soil, suggests that seedlings growing in both types of environments will be exposed to conditions of moisture stress for varying periods of time.

The relative availability of soil moisture to plants has been the subject of much controversy. However, most investigators now believe that as the amount of soil moisture is reduced, moisture stresses are increased, limiting the uptake of water by the plant and subsequently reducing growth.

Kramer (1956) stated that the availability of soil moisture depends largely on its diffusion pressure deficit. Soil moisture tension is produced by gravitational, hydrostatic, osmotic, and capillary forces and can be expressed in atmospheres of negative pressure. For all practical purposes, this would be equivalent to the diffusion pressure deficit, providing the salt content of the soil was not high. The diffusion pressure deficit increases as moisture leaves the soil, and the pressure gradient from root to soil decreases. The decrease in the pressure gradient causes a decrease in the amount of water absorbed, and, as the diffusion pressure deficits of the soil and roots become equal, absorption stops. Slatyer (1957) presented an explanation of the wilting point that differed somewhat from Kramer's explanation. He stated that as a plant depletes the soil water reservoir, the total soil moisture stress increases, and the diffusion pressure deficit of the plant must also increase to maintain turgor pressure. The progressive increase in stress will continue until the total soil moisture stress reaches a level equivalent to the osmotic pressure in the plant leaves. At this point, the total soil moisture stress and the diffusion pressure deficit are also equal and the turgor pressure is zero and permanent wilting occurs. This suggests that the permanent wilting point is dependent upon the osmotic characteristics of different plant species in different habitats and has a potential range of 5-200 atmospheres.

The views of Kramer and Slatyer can be substantiated by the findings of many experiments. Schopmeyer (1939) found that transpiration rates of loblolly and shortleaf pines decreased as soil moisture decreased until the rate at the calculated wilting coefficient was only 15.8 per cent of that at field capacity. Martin (1940) observed that transpiration of sunflowers was not affected until approximately two-thirds of the available water had been removed. Denmead and Shaw (1962) found that transpiration rates of corn were reduced at soil moisture tensions of .3-2 bars under conditions favoring high transpiration rates. Schneider and Childers (1941) found that transpiration and photosynthesis rates of potted apple trees at wilting point dropped to 13% of the original rate at field capacity.

The effect of available moisture on metabolic processes can also be shown by the effect on the total growth of a plant. A review of soil moisture regime experiments by Stanhill (1957) showed that of 80 papers describing moisture regime investigation 66 experiments found that plant growth showed a significant response to different levels of available moisture and 14 indicated no response. The greatest yield was found to be associated with the wettest regimes.

Wenger (1952) found that both height growth and total fresh weight of sweetgum, loblolly pine and shortleaf pine decreased significantly with decreasing available soil moisture.

Kozlowski (1949) found that dry weight and size of the root systems of potted overcup oak and loblolly pine seedlings were reduced when subjected to a moisture stress slightly above their wilting points.

Dickson (1962) grew four bottomland hardwood species (pin oak, sycamore, green ash, and tupelo gum) under moisture conditions ranging from saturation to wilting point. He found that as the intensity of the soil moisture stress increased there was a reduction in growth of all species tested when compared to the well-watered condition.

DESCRIPTION OF THE STUDY AREA

Location

Prince Edward County is in the south-central part of Virginia. Farmville, the county seat, is about 65 miles southwest of Richmond and about 45 miles east of Lynchburg.

Climate

Prince Edward County has an average annual rainfall of approximately 40 inches. Although the rainfall is distributed well throughout the year, November and June are the average driest and wettest months respectively. Average annual temperature is 57.6° but summer and winter temperatures are usually subject to considerable variation. The average reported frost-free season is 191 days and the normal growing season usually extends from April 16 to October 24.

Physiography and Relief

Prince Edward County is an upland plain entirely within the Piedmont province of the eastern United States (Fenneman, 1938). A gently rolling topography is characteristic of the lower Piedmont. Unbroken slopes greater than 15 per cent are uncommon. The County is underlain by metamorphosed pre-Cambrian rocks of sedimentary and igneous origin, Lower Cambrian quartzites and triassic sediments (Jonas and Watkins, 1932).

The granite, gneiss, and schist of the County support ridges that gradually slope toward the streams. The more important soil series derived from these rocks include Cecil, Appling, Madison, Lloyd, Durham, Vance, Helena, and Fluvana (Henry *et al.*, 1958).

Cecil Soil

The Cecil soils have formed in parent material derived from granite gneiss, mica gneiss, granite and mica schist. They are widely distributed in the Piedmont region of Virginia, the Carolinas, Georgia, and Alabama.

In profile characteristics, Cecil soils typically have red clay B horizons and light colored sandy loam A horizons. These soils have a high degree of horizon differentiation and are representative of the Red-Yellow Podzolic Great Soil Group.

The following general profile description applied to the typical Cecil profile of a cultivated field:

Surface soil --

0 to 11 inches, yellowish-brown friable fine sandy loam; weak fine granular structure; a few angular quartz fragments. The lowest part is reddish-yellow and contains some clay.

Subsoil --

11 to 54 inches, red firm clay, sticky when wet; moderate medium blocky structure; a few mica flakes; faint mottlings similar to those in the parent material in the lower part.

Parent material --

54 to 60 inches, mottled reddish-yellow and yellowish-brown friable clay loam; moderate medium subangular block structure.

60 inches +, soft decomposed schist and granitic rock.

METHODS AND PROCEDURES

Part I. Old-Field Succession Study

Four seral stages representing the old-field successional pattern on the Piedmont areas of Virginia and the Carolinas were arbitrarily chosen for sampling in part one of the study. The seral stages chosen were as follows:

1. Abandoned fields - two to five years since subjected to agricultural use.
2. Young pine stands - Virginia pine stands 10-20 years of age that had regenerated naturally on abandoned farm land and had formed closed canopies.
3. Mature pine stand - Virginia pine stands 50-70 years of age that had regenerated naturally on abandoned farm land.
4. Climax oak-hickory stands.

Three uniform sites were located for each of the above successional stages; two of the three sites were randomly chosen for the actual sampling. All sites were located on moderately eroded Cecil fine sandy loam soils with slopes of two to five per cent.

The soil samples used in the experiment consisted of large cores of undisturbed soil collected in number 10 tin cans (6 inches in diameter and 7 inches high) according to the procedure described by Clark (1961).

The open tops of the cans were pressed firmly against the soil surface and the litter, grass, etc. cut with a knife. The cans were then driven flush to the surface with a hammer and a two-inch thick block of wood. Each can was then dug from the ground and the excess soil shaved off the core bottom with a knife. The presence of rocks and roots accounted for the loss of about one half of the cans; however, an adequate number of usable samples were obtained from each location. The most uniform samples from the two locations representing each seral stage were then pooled and 12 cans were randomly chosen for use in the experiment. Thus a total of 48 cans were used.

The experiment, conducted in a greenhouse to control moisture, light, and temperature,was set up in a completely randomized design with four observations for each of the 12 species-stage combinations.

The samples were rerandomized every two weeks to reduce any possible positional effects. In order to prevent excess leaching and washing of the soil due to repeated waterings, the sample cans were placed in aluminum cake pans and watered from below. Consequently, at no time during the course of the experiment was soil moisture a limiting factor.

Soil samples (representing the eight collecting sites) taken from the sample cans at the conclusion of the experiment were used to determine texture, organic matter content, pH, cation exchange capacity, exchangeable bases, total phosphorous, and total nitrogen. Soil texture was determined by the Bouyoucos hydrometer method. Per cent organic matter was determined by the Schollenberger wet combustion method as described by Wilde and Voigt (1955). Cation exchange capacity was determined by the methods described by Rich (1962).

Exchangeable Ca, Mg, and K were determined by use of the flame photometer. Total phosphorous was determined by the fractionation method outlined by Chang and Jackson (1957). Total nitrogen was determined by use of the Coleman nitrogen gas analyzer. Results of these analyses are shown in Table 1.

