The Relative Growth of Three Forest Tree Species on Soils Associated with Different Successional Stages in Virginia

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ABSTRACT: The objective of this study was to evaluate the relative effects of soils associated with old-field succession upon the growth of three indigenous tree species, Virginia pine (*Pinus virginiana* Mill.), loblolly pine (*Pinus taeda* L.), and yellow poplar (*Liriodendron tulipifera* L.). Seedlings were transplanted into undisturbed cores of soil removed from locations representing stages of the old-field successional pattern of the southern Piedmont region of Virginia: abandoned fields, 10- to 20-year-old pine stands, 50- to 70-year-old pine stands, and climax oak-hickory stands. All samples were of Cecil fine sandy loam soils.

Height growth and total dry-weight production of yellow poplar were significantly greater on soils from the old-field and young pine sites. Little growth of yellow poplar seedlings occurred on soils from the mature pine and climax hardwood sites.

Loblolly and Virginia pine seedlings produced significantly greater height growth on soils from the young pine sites; however, no significant differences in total dry-weight production occurred between these species on any of the four sites.

The largest shoot/root ratios produced by the pine species were associated with soils from the 10- to 20-year pine sites while yellow poplar showed little variation with respect to site. No significant differences were found between mean shoot/root ratio values of yellow poplar seedlings grown on soils from the four sites.

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

INTRODUCTION

Although considerable research has been devoted to studying the succession of natural plant communities in the Piedmont region of southeastern United States, the role of soil changes associated with changes in plant associations is not clearly understood. The purposes of this study were: a) to evaluate the relative effects on tree growth of soils associated with different successional stages, and b) to demonstrate the possibility of using intact soil samples to evaluate the importance of changes in soil characteristics associated with old-field successional stages.

The general old-field successional patterns of the upland Piedmont region have been described by Oosting (1942). Various herbaceous

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taxa are replaced by fast-growing pioneer pine species and, in turn, are succeeded by climax oak-hickory types.

Although numerous environmental factors are associated with plant succession, the changes in soil characteristics presumably contribute to the transition of forest communities toward the climax association. Litter deposition, organic matter incorporation, and increases in porosity and infiltration rates have been suggested as the more important changes occurring during the succession (Clements, 1931; Billings, 1938; Auten, 1939, 1941, 1945).

Measurable changes in physical and chemical soil characteristics occur during successional changes (Billings, 1938; Coile, 1940; Auten, 1939, 1941, 1945; Scott, 1955); however, the importance of these changes as a determining factor in the replacement of one species by another has not been definitely established.

Coile (1940) contended that factors such as seed dispersal and rooting characteristics of the particular species under shade and open conditions were of greater significance than soil changes in the establishment and replacement of the various successional stages. Hardwood seeds were found to have a smaller dispersion radius and were more susceptible to desiccation than pine seed. Hardwood seedlings were found to have more vigorous root systems under shade conditions than pine.

Bormann (1953) has shown that pine seedlings are more tolerant to the high-temperature, low-moisture extremes of old-field sites than hardwood seedlings, and several writers have shown that under shaded conditions pine seedlings do not produce adequate root growth to compete for soil moisture (Kramer and Decker, 1944; Kramer *et al.*, 1952; Kozlowski, 1949; Bourdeau, 1954).

It also has been demonstrated that hardwood seedlings may not grow well on old-field sites, but will make adequate growth on sites that have not been depleted by agricultural use (Minckler and Chapman, 1948; Minckler, 1946, 1952; Ryker, 1958).

METHODS

Four serial stages representing the old-field successional pattern of the southern Piedmont region of Virginia were arbitrarily chosen for sampling, as follows:

1. Abandoned fields—cropland abandoned for 2 to 5 years.
2. Young pine stands—Virginia pine stands, 10 to 20 years of age, that had regenerated naturally on abandoned farmland and had formed closed canopies.
3. Mature pine stands—Virginia pine stands, 50 to 70 years of age, that had regenerated naturally on abandoned farmland.
4. Climax oak-hickory stands.

Two uniform sites were sampled for each stage. All sites were located on moderately eroded Cecil fine sandy loam soils with slopes of 2 to 5%. Much of the A_1 horizon was missing on the old-field soils.

SAMPLING

The soil samples consisted of large cores of undisturbed soil collected in no. 10 food cans (6 inches in diameter and 7 inches tall) according to the procedure described by Clark (1961). The litter was left intact.