The tree species used in the experiment were loblolly pine (*Pinus taeda* L.), Virginia pine (*Pinus Virginiana* Mill.), and yellow-poplar (*Liriodendron tulipifera* L.). Seedlings of these species were germinated in perlite and planted in the sample cans on June 14, 1962. After establishment, the seedlings were thinned to three healthy, uniform individuals per can. Artificial light was supplied during the evening to insure a constant 16 hour photoperiod. The experiment was started on June 20, 1962, and continued until October 2, 1962. The total experimental period was 105 days.

Part II. Moisture Stress Study

The Cecil soil used in part two, or the moisture stress portion, of the study was obtained from one of the old-field sites sampled in part one of the study. The soil was collected in bulk from the upper six inches of the profile. The soil was then sieved through a one-quarter inch mesh screen to insure uniformity of samples for accurate weight and soil moisture determinations.

Analyses were made to determine the one-third atmosphere, and 15 atmospheres moisture values. Texture and per cent and organic matter for the soil had been previously determined in the soil analysis for part one of the study. The one-third atmosphere moisture value was

Table 1. Chemical and physical properties of the 0-6 inch soil layer for each location of the four successional stages[1/]

Successional stage and location		pH	C.E.C. me./100g	Exchangeable cations, me./100g Ca	Mg	K	Organic matter, %	Total P, ppm	N, %	Particle size distribution, % Sand	Silt	Clay
OF	I	4.4	4.0	1.07	0.33	0.20	1.6	80	0.060	60.0	21.0	19.0
	II	4.9	4.3	0.93	0.17	0.15	1.5	67	0.066	65.0	19.7	15.3
10-20	I	4.7	4.3	0.52	0.21	0.21	1.5	66	0.073	66.0	16.4	17.6
	II	4.7	4.7	0.40	0.10	0.11	2.0	66	0.065	68.0	17.4	13.6
50-70	I	5.2	7.3	0.60	0.30	0.21	3.2	57	0.074	65.0	19.0	16.0
	II	4.9	6.9	0.80	0.19	0.09	2.0	60	0.070	66.0	19.4	14.6
Hwd	I	4.8	7.5	0.53	0.13	0.12	3.5	59	0.080	70.0	24.4	13.6
	II	4.1	6.5	0.58	0.24	0.22	2.7	64	0.070	68.0	23.4	16.6

[1/] OF - Old-field stage; 10-20 - 10-20 year pine stage; 50-70 - 50-70 year pine stage; Hwd - Hardwood stage; I - Location I; II - Location II.

determined by using the suction plate apparatus described by Richards and Weaver (1943). The determination of the wilting point was approximated at 15 atmospheres by use of the pressure membrane device described by Richards (1941).

The physical properties of the Cecil soil are outlined in Table 2. The one-third atmosphere and 15 atmosphere values correspond with the average values obtained for sandy loam soils by Broadfoot and Burke (1958). Although the permanent wilting values were not determined for the species used in the experiment, the 15 atmospheres moisture value was assumed to represent the permanent wilting point.

The tree species used were the same as the species named in part one of the study. The seedlings were transplanted into the sample cans on June 15, 1962. Each sample can contained 3,450 grams of oven-dry soil. The seedlings were watered daily to the calculated one-third atmosphere moisture level until the roots of the seedlings had completely permeated the soil. The seedlings were then thinned to obtain three uniform seedlings per can. Artificial light was supplied during the evenings to insure a 16 hour day. The experiment was started on August 1, 1962, and was terminated on October 2, 1962; a period of 63 days.

The moisture regimes used were:

1. One-third atmosphere - return to calculated one-third atmosphere value daily.
2. 50% - return to one-third atmosphere value when 50% or more of the available water had been removed.

Table 2. Physical properties of soil used for moisture stress study

Property	Range	Mean*
1/3 atmosphere	15.31-15.57	15.40
15 atmospheres	4.46-4.51	4.48
Sand, %	62-66	65
Silt, %	18.4-20.4	19.7
Clay, %	13.6-17.6	15.3
Organic matter, %	1.4-1.6	1.5

*All values are the mean's of four observations.

3. 15 atmospheres - return to one-third atmosphere value when the calculated 15 atmospheres value had been reached.

The amount of available water was determined by weighing the can plus soil each day. These weights were used to indicate when and how much water was needed to reach the desired moisture level for the start of a new cycle.

This part of the experiment was replicated four times in a completely randomized design. The sample cans were rerandomized every two weeks to reduce possible positional effects on the seedlings.

At the conclusion of each experiment, the seedlings from the sample cans were carefully washed from the soil and the following data were collected:

1. Height growth during the experiment
2. Dry weights of roots and tops
3. Shoot/root ratios of the dry weights
4. Extent of root and root hair development
5. General observations on mortality, appearance, and color

The data obtained were statistically analyzed to test differences between variables. The variables tested were tree species and successional stages in part one; tree species and moisture levels for part two. Differences between mean values were separated by using the Duncan Multiple Range test.

RESULTS

The results of each separate experiment are given below. The differences in growth of the three species was evaluated separately based upon the following criteria: total dry weight, height growth, dry weight of shoots, dry weight of roots, and dry-weight shoot/root ratios.

Part I. Old-Field Succession Study

Effects of Successional Stage on Total Dry Weight

The effect of successional stages on the dry weight production of the species concerned is illustrated in Fig. 1.

The greatest amount of dry weight production for yellow-poplar was produced in soils taken from the old-field site (Table 3). The amount of dry material produced in the cans taken from old-field site was significantly greater (1% level) than that produced by yellow-poplar in cans taken from all other sites. Yellow-poplar dry weight production in soils from the 10-20 year pine site was highly significant (1% level) from yellow-poplar seedlings grown in soils from the 50-70 year pine and the hardwood stands. No significant differences in yellow-poplar dry weight production were found between the 50-70 year pine and the hardwood sites.

No significant differences in total dry weight production of loblolly and Virginia pine seedlings were obtained for any of the four sites (Table 3).

Table 3. Individual differences in the mean total dry weights produced by three species grown on soils from four successional stages[1]/[2]/

	Means	YP OF 1.84	YP 10-20 1.02
YP-OF	1.84	--	--
YP 10-20	1.02	0.82**	--
Va 10-20	0.59	1.25**	0.43*
Lob 10-20	0.56	1.28**	0.46*
Lob Hwd	0.56	1.28**	0.46*
Lob 50-70	0.34	1.50**	0.68**
Lob OF	0.31	1.53**	0.71**
Va OF	0.22	1.62**	0.80**
Va 50-70	0.19	1.65**	0.83**
Va Hwd	0.17	1.67**	0.85**
YP 50-70	0.16	1.68**	0.86**
YP Hwd	0.14	1.79**	0.88**

[1]/YP - Yellow-poplar; Lob - Loblolly pine; Va - Virginia pine; OF - Old field; 10-20 - 10-20 year pine; 50-70 - 50-70 year pine; Hwd - Hardwood

[2]/Mean values in grams for four observations of each treatment.