Uniform samples from the two sites representing each stage were pooled and 12 cans were randomly selected for use in the study. A total of 48 soil samples were used.

ANALYSIS OF SOILS

Soil samples excluding the litter were taken from the sample cans at the conclusion of the experiment and used for chemical and physical soil analyses. Soil texture was determined by the Bouyoucos hydrometer method (Anonymous, 1965). Per cent organic matter was determined by the Scholenberger wet combustion method as described by Wilde and Voigt (1955). Total cation-exchange capacity was obtained by the method described by Rich (1961). The flame photometer was used to determine exchangeable Ca, Mg, and K. Total phosphorus was determined by fractionation using the procedure described by Chang and Jackson (1957). Per cent nitrogen was obtained by use of the Coleman nitrogen gas analyzer. Results of the soil analyses are shown in Table 1.

TEST DESIGN AND DATA ANALYSIS

The study was conducted under greenhouse conditions to minimize variations in moisture, light, and temperature. Sample cans were arranged in a completely randomized design with four observations of

TABLE 1.—Chemical and physical properties of the 0-6-in soil layer for the four successional stages[1 2]

Successional stage and location	*p*H	C.E.C. me./100g	Exchangeable cations, me./100g Ca	Mg	K
OF	4.6	4.2	1.00	0.25	0.18
10-20	4.7	6.5	0.46	0.16	0.16
50-70	5.0	7.1	0.70	0.24	0.15
Hwd.	4.4	7.0	0.56	0.18	0.17

[1] OF = Old-field stage; 10-20 = 10-20-year pine stage; 50-70 = 50-70-year pine stage; Hwd. = Hardwood stage.

[2] Each figure is a mean of two composite samples representing each successional stage.

TABLE 1.—(continued)

Successional stage and location	Organic matter, %	Total P, ppm	N, %	Particle size distribution, % Sand	Silt	Clay
OF	1.6	74	0.063	62.0	20.4	17.6
10-20	1.8	66	0.069	67.0	17.4	15.6
50-70	2.6	58	0.072	66.0	19.2	14.8
Hwd.	3.1	62	0.075	69.0	15.9	15.1

each of the 12 species-stage combinations. The samples were rerandomized every two weeks to reduce positional effects. To prevent excessive leaching and washing of the soil due to repeated watering, the cans of soil were placed in aluminum cake pans and watered from below. Consequently, soil moisture was not a limiting factor during the course of the experiment.

Artificial light was supplied during the evening hours to insure a constant 16-hr photoperiod.

Seedlings of the three taxa were germinated in perlite and subsequently transplanted into the sample soils in June 1962. After establishment, the seedlings were thinned to three healthy, uniform individuals per can and grown for 105 days.

At the conclusion of the study, the seedlings were washed from the sample cans and the following data recorded: 1) height growth during the experiment; 2) oven-dry weights of roots and tops; 3) dry-weight shoot/root ratios; and 4) general observations on root mortality, mycorrhiza development, appearance, and color.

The quantified data were treated as random and statistically analyzed to test differences among tree species and successional stages. Differences among mean values at both the 5% and 1% levels were tested using the Duncan Multiple Range Test (Duncan, 1955).

RESULTS

EFFECTS OF SUCCESSIONAL STAGE UPON TOTAL DRY WEIGHT

The major differences in seedling parameters are presented in Table 2. For a detailed analysis of individual statistical differences see Graney (1964).

The effect of soils from successional stages on the dry-weight production of yellow poplar indicates that the greatest dry-weight production was associated with soils taken from the old-field site. The amount of dry material produced was significantly greater (1% level) than that produced in soils from the 10- to 20-year pine site and was also significantly different (1% level) from seedlings grown in soils from the 50- to 70-year pine and the hardwood sites. No significant differences in yellow poplar dry weights were found between the 50- and 70-year pine and the hardwood sites, nor in the total dry-weight production of loblolly and Virginia pine seedlings among any of the four sites.

EFFECTS OF SUCCESSIONAL STAGE ON SHOOT GROWTH

Best height growth of yellow poplar occurred on soils taken from the 10- to 20-year pine and old-field sites (Table 2). Height differences between these sites were not significant; however, seedlings from both sites were significantly taller than yellow poplar seedlings grown on soils from the remaining two sites.

Maximum height growth of loblolly pine was associated with soils from the 10- to 20-year pine site. Height growth produced by loblolly seedlings on soils from the 10- to 20-year pine site was significantly greater than seedlings grown on soils from the remaining three sites. Height growth produced in soils from the hardwood site was significantly greater when compared with the old-field site. No significant differences were obtained between the old-field and 50- to 70-year pine sites.

Virginia pine grown on soils from the 10- to 20-year pine site grew significantly taller than seedlings of the same species grown on soils from the other three sites. No significant differences were obtained from comparisons of the old-field, 50- to 70-year pine, and hardwood sites.

DRY WEIGHT OF SHOOTS AND ROOTS

Maximum dry-shoot weight of yellow poplar occurred in soils from the old-field site. Shoot weight from that site was significantly greater

TABLE 2.—The mean heights, total dry weights, shoot dry weights, root dry weights, and shoot/root ratios of three species grown on soils from four successional stages[1]

	Heights (cm)	Total dry wts. (g)	Shoot wts. (g)
Yellow poplar—old fields	9.85	1.84	0.96
Yellow poplar—10-20-year pine	8.32	1.02	0.58
Yellow poplar—50-70-year pine	1.15	0.16	0.08
Yellow poplar—hardwood stands	1.52	0.14	0.08
Loblolly pine—old fields	4.18	0.31	0.20
Loblolly pine—10-20-year pine	10.55	0.56	0.40
Loblolly pine—50-70-year pine	4.82	0.34	0.22
Loblolly pine—hardwood stands	6.35	0.56	0.41
Virginia pine—old fields	2.30	0.22	0.12
Virginia pine—10-20-year pine	6.12	0.59	0.39
Virginia pine—50-70-year pine	2.20	0.19	0.20
Virginia pine—hardwood stands	1.75	0.17	0.09

[1] Each figure is a mean of four observations.

TABLE 2.—(continued)

	Root wts. (g)	Shoot/root ratio dry wts. (g)
Yellow poplar—old fields	0.87	1.24
Yellow poplar—10-20-year pine	0.44	1.54
Yellow poplar—50-70-year pine	0.08	1.02
Yellow poplar—hardwood stands	0.07	1.10
Loblolly pine—old fields	0.11	0.91
Loblolly pine—10-20-year pine	0.16	2.72
Loblolly pine—50-70-year pine	0.13	1.83
Loblolly pine—hardwood stands	0.15	2.62
Virginia pine—old fields	0.10	1.36
Virginia pine—10-20-year pine	0.20	1.78
Virginia pine—50-70-year pine	0.09	1.31
Virginia pine—hardwood stands	0.08	1.24

than the shoot weights of the yellow poplar seedlings grown on soils from the remaining three sites. Shoot weights of the yellow poplars growing on the 10- to 20-year pine soils were greater than shoot weights from the 50- to 70-year pine and hardwood sites, but the latter sites were not different from each other.

No significant differences in dry-shoot weights were obtained for the loblolly seedlings grown on soils from any of the four sites.

Shoot weights of Virginia pine seedlings grown on soils from the 10- to 20-year pine site were significantly greater than corresponding weights produced by seedlings on soils from the old-field and hardwood sites. No other significant differences were obtained among Virginia pine data.

The greatest root growth produced by the three species were generally associated with the soils taken from the old-field and 10- to 20-year pine sites (Table 2).

Yellow poplar dry root material produced on the soils taken from the old-field site was significantly greater than that of similar seedlings from all other sites. Root weights of yellow poplar from the 10- to 20-year pine soils were significantly greater than those from the 50- to 70-year pine and hardwood soils, but the latter sites were not significantly different.

Greatest dry-root weight production for loblolly and Virginia pine seedlings occurred on the soils taken from the 10- to 20-year pine site, but the differences among sites within each species were not significant.

The largest shoot/root ratios produced by the pine species were associated with soils from the 10- to 20-year pine site while yellow poplar showed little variation with respect to site (Table 2).

No significant differences were found between mean shoot/root ratio values of yellow poplar seedlings grown on soils from the four sites.

The largest shoot/root ratios of loblolly seedlings were produced by seedlings growing on soils from the 10- to 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 when compared to the loblolly seedlings from the remaining two sites. The old-field and 50- to 70-year pine sites were not significantly different.