*Significant at 5% level

**Significant at 1% level

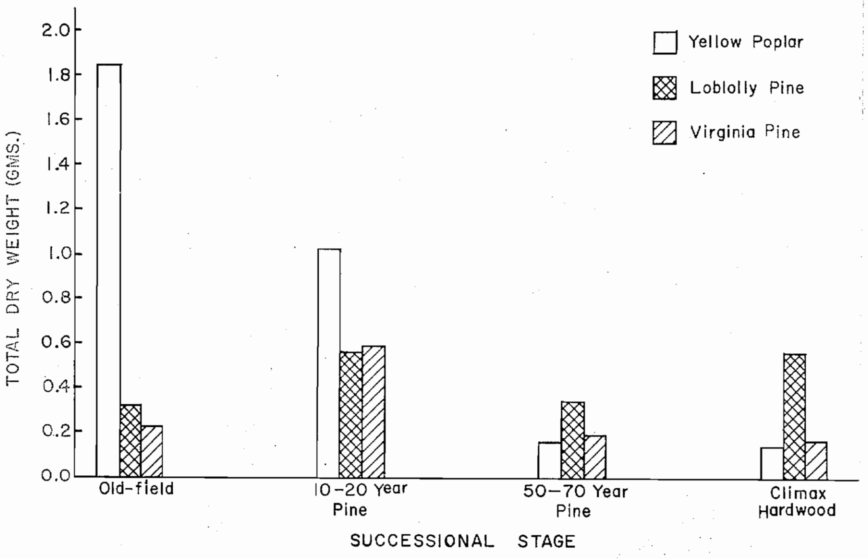

Fig. 1. The relationship of total dry weight production of three tree species to successional stages in the Virginia Piedmont.

Effects of Successional Stage on Shoot Growth

Effect on height growth. The greatest height growth for all species was generally associated with the soils taken from the old-field, and 10-20 year pine sites (Fig. 2).

Greatest height growth for yellow-poplar occurred in cans taken from the 10-20 year pine and old-field sites (Table 4). Differences in height growth between these sites were not significant; however, both were significantly greater (1% level) than the height growth of yellow-poplar seedlings grown in soils from the 50-70 year pine and hardwood sites.

Maximum height growth for loblolly pine was associated with soils from the 10-20 year pine site. Height growth produced by loblolly pine seedlings in cans taken from the 10-20 year pine site was significantly greater (1% level) than the height growth of loblolly seedlings grown in cans from the remaining three sites (Table 4). Height growth produced in cans from the hardwood site was significantly greater at the 5% level when compared with the old-field site. No significant differences were obtained from a comparison of loblolly height growth produced in soils from the old field and 50-70 year pine sites.

Virginia pine grown in soils from the 10-20 year pine site produced significantly greater (5% level) height growth than seedlings of the same species grown in soils from the other three sites (Table 4). No significant height growth differences were obtained from comparisons of the old field, 50-70 year pine, and hardwood sites.

Table 4. Individual differences in the mean height growth values of three species grown on soils from four successional stages[1]/[2]

	Means	Lob 10-20 10.55	YP OF 9.85	YP 10-20 8.32	Lob Hwd 6.35	Va 10-20 6.12	Lob 50-70 4.82
Lob 10-20	10.55	--	--	--	--	--	--
YP-OF	9.85	.70	--	--	--	--	--
YP 10-20	8.32	2.23	1.53	--	--	--	--
Lob Hwd	6.35	4.20**	3.50*	1.97	--	--	--
Va 10-20	6.12	4.43**	3.73*	2.20	.23	--	--
Lob 50-70	4.82	5.73**	5.03**	3.50*	1.53	1.30	--
Lob OF	4.18	6.37**	5.67**	4.14*	2.17	1.94	.64
Va OF	2.30	8.25**	7.55**	6.02**	4.05*	3.82*	2.52
Va 50-70	2.20	8.35**	7.65**	6.12**	4.15*	3.92*	2.62
Va Hwd	1.75	8.80**	8.10**	6.57**	4.60**	4.37**	3.07
YP Hwd	1.52	9.03**	8.33**	6.80**	4.83**	4.60**	3.30*
YP 50-70	1.15	9.40**	8.70**	7.17**	5.20**	4.97**	3.67*

[1] YP - Yellow-poplar; Lob - Loblolly pine; Va - Virginia pine; OF - Old field; 10-20 - 10-20 year pine; 50-70 - 50-70 year pine; Hwd - Hardwood

[2] Mean values in cm. for four observations of each treatment.

*Significant at 5% level.

**Significant at 1% level.

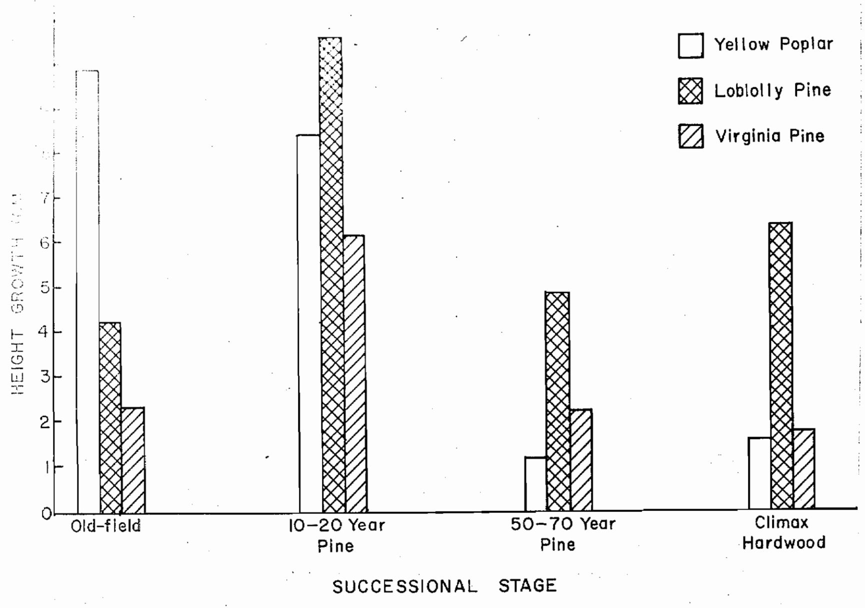

Fig. 2. The relationship of the height growth of three tree species to successional stages in the Virginia Piedmont.

Effects on dry weight of shoots. Maximum dry shoot weight for yellow-poplar occurred in cans taken from the old-field site. Yellow-poplar shoot weight for this site was significantly greater (1% level) than the shoot weights of the yellow-poplar seedlings grown in soils from the remaining three sites (Table 5). Shoot weights of the yellow-poplars grown in the 10-20 pine soils were greater (1% level) than the yellow-poplar shoot weights from the 50-70 year pine site and the hardwood site, but no significant differences were found between the 50-70 year pine and hardwood sites.

No significant differences in dry shoot weights were obtained for the loblolly seedlings grown in soils from the four sites (Table 5).

The shoot weights of Virginia pine seedlings grown in cans from the 10-20 year pine site were significantly greater (5% level) than corresponding weights produced by the Virginia pine seedlings in soils from the old field and hardwood sites (Table 5). No significant differences in Virginia pine shoot weights were obtained from comparisons of the old field, 50-70 year pine, and hardwood sites.

Effect of Successional Stage on Dry Weight of Roots

The greatest root growth produced by the three species was generally associated with the soils taken from the old-field and 10-20 year pine sites.

Yellow-poplar produced the greatest amount of dry root material in the cans taken from the old-field site. Root production for the yellow-poplar seedlings grown in soils from the old-field site was found to be significantly more (1% level) than that of the yellow-poplar

Table 5. Individual differences in the mean shoot dry weight values of three species grown on soils from four successional stages[1/][2/]

	Means	YP OF 0.96	YP 10-20 0.58	Lob Hwd 0.41	Lob 10-20 0.40	Va 10-20 0.39
YP-OF	0.96	--	--	--	--	--
YP 10-20	0.58	0.38**	--	--	--	--
Lob Hwd	0.41	0.55**	0.17	--	--	--
Lob 10-20	0.40	0.56**	0.18	0.01	--	--
Va 10-20	0.39	0.57**	0.19	0.02	0.01	--
Lob 50-70	0.22	0.74**	0.36**	0.19	0.18	0.17
Va 50-70	0.20	0.76**	0.38**	0.21	0.20	0.19
Lob OF	0.20	0.76**	0.38**	0.21	0.20	0.19
Va OF	0.12	0.84**	0.46**	0.29*	0.28*	0.27*
Va Hwd	0.09	0.87**	0.49**	0.32*	0.31*	0.30*
YP Hwd	0.08	0.88**	0.50**	0.33*	0.32*	0.31*
YP 50-70	0.08	0.88**	0.50	0.33*	0.32*	0.31*

[1/] YP - Yellow-poplar; Lob - Loblolly pine; Va - Virginia pine; OF - Old field; 10-20 - 10-20 year pine; 50-70 - 50-70 year pine; Hwd - Hardwood.