The largest shoot/root ratios produced by Virginia pine seedlings were associated with the soils from the 10- to 20-year pine site. The ratios for this site were greater than the ratios of the Virginia pine seedlings grown on soils from the old-field and hardwood sites. Shoot/root ratios of the Virginia pine seedlings grown on soils from the old-field, 50- to 70-year pine, and hardwood sites were not significantly different.

DISCUSSION

Perhaps the most important factor illustrated by the results is the highly significant interactions between the species and the soils. One species may grow best on soils taken from one successional stage but grow least on soils from another stage. The total dry-weight values illustrate this interaction. For example, yellow poplar produced the best growth on soils from the old-field and poorest on soils from the climax hardwood stands. On the other hand, loblolly pine exhibited the best growth on climax hardwood soils.

Although the conditions of this experiment do not allow direct correlation to field conditions, it is interesting to note possible implications to realistic successional situations. Yellow poplar, because of its superior juvenile height growth, seems to have a competitive advantage on old fields of Cecil soil. Loblolly pine, on the other hand, apparently has a distinct competitive advantage over the other two species during later stages of succession.

The excellent growth produced by yellow poplar on the soils from the old-field and young pine stages tends to substantiate the findings of Coile (1940) and Bormann (1953). Both suggested that factors other than soil characteristics were responsible for initial dominance of pine on abandoned areas. Coile observed that, from the standpoint of mineral soil characteristics alone, the abandoned fields would probably be more favorable for the 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 factors such as light, temperature, and moisture were controlled. Other important factors such as seed dispersal, resistance of seed to desiccation, and damage by rodents also could contribute to the success or failure of seedling establishment on abandoned areas. A separate study (Graney, 1964), for example, indicated that tulip poplar is quite responsive to different levels of available moisture. Growth of seedlings rewatered to an approximate field capacity significantly exceeded the growth of similar seedlings that were not rewatered until 50% or more of the soil moisture was depleted. Virginia and loblolly pine also are likely to respond differently to soil-moisture levels although there were no observed differences in the study cited above.

The failure of the yellow poplar to grow on 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 growing on undisturbed forest soils, it would seem that the soils present on these sites would favor seedling growth when light and moisture are not limiting. Nutrient analysis of the tops of the seedlings from the mature pine and climax hardwood soils showed them to be extremely low in phosphorus when compared to the phosphorus content of the yellow poplar seedlings grown in soils from the old-field and young pine stages (Table 3). The total soil phosphorus analysis (Table 1) showed only minor differences in the phosphorus content of all the sites; however, since it is known that phosphorus availability in acid soils decreases with time (Russell, 1961), it is possible that the phosphorus present in the soils from the later successional stages was less available to the yellow poplar seedlings.

Although loblolly pine produced the best growth on soils taken from the young pine, mature pine, and hardwood sites, the larger shoot/root relationship of loblolly seedlings on the young pine and hardwood sites probably limits their chances of survival.

The amount of mycorrhizae was much lower on the pine seedlings growing in abandoned-field soils than that of the remaining three sites and probably accounts for the lower initial growth.

Although all species grew well on soils taken from pine stands, the nutrient levels were no higher than, and generally lower than those of the other stages. Apparently a greater availability of one or more of the nutrients, possibly phosphorus, was responsible for the greater growth. The tops of all species grown on the young pine soils were somewhat higher in phosphorus (Table 3).

The inability of Virginia pine seedlings to grow well on the abandoned-field soils is not clearly understood since Virginia pine is the pioneer tree species of the area from which the soil samples were taken. The balance between shoots and roots of Virginia pine was more favorable than for loblolly pine on all soils; however, the general growth and appearance of the Virginia pine seedlings were poor when compared to the loblolly seedlings. The presence of mycorrhizae was less on Virginia pine seedlings than on loblolly seedlings.

TABLE 3.—Nutrient contents in % of dry weight of the tops of three species grown in soils from four successional stages[1]

Successional	Yellow poplar					Loblolly pine				
stage	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
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
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
Hardwood stands	1.79	0.033	1.15	0.28	0.180	1.95	0.102	0.75	0.18	0.068

[1] Each figure represents a mean of four observations.

TABLE 3.—(continued)

Successional	Virginia pine				
stage	N	P	K	Ca	Mg
Old fields	1.10	0.090	0.76	0.22	0.067
10-20-year pine stands	1.38	0.142	0.72	0.08	0.045
50-70-year pine stands	1.38	0.096	0.67	0.12	0.063
Hardwood stands	1.50	0.088	0.40	0.14	0.058

REFERENCES

ANONYMOUS. 1965. Methods of soil analysis. Agronomy Monog. No. 9. C. A. Black *et al.* (ed.) Amer. Soc. Agron. 562-567.

AUTEN, J. T. 1939. Reconstruction of the hardwood forest soil by vegetative covers. *Soil Sci. Soc. Amer. Proc.,* 4:245.

———. 1941. Black locust, pines, and sassafras as builders of forest soil. *Central States Forest Exp. Sta. Tech. Note,* No. 32. 9 p.

———. 1945. Relative influences of sassafras, black locust, and pines on old-field soils. *J. Forest.,* **43**:441-446.

BILLINGS, W. B. 1938. The structure and development of old-field shortleaf pine stands and certain associated physical properties of the soil. *Ecol. Monogr.,* **8**:437-499.

BORMANN, F. H. 1953. Factors determining the role of loblolly pine and sweetgum in early upland old-field succession in the piedmont of North Carolina. *Ibid.,* **23**:339-358.

BOURDEAU, P. F. 1954. Oak seedling ecology determining segregation of species in piedmont oak-hickory forests. *Ibid.,* **24**:297-320.

CHANG, S. C. AND M. L. JACKSON. 1957. Phosphorous fractionation. *Soil Sci.,* **84**:133-136.

CLARK, F. B. 1961. Pot culture — an aid to site evaluation. *Proc. Indiana Acad. Sci.,* **70**:234-237.

CLEMENTS, F. E. 1931. Investigations in ecology. *Carnegie Inst. Wash. Year B.,* **30**:266-275.

COILE, T. S. 1940. Soil changes associated with loblolly pine succession on abandoned agricultural land of the piedmont plateau. *Duke Univ. School of For. Bull.,* No. 5. 85 p.

DUNCAN, DAVID B. 1955. Multiple range and multiple F-tests. *Biometrics,* **11**:1-42.

GRANEY, D. L. 1964. The relative effect of soil changes associated with old-field succession and available soil moisture upon the growth of three upland tree species. Master of Science thesis, Virginia Polytechnic Institute, Blacksburg, Va. 81 p.

KOZLOWSKI, T. T. 1949. Light and water in relation to growth and competition of forest tree species. *Ecol. Monogr.,* **19**:207-231.

KRAMER, P. J. AND J. P. DECKER. 1944. Relation between light intensity and rate of photosynthesis of loblolly pine and certain hardwoods. *Plant Physiol.,* **19**:350-359.

———, H. J. OOSTING AND C. F. KORSTIAN. 1952. Survival of pine and hardwood seedlings in forest and open. *Ecology,* **33**:427-430.

MINCKLER, L. S. 1946. Old-field reforestation in the great Appalachian valley as related to some ecological factors. *Ecol. Monogr.,* **16**:87-108.

———. 1952. Comparative success of conifers and hardwoods on two old-field sites in southern Illinois. *Central States Forest Exp. Sta.,* Sta. Note No. 67. 2 p.

——— AND A. G. CHAPMAN. 1948. Tree planting in the Central, Piedmont and Southern Appalachian Regions. *U.S. Dep. Agr. Farmers' Bull.,* 1944. 39 p.

OOSTING, H. J. 1942. An ecological analysis of the plant communities of Piedmont, North Carolina. *Amer. Midl. Natur.,* **28**:1-26.

RICH, C. J. 1961. Calcium determination for cation-exchange capacity measurements. *Soil Sci.,* **92**:226-231.

RUSSELL, E. W. 1961. Soil conditions and plant growth. Longmans, Green & Co., London. 688 p.

RYKER, R. A. 1958. Conifers vs. hardwoods on old-field sites. *Central States Forest Exp. Sta.,* Sta. Note 122. 2 p.

SCOTT, D. R. M. 1955. Amount and chemical composition of organic matter contributed by overstory and understory vegetation to forest soil. *Yale Univ. Sch. Forest. Bull.,* No. 62. 73 p.

WILDE, S. A. AND G. K. VOIGT. 1955. Analysis of soils and plants for foresters and horticulturists. J. W. Edwards Publishers, Inc., Ann Arbor, Mich. 117 p.

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