[2/] Mean values in grams for four observations of each treatment.

*Significant at 5% level.

**Significant at 1% level.

seedlings grown in soils from all other sites (Table 6). Root weights of yellow-poplar seedlings grown in the 10-20 year pine site soils were significantly greater (1% level) than yellow-poplar seedlings grown in the 50-70 year pine and the hardwood soils, but the latter sites were not significantly different.

Greatest dry root weight production for loblolly and Virginia pine seedlings occurred in the cans taken from the 10-20 year pine site, but the differences between sites within each species were not significant (Table 6).

Effect of Successional Stage on Dry-Weight Shoot/Root Ratios

The largest shoot/root ratios produced by the pine species were associated with soils from the 10-20 year pine sites while yellow-poplar showed little variation with respect to site (Fig. 3).

No significant differences were found between mean shoot/root ratio values for yellow-poplar seedlings grown in soils from the four sites (Table 7).

The largest shoot/root ratios for loblolly seedlings were produced by the seedlings grown in soils from the 10-20 year pine, and hardwood sites. The mean ratio values for these sites were not significantly different from each other, but they were highly significant (1% level) when compared to the mean ratio values of the loblolly seedlings grown in the old field and 50-70 year pine sites (Table 7). The old field and 50-70 year pine sites were not significantly different.

The largest shoot/root ratios produced by Virginia pine seedlings were associated with the cans taken from the 10-20 year pine site.

Table 6. Individual differences in the mean root dry weight values of three species grown on soils from four successional stages[1]/[2]/

	Means	YP OF 0.87	YP 10-20 0.44
YP-OF	0.87	--	--
YP 10-20	0.44	0.43**	--
Va 10-20	0.20	0.67**	0.24**
Lob 10-20	0.16	0.71**	0.28**
Lob Hwd	0.15	0.72**	0.29**
Lob 50-70	0.13	0.74**	0.31**
Lob-OF	0.11	0.76**	0.33**
Va-OF	0.10	0.77**	0.34**
Va 50-70	0.09	0.78**	0.35**
Va Hwd	0.08	0.79**	0.36**
YP 50-70	0.08	0.79**	0.36**
YP Hwd	0.07	0.80**	0.37**

[1]/YP - Yellow-poplar; Lob - Loblolly pine; Va - Virginia pine; OF - Old field; 10-20 - 10-20 year pine; 50-70 - 50-70 year pine; Hwd - Hardwood.

[2]/Mean values in grams for observations of each treatment.

*Significant at 5% level.

**Significant at 1% level.

Table 7. Individual differences in mean shoot/root ratios for seedlings of three species grown on soils from four successional stages[1/][2/]

	Means	Lob 10-20 2.72	Lob Hwd 2.62	Lob OF 1.91	Lob 50-70 1.83	Va 10-20 1.78
Lob 10-20	2.72	--	--	--	--	--
Lob Hwd	2.62	0.10	--	--	--	--
Lob OF	1.91	0.81**	0.71**	--	--	--
Lob 50-70	1.83	0.89**	0.79**	0.08	--	--
Va 10-20	1.78	0.94**	0.84**	0.13	0.05	--
YP 10-20	1.54	1.18**	1.08**	0.37	0.29	0.24
Va OF	1.36	1.36**	1.26**	0.55*	0.47	0.42
Va 50-70	1.31	1.41**	1.31**	0.60*	0.52*	0.47*
YP OF	1.24	1.48**	1.38**	0.67*	0.59*	0.54*
Va Hwd	1.24	1.48**	1.38**	0.67*	0.59*	0.54*
YP Hwd	1.10	1.62**	1.52**	0.81**	1.73*	0.68*
YP 50-70	1.02	1.70**	1.60**	0.89**	1.81**	0.76**

[1/] YP - Yellow-poplar; Lob - Loblolly pine; Va - Virginia pine; OF - Old field; 10-20 - 10-20 year pine; 50-70 - 50-70 year pine; Hwd - Hardwood.

[2/] Mean values for four observations of each treatment.

*Significant at 5% level.

**Significant at 1% level.

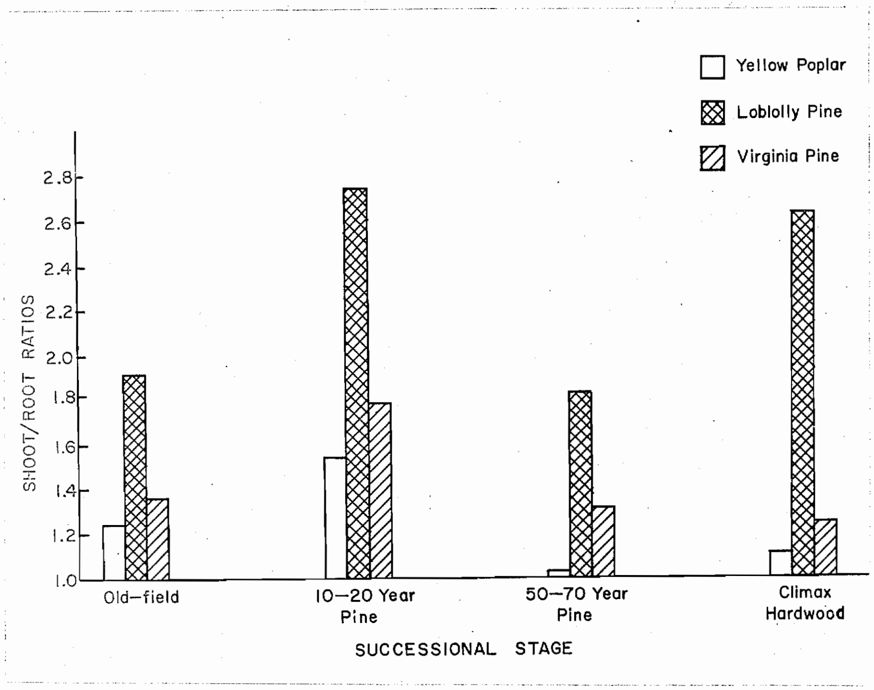

Fig. 3. The relationship of the shoot/root ratios of three tree species to successional stages in the Virginia Piedmont.

The ratios produced in soils from this site were greater (5% level) than the ratios of the Virginia pine seedlings grown in soils from the old field and hardwood sites (Table 7). Shoot/root ratios of the Virginia pine seedlings grown in cans taken from the old field, 50-70 year pine, and hardwood sites were not significantly different.

Part II. Moisture Stress Study

Effect of Moisture Stress on Total Dry Weight

The effect of increasing soil moisture stress on the dry weight production of yellow-poplar and the pine species is illustrated in Fig. 4.

The yellow-poplar 1/3 atmosphere moisture regime produced significantly more dry weight (1% level) than the other two treatments (Table 8). Total dry weight of the 50% yellow-poplar treatment was significantly greater than the yellow-poplar 15 atmospheres treatment.

No significant differences were obtained between any of the Virginia and loblolly pine treatments (Table 8).

Effects of Moisture Stress on the Growth of Shoots

Effect on height growth. Height growth of yellow-poplar decreased with increasing soil moisture stress while the pine species showed little significant variation (Fig. 5).

Maximum height growth of yellow-poplar was produced in association with the 1/3 atmosphere regime. Height growth comparisons for all yellow-poplar treatments were significant at the 1% level (Table 9).

No significant differences were found between the three loblolly pine treatments at the 1% level; however, the height growth production

Table 8. Individual differences of mean total dry weight values of three species subjected to three moisture regimes[1][2]

	Means	YP 1/3 4.74	YP 50% 3.37	YP 15 1.61
YP 1/3	4.74	--	--	--
YP 50%	3.37	1.37**	--	--
YP 15	1.61	3.13**	1.76**	--
Lob 50%	0.51	4.23**	2.86**	1.10**
Va 15	0.44	4.30**	2.93**	1.17**
Lob 15	0.43	4.31**	2.94**	1.18**
Lob 1/3	0.42	4.32**	2.95**	1.19**
Va 1/3	0.35	4.39**	3.02**	1.26**
Va 50%	0.31	4.43**	3.06**	1.30**

[1] YP - Yellow-poplar; Lob - Loblolly pine; Va - Virginia pine; 1/3 - 1/3 atmosphere; 50% - 50% available water; 15 - 15 atmospheres.

[2] Mean values in grams for four observations of each treatment.

*Significant at 5% level.

**Significant at 1% level.

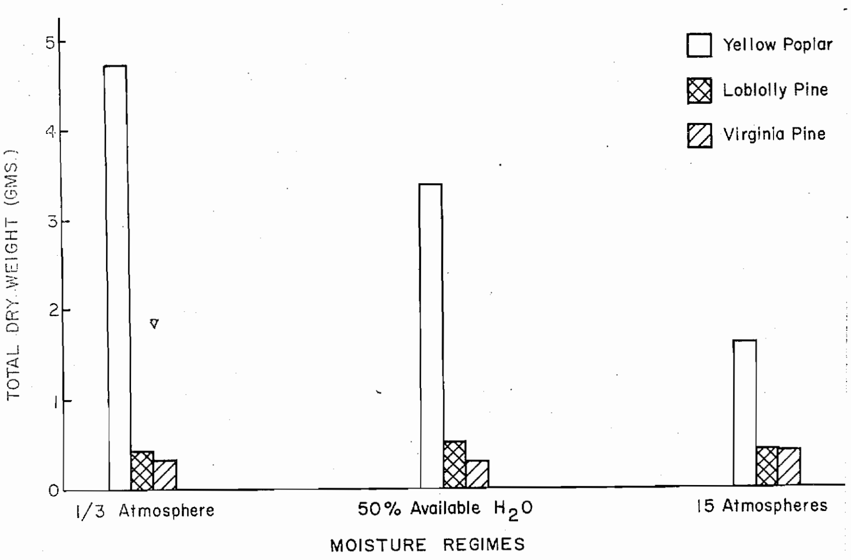

Fig. 4. The relationship of three moisture regimes to the total dry weight production of three tree species.

Table 9. Individual differences in the mean height growth values of three species subjected to three moisture regimes[1]/[2]/

	Means	YP 1/3 16.05	YP 50% 12.42	YP 15 6.35	Lob 50% 5.12
YP 1/3	16.05	--	--	--	--
YP 50%	12.42	3.63**	--	--	--
YP 15	6.35	9.79**	6.07**	--	--
Lob 50%	5.12	10.93**	7.30**	1.23	--
Lob 1/3	4.60	11.45**	7.82**	1.75	0.52
Lob 15	3.50	12.55**	8.92**	2.95	1.62
Va 1/3	2.45	13.60**	9.97**	3.90*	2.67
Va 50%	1.90	14.15**	10.52**	4.45**	3.22*
Va 15	1.70	14.35**	10.72**	4.65**	3.42*

[1]/YP - Yellow-poplar; Lob - Loblolly pine; Va - Virginia pine; 1/3 - 1/3 atmosphere; 50% - 50% available moisture; 15 - 15 atmospheres.

[2]/Mean values in cm. for four observations of each treatment.

*Significant at 5% level.

**Significant at 1% level.

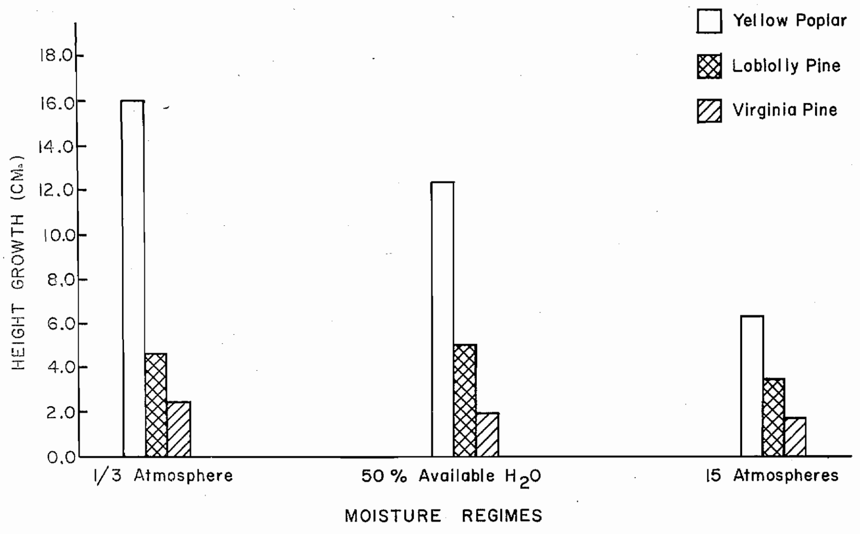

Fig. 5. The relationship of three moisture regimes to the height growth of three tree species.

for the 1/3 atmosphere and 50% treatments were significantly greater (5% level) than that of the 15 atmospheres treatment (Table 9).

No significant differences were obtained for height growth of Virginia pine subjected to the three treatments (Table 9).

Effect on dry weight. The maximum dry weight production for yellow-poplar was associated with the 1/3 atmosphere treatment (Table 10). Dry weight production decreased progressively from the 1/3 atmosphere to the 15 atmospheres treatment. Statistical comparisons showed that all yellow-poplar treatments were significantly different at the 1% level.

No significant differences were obtained between any of the loblolly and Virginia pine treatments (Table 10).

Effect of Moisture Stress on the Dry Weight of the Roots

Root production for yellow-poplar increased through the treatment series 15 atmospheres, 50%, and 1/3 atmosphere while the pine species showed no significant reaction to the treatment levels.

Yellow-poplar produced maximum dry root weight when subjected to the 1/3 atmosphere moisture treatment. Dry weight production decreased progressively from the 1/3 atmosphere to the 15 atmospheres treatment (Table 11). All yellow-poplar treatments were highly significant from each other at the 1% level.

Loblolly and Virginia pine showed no significant differences in dry weight production between any of the treatments (Table 11).

Table 10. Individual differences in the mean shoot dry weight values of three species subjected to three moisture regimes[1]/[2]/

	Means	YP 1/3 2.20	YP 50% 1.65	YP 15 0.88
YP 1/3	2.20	--	--	--
YP 50%	1.65	0.55**	--	--
YP 15	0.88	1.32**	0.77**	--
Lob 50%	0.34	1.86**	1.31**	0.54**
Va 15	0.29	1.91**	1.36**	0.59**
Lob 15	0.28	1.92**	1.37**	0.60**
Lob 1/3	0.25	1.95**	1.40**	0.63**
Va 1/3	0.20	2.00**	1.45**	0.68**
Va 50%	0.19	2.01**	1.46**	0.69**

[1]/YP - Yellow-poplar; Lob - Loblolly pine; Va - Virginia pine; 1/3 - 1/3 atmosphere; 50% - 50% available moisture; 15 - 15 atmospheres.

[2]/Mean values in grams for four observations of each treatment.

*Significant at 5% level.

**Significant at 1% level.

Table 11. Individual differences in the mean root dry weight values of three species subjected to three moisture regimes[1]/[2]/

	Means	YP 1/3 2.54	YP 50% 1.72	YP 15 0.73
YP 1/3	2.54	--	--	--
YP 50%	1.72	0.82**	--	--
YP 15	0.73	1.81**	0.99	--
Lob 1/3	0.17	2.37**	1.55**	0.56*
Lob 50%	0.17	2.37**	1.55**	0.56*
Va 1/3	0.15	2.39**	1.57**	0.58*
Va 15	0.15	2.39**	1.57**	0.58*
Lob 15	0.14	2.40**	1.58**	0.59*
Va 50%	0.12	2.42**	1.60**	0.61*

[1]/YP - Yellow-poplar; Lob - Loblolly pine; Va - Virginia pine; 1/3 - 1/3 atmosphere; 50% - 50% available moisture; 15 - 15 atmospheres.

[2]/Mean values in grams for four observations of each treatment.

*Significant at 5% level.

**Significant at 1% level.

Effects of Moisture Stress on Dry-Weight Shoot/Root Ratios

The effect of increasing soil moisture stress upon the shoot/root ratios of the three species is illustrated in Fig. 6.

The yellow-poplar produced the smallest shoot/root ratios of the three species, and the yellow-poplar 1/3 atmosphere treatment had the smallest ratio. The 15 atmospheres yellow-poplar treatment showed the largest ratio. No significant difference was obtained between the yellow-poplar 1/3 and 50% treatments; however, the 15 atmospheres treatment ratios were greater at the 5% level than the 1/3 atmosphere treatment ratios (Table 12).

The largest ratios for the loblolly pine seedlings were associated with the 50% and 15 atmospheres treatment (Table 12). Although these treatments were not significantly different from each other, both were different at the 1% level from the 1/3 atmosphere treatment.

Virginia pine also produced the largest ratio in association with the 15 atmospheres treatment. The 15 atmospheres ratio was significantly different from the 1/3 atmosphere treatment (1% level) and different from both the 1/3 atmosphere and 50% treatments at the 5% level (Table 12).

Table 12. Individual differences in the mean dry weight shoot/root ratios for individual seedlings of three species subjected to three moisture regimes[1][2]

		Lob	Lob	Va	Lob	Va	Va	YP
		50%	15	15	1/3	50%	1/3	15
	Means	1.95	1.94	1.84	1.48	1.45	1.31	1.28
Lob 50%	1.95	--	--	--	--	--	--	--
Lob 15	1.94	0.01	--	--	--	--	--	--
Va 15	1.84	0.11	0.10	--	--	--	--	--
Lob 1/3	1.48	0.47*	0.46*	0.36*	--	--	--	--
Va 50%	1.45	0.50*	0.49*	0.39*	0.03	--	--	--
Va 1/3	1.31	0.64**	0.63*	0.53*	0.17	0.14	--	--
YP 15	1.28	0.67**	0.66**	0.56*	0.20	0.17	0.03	--
YP 50%	1.06	0.89**	0.88**	0.78**	0.36	0.39	0.25	0.22
YP 1/3	0.88	1.07**	1.06**	0.96**	0.60*	0.57*	0.43*	0.40*

[1] YP - Yellow-poplar; Lob - Loblolly pine; Va - Virginia pine; 1/3 - 1/3 atmosphere; 50% - 50% available moisture; 15 - 15 atmospheres.

[2] Mean values for four observations of each treatment.

*Significant at 5% level.

**Significant at 1% level.

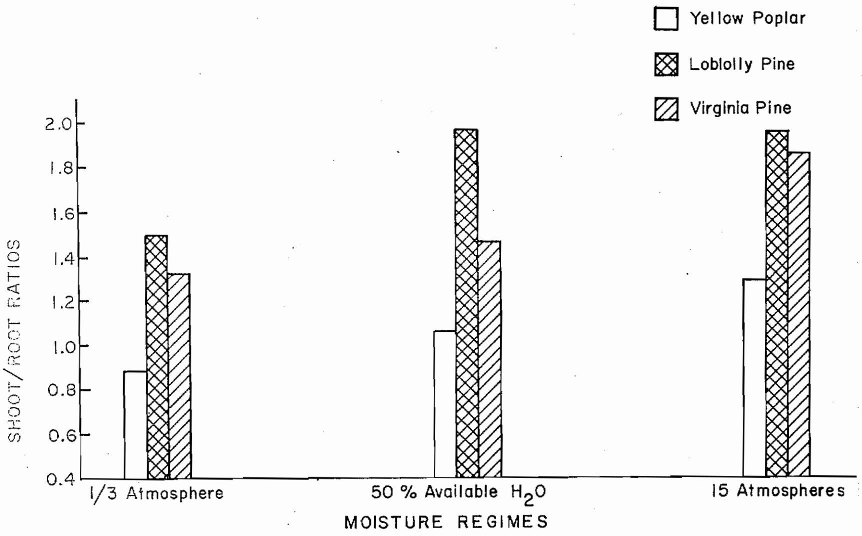

Fig. 6. The relationship of three moisture regimes to the shoot/root ratios of three tree species.

DISCUSSION

The study was directed primarily toward the relative effect of changes in soil characteristics on seedling growth as demonstrated by growth variations of species grown in soils taken from progressive successional stages ranging from abandoned fields to the climax oak-hickory stage. The scope of this experiment did not include evaluation of the physical and chemical changes separately and their individual correlation with growth differences exhibited by the species involved.

Perhaps the most important factor illustrated by this experiment is the highly significant interaction between the species and the soils. One species may grow the best in soils taken from one successional stage and grow the least in soils from another stage. The total dry weight graph for yellow-poplar and other species in Fig. 1 illustrates this interaction. For example, yellow-poplar grew the best in soils taken from the old-fields and poorest in soils from the climax hardwood forest; whereas loblolly pine exhibited the best growth in climax hardwood sites. Growth of yellow-poplar increased through the successional series hardwood, 50-70 year pine, 10-20 year pine, and old-field, while growth increased for loblolly pine through the series old-field, 50-70 year pine, hardwood, and 10-20 year pine. Growth of Virginia pine increased through the series hardwood, 50-70 year pine, old-field, and 10-20 year pine.

If early juvenile height growth is an indicator as to which species will have the competitive advantage on a given area, it is obvious that, other environmental factors except soil being equal, yellow-poplar could become the dominant pioneer species on an abandoned field. Loblolly pine, on the other hand, would have a distinct competitive advantage over the other two species during later stages of the succession.

The excellent growth produced by yellow-poplar in the soils taken from the old-field and young pine stages tends to substantiate the findings of Coile (1940) and Bormann (1953) who found that factors other than soil characteristics were responsible for the initial dominance on abandoned areas. Coile observed that, from the standpoint of mineral soil characteristics alone, the abandoned fields would probably be more favorable for growth of all seedlings because of lower carbon/nitrogen ratios, and, thus, the possibility of more available nitrogen.

Since the experiment was conducted under greenhouse conditions, variable environmental factors such as temperature and moisture were controlled. Other important factors such as seed dispersal, resistance of seed to dessication, and damage by rodents could also contribute to the success or failure of establishment of seedlings on abandoned areas. It is probably a combination of these factors that prevent dominance by hardwood species on abandoned field sites.

The failure of the yellow-poplar seedlings to grow in the soils taken from the mature pine and the climax hardwood sites is difficult to explain. Although little is known of the actual growth rates and characteristics of seedlings grown in undisturbed forest soils, it would seem the mull humus type present on these sites would favor seedling growth when light and moisture are not limiting. Nutrient analysis of the tops of the seedlings grown in the mature pine and climax hardwood soils showed them to be extremely low in phosphorous when compared to the phosphorous content of the yellow-poplar seedlings grown in soils from the old-field, and young pine stages (Appendix Table 11). The total soil phosphorous analysis (Table 1) showed little differences in the phosphorous content of all the sites; however, since it is known that phosphorous availability in acid soils decreases with time (Russell 1961), it is possible that the phosphorous present in the soils from the later successional stages was less available to the yellow-poplar seedlings. Physical and chemical soil factors other than phosphorous may have influenced the growth of the yellow-poplar seedlings in the old pine, and hardwood soils, however, the phosphorous deficiency of the seedling tissue seemed to be the most readily apparent answer for the lack of growth.

Loblolly pine produced the best growth in soils taken from the young pine, mature pine, and hardwood sites, and least growth in the abandoned field soils. However, since survival of seedlings growing in later successional stages would depend upon their ability to compete with established vegetation for water, loblolly pine would still be at a disadvantage. Fig. 3 shows the shoot/root ratio relationships of loblolly pine and the other species for each of the successional stages. It becomes apparent that the unbalanced shoot/root relationship for loblolly pine on the young pine and hardwood sites would be a detriment to its chances of survival if moisture became limiting and root competition became severe. The lag in the growth of the loblolly pine seedlings grown in the abandoned field soils is not clearly understood, although the seedlings seemed to have a more favorable balance in their ratio of tops to roots. The degree of mycorrhizal infection was much lower in the pine seedlings grown in abandoned field soils than that of the remaining three sites. This may have had some affect upon the forraging ability of the seedlings.

Virginia pine grew well only in soils taken from the young pine stands. Apparently the soil conditions existing in the young pine stands were generally favorable for growth. All species grew well in these soils while there was a wide variation in growth by species in soils from the remaining stages. Nutrient levels were no higher than, and generally lower than that of the remaining sites, so the explanation must lie in a greater availability of one or more of the nutrients, possibly phosphorous since the tops of all species growing in the young pine soils were somewhat higher in phosphorous (Appendix Table 11).

The inability of the Virginia pine seedlings to grow well in the abandoned field soils is not clearly understood since Virginia pine is the pioneer species in the area from which the soil samples were taken. Although the balance between shoots and roots was more favorable on all soils than that of loblolly pine, the general growth and appearance of the Virginia pine seedlings was poor compared to the loblolly pine seedlings. The degree of mycorrhizal infection was also less in Virginia pine seedlings than the loblolly.

The relative response of the species to varying degrees of soil moisture stress was demonstrated in the second phase of the experiment.

The relationship between dry weight production and available moisture is illustrated in Fig. 4. Growth of yellow-poplar seedlings was closely correlated with available moisture but the pines showed an erratic behavior. Growth increased for yellow-poplar through the treatment series 15 atmospheres, 50%, and 1/3 atmosphere, while the growth of loblolly pine increased through the series 15 atmospheres, 1/3 atmosphere, and 50%. Virginia pine showed little sensitivity to any of the treatments.

Early height growth is an important factor in the subsequent growth and survival to seedlings. Since the tallest seedlings receive the most light, they would have a definite competitive advantage over surrounding seedlings. Since early height growth is an important criteria for survival, it is apparent why yellow-poplar is commonly found on the moist but well-drained cove areas where extreme moisture stress conditions are less likely to occur.

Explanation of the response of loblolly and Virginia pine seedlings to the varying degrees of moisture stress creates something of a problem. For all practical purposes, the Virginia pine seedlings did not grow and the loblolly seedlings grew only slightly at the 1/3 atmosphere and 50% levels. In no case did growth of the pines approach that of the yellow-poplar. These results are in direct contrast with the findings of Wenger (1952). Wenger found that loblolly and shortleaf pine seedlings grew best when subjected to the well watered condition and poorest under the wilting point regime, and under all conditions the height growth of the pines was greater than that of sweetgum seedlings grown under similar moisture conditions.

It is possible that the initial shock of transplanting affected the cotyledon stage pine seedlings more than the cotyledon stage yellow-poplar seedlings (although both were nearly the same age and size and subjected to the same conditions) and, as a result, the pine seedlings did not exhibit normal growth patterns under the treatment conditions.

The roots of the seedlings of both pine species appeared healthy and were well distributed throughout the sample cans. Thus the lack of growth of the pine seedlings must be attributed to factors other than root development.

A direct relationship exists between the root systems and shoot systems. A reduction in the size of the root system tends to cause a corresponding reduction in the size of the tops due to a reduced water supply; a small shoot system tends to reduce the size of the root system due to the reduction of the carbohydrate supply. The most efficient shoot/root ratio in respect to balanced growth varies with the environmental conditions and with the hereditary growth patterns of the individual species. The pine seedlings produced consistantly higher shoot/root ratios than yellow-poplar seedlings; however, the seedlings of all three species produced the smallest shoot/root ratios in association with the 1/3 atmosphere regime.

An interesting association was found to exist between increasing moisture stress and the shoot/root ratios of both pine species and yellow-poplar. Shoot/root ratios of all species increased significantly as the severity of the moisture stress increased (Fig. 6). A similar increase in the shoot/root ratios of sycamore seedlings with increasing moisture stress was obtained by Dickson (1962).

Wenger (1952) observed that loblolly and shortleaf pine shoot/root ratios changed very little as moisture stress increased. It would appear that an increase in the shoot/root ratio would be a detriment and would decrease the species resistance to increasing moisture stress.

Many experiments have shown that growth is significantly reduced before the wilting point is reached (Martin, 1940; Kozlowski, 1949; Dickson, 1962). This was found to be true for yellow-poplar, but loblolly and Virginia pine demonstrated no significant response to varying moisture regimes.

SUMMARY AND CONCLUSIONS

Seedlings of three upland tree species--yellow-poplar, loblolly pine, and Virginia pine--were grown in intact soil samples taken in gallon cans from four stages of the secondary successional pattern common to the southern Piedmont area of Virginia. All areas sampled were located on Cecil fine sandy loam soils that were uniform with respect to slope, aspect, and degree of erosion.

The successional stages sampled were:

1. Abandoned fields (two to five years since subjected to agricultural use).
2. Young pine stands (Virginia pine stands 10-20 years of age that have regenerated naturally on abandoned farm land and have formed a closed canopy).
3. Mature pine stands (Virginia pine stands 50-70 years of age that have regenerated naturally on abandoned farm land).
4. Climax oak-hickory stands.

Light, temperature, and moisture were controlled in the greenhouse. Therefore, the growth of the seedlings would indicate the favorability of soil changes for growth of one or more of the species.

Yellow-poplar produced maximum height and dry weight growth in soils taken from the abandoned field and young pine sites. Total dry weight of yellow-poplar was significantly greater than that of the pines, but loblolly pine equaled yellow-poplar in height growth in soils taken from the young pine site. Poorest yellow-poplar growth was obtained in soils taken from the mature pine, and hardwood sites. Tissue analysis of the tops of these seedlings revealed an extremely low phosphorous content. Therefore, the lack of growth of yellow-poplar on these sites could be attributed to a phosphorous deficiency. From the standpoint of soil characteristics alone, the early stages of the successional pattern seem to favor growth of yellow-poplar.

Loblolly pine seedlings grew best in soils taken from the young pine, and hardwood sites, and least in soils taken from the abandoned fields. The loblolly pine seedlings grown in the abandoned field soils, although smaller, had a more favorable balance between tops and roots than the loblolly seedlings grown in soils from the other stages. The large shoot/root ratios produced by the loblolly seedlings in the young pine, and hardwood soils would probably detract from any possible advantage they obtained in rapid early height growth.

Virginia pine seedlings grew best in soils taken from the young pine and abandoned field sites, and least in soils taken from the mature pine and hardwood sites. Although best growth of Virginia pine seedlings was obtained in soils taken from the earlier successional stages, the growth of yellow-poplar seedlings, in the same soils, was significantly greater than that of Virginia pine.

The effect of soil moisture conditions upon the growth of the three species was determined in the second phase of the experiment.

The three species--yellow-poplar, loblolly pine, and Virginia pine--were planted in gallon cans of sandy loam soil and subjected to varying soil moisture regimes.

The different soil moisture regimes were:

1. 1/3 atmosphere (return to 1/3 atmosphere moisture level daily).
2. 50% (return to 1/3 atmosphere moisture when 50% or more of the available water had been removed).
3. 15 atmospheres (return to 1/3 atmosphere moisture level when the 15 atmospheres moisture content had been reached.

The species reaction to the different moisture regimes were an indication of their reaction to various upland soil moisture conditions.

Growth of yellow-poplar was directly correlated with the availability of soil moisture. Height growth and total dry weight production increased significantly through the treatment series 15 atmospheres, 50%, and 1/3 atmosphere as soil moisture stress decreased. Optimum site conditions for yellow-poplar should be on well watered but well drained areas where extreme moisture conditions do not occur.

Soil moisture availability had no significant affect on the growth of loblolly and Virginia pine seedlings. Growth of both species was generally poor for all treatments and it is believed that some factor other than the growth habits of these pine seedlings was responsible for the lack of differences among treatments.

All three species exhibited increasing shoot/root ratios with increasing soil moisture stress. The differences between the ratios at the 15 atmospheres and 1/3 atmosphere moisture regimes were significant with all species but more striking in the pines.

Changes in the characteristics of soils associated with the secondary successional pattern of the southern Piedmont area of Virginia are the result and not the cause of the successive change of dominant species. Environmental factors such as light, temperature, and moisture, plus other factors such as species tolerance, seed dispersal, and resistance to dessication are probably the dominant factors in determining the successional pattern of abandoned fields in the Virginia Piedmont.

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APPENDIX

Table I. Analysis of variance of height growth of three species grown on soils from four successional stages

Source	d. f.	S. S.	M. S.	F
Stages	3	236.04	78.68	18.82
Species	2	93.41	46.70	11.17
St. x Sp.	6	157.37	26.23	6.28
Error	36	150.69	4.18	
Total	47	637.51		

Table II. Analysis of variance of total dry weight of three species grown on soils from four successional stages

Source	d. f.	S. S.	M. S.	F
Stages	3	2.98	0.99	11.79
Species	2	2.10	1.05	12.50
St. x Sp.	6	5.56	0.93	11.07
Error	36	3.02	0.084	
Total	47	13.66		

Table III. Analysis of variance of shoot dry weights for three species grown on soils from four successional stages

Source	d. f.	S. S.	M. S.	F
Stages	3	0.98	0.33	11.00
Species	2	0.50	0.25	8.33
St. x Sp.	6	1.64	0.27	9.00
Error	36	1.04	0.03	
Total	47	4.16		

Table IV. Analysis of variance of root dry weights of three species grown on soils from four successional stages

Source	d. f.	S. S.	M. S.	F
Stages	3	0.59	0.20	10.00
Species	2	0.60	0.30	15.00
St. x Sp.	6	1.19	0.20	10.00
Error	36	0.65	0.02	
Total	47	3.03		

Table V. Analysis of variance of shoot:root ratios of three species grown on soils from four successional stages

Source	d. f.	S. S.	M. S.	F
Stages	3	2.77	0.92	7.67
Species	2	9.77	4.98	41.50
St. x Sp.	6	1.27	0.21	1.75
Error	36	4.15	0.12	
Total	47	18.16		

Table VI. Analysis of variance of height growth of three species subjected to three moisture regimes

Source	d. f.	S. S.	M. S.	F
Moisture	2	92.95	46.48	12.20
Species	2	598.24	299.12	78.51
M. x Sp.	4	105.95	26.49	6.95
Error	27	102.90	3.81	
Total	35	900.04		

Table VII. Analysis of variance of total dry weights of three species subjected to three moisture regimes

Source	d. f.	S. S.	M. S.	F
Moisture	2	6.19	3.10	10.33
Species	2	91.94	45.97	153.23
M. x Sp.	4	13.63	3.41	11.37
Error	27	7.99	0.30	
Total	35	219.75		

Table VIII. Analysis of variance of shoot dry weights for three species subjected to three moisture regimes

Source	d. f.	S. S.	M. S.	F
Moisture	2	0.98	0.49	8.17
Species	2	13.90	6.95	115.83
M. x Sp.	4	2.57	0.64	10.67
Error	27	1.62	0.06	
Total	35	19.08		

Table IX. Analysis of variance of root dry weights for three species subjected to three moisture regimes

Source	d. f.	S. S.	M. S.	F
Moisture	2	2.26	1.13	11.30
Species	2	18.34	9.17	91.70
M. x Sp.	4	4.35	1.09	10.90
Error	27	2.82	0.10	
Total	35	27.78		

Table X. Analysis of variance of shoot:root ratios of seedlings of three species subjected to three moisture regimes

Source	d. f.	S. S.	M. S.	F
Moisture	2	1.29	0.64	8.00
Species	2	3.14	1.57	19.63
M. x Sp.	4	0.21	0.05	0.63
Error	27	2.22	0.08	
Total	35	6.86		

Table XI. Nutrient contents of the tops of three species grown in soils taken from four successional stages[1]

Successional stage	Yellow-poplar					Loblolly pine					Virginia pine				
	N	P	K	Ca	Mg	N	P	K	Ca	Mg	N	P	K	Ca	Mg
Old-fields	1.30	0.122	1.17	0.79	0.230	1.45	0.128	0.97	0.11	0.070	1.10	0.090	0.76	0.22	.067
10-20 year pine stands	1.33	0.120	1.42	0.66	0.255	1.63	0.145	0.92	0.11	0.055	1.38	0.142	0.72	0.08	.045
50-70 year pine stands	1.63	0.043	1.35	0.36	0.318	1.96	0.080	0.67	0.12	0.080	1.38	0.036	0.67	0.12	.063
Hardwood stands	1.79	0.033	1.15	0.28	0.180	1.95	0.102	0.75	0.18	0.068	1.50	0.088	0.40	0.14	.058

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[1] All values in % of dry weight.

VITA

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ABSTRACT

of

THE RELATIVE EFFECT OF SOIL CHANGES ASSOCIATED WITH OLD-FIELD SUCCESSION AND AVAILABLE MOISTURE UPON THE GROWTH OF THREE UPLAND TREE SPECIES

by

David Lee Graney

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ABSTRACT

The primary objectives of this study were to determine the relative effects of (1) changes in soil characteristics associated with old-field succession and (2) available moisture upon the growth of three upland tree species.

Two month old seedlings of yellow-poplar, loblolly pine, and Virginia pine were transplanted into undisturbed cores of soil taken from locations representing the old-field successional pattern on the southern Piedmont region of Virginia. The successional stages sampled were abandoned fields, 10-20 year old pine stands, 50-70 year old pine stands, and climax oak-hickory stands. All sites were located on Cecil fine sandy loam soils.

The experiment was conducted under greenhouse conditions.

Height growth and total dry weight production for yellow-poplar were significantly greater in soils taken from the old-field and young pine sites. Little or no growth was observed for yellow-poplar seedlings grown in soils taken from the mature pine and climax hardwood sites.

Loblolly and Virginia pine seedlings produced significantly greater height growth in soils taken from the young pine sites; however, no significant differences in total dry weight production were obtained for these species on any of the four sites. The greatest degree of mycorrhizal infection for all species was associated with the latter successional stages while the seedlings grown in the abandoned field soils showed the least mycorrhizal infection.

The effect of available moisture upon the growth of the three species was determined by subjecting 3 month-old potted yellow-poplar, loblolly pine, and Virginia pine seedlings to three moisture regimes. The moisture regimes were 1/3 atmosphere, 50% available moisture, and 15 atmospheres.

Height growth and dry weight production for yellow-poplar decreased significantly through the treatment series 1/3 atmosphere, 50%, and 15 atmospheres.

The pine species exhibited generally poor growth and showed no significant reactions to the moisture treatments.

The dry-weight shoot/root ratios of all species became significantly larger as the moisture stress increased from the 1/3 atmosphere treatment to the 15 atmospheres treatment.