WATER AND LIGHT IN RELATION TO PINE REPRODUCTION

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Introduction

Seedlings of certain species of pine often become established along the margins of forests (fig. 1) although they rarely become established within the forests. Seedlings growing at the margin must compete for water and minerals with the roots of trees comprising the stand but they are exposed to light of much higher intensity than if they were growing in the interior of the stand. These circumstances provide an opportunity to study the relative importance of light and water with respect to the establishment of pine seedlings.

It is well known that in the Piedmont pine (*Pinus taeda* L., *P. echinata* Mill., *P. virginiana* Mill.) usually fails to reproduce under either pine or hardwood stands while many species of hardwoods grow under both pines and hardwoods. It was generally assumed at one time that failure of tree seedlings to survive under a forest canopy was the result of lack of light, and species failing to survive under such conditions were described as shade intolerant. Results of certain trenched-plot experiments performed during the past 40 years have been interpreted, however, as indicating that lack of water is more important than shade in the failure of seedlings to survive. It has been observed that if small areas under forest stands are protected from the root competition of the surrounding vegetation by trenching, seedlings of intolerant species sometimes become established. The only demonstrable environmental difference between such trenched plots and adjacent untrenched control plots is that the trenched plots usually contain more available soil moisture during periods of drought. It has therefore been argued that lack of available soil moisture rather than lack of light is responsible for the failure of intolerant species, such as many species of pine, to become established under a forest canopy.

It seemed probable to the writers that the supply of water is as low in the marginal zone where pine seedlings survive as it is within the forest where they fail to survive. If this were true it would suggest that pine seedlings are able to become established in the margin of a forest because they are exposed to higher light intensity than within the stand. In other words, possibly pine seedlings are more drought resistant in the open than in the shade. Therefore, it was decided to measure the moisture content of the soil along a transect extending from within the forest across the marginal fringe of pines into an adjacent open field to learn whether significant differences exist.

Methods

Three stands of shortleaf pine (*Pinus echinata* Mill.) were selected which were bordered by fields that had not been cultivated for several years. One field (station 3) was in the broom-sedge stage of succession (Oosting, '42) but had been planted with pine seedlings. The other two fields (stations 1 and 2) had been lying fallow much longer, but succession on them was held in check by periodic mowings.

The pine stands were mature, or overmature, ranging in age from 60 to 120 years. As a result there was a well-developed understory of hardwoods with deciduous shrubs and hardwood reproduction abundant in the lower strata. There was no evidence of pine reproduction in recent years within the stands. Along the margins of the stands, however, were numerous young pines ranging in size from seedlings up to small trees 10–12 feet tall (figs. 1, 2). These were distributed in a

FIG. 1. Mixed pine-hardwood stand showing line of young shortleaf pine at margin.

narrow strip, usually not more than 1–2 feet wide at a distance of 6–10 feet from the bases of the dominant trees but well within the outer extent of the crowns of the marginal trees. Although young pines occur in margins of all exposures, north and northwest margins were selected for study because they receive the least light.

Points were selected within these margins where young pines were flourishing and where there were no depressions or drainage lines to affect soil moisture. Through each of two such points at station 1, one at station 2, and two at station 3, a line was run from well inside the stand out into the open field. Measuring from the point where young pines grew, markers were put on this line in the field at 6, 12, 18, and 40 feet. Inside the stand points were marked at 13 and 35 feet. Some slight irregularities in these distances were necessary because of clumps of trees inside the stand, or because of slight depressions or eroded spots in the fields. These lines of sampling points were termed transects.

Soil samples, obtained with an auger, were taken in pairs at depths of 6 and 15 inches at each of the sampling points on all five transects, each complete set of samples being obtained in a single day. The samples were dried at 110° C., and their water content was expressed as a percentage of the dry weight. The average of each pair of samples was taken as the water content for each depth at the time of sampling. Three such series of samples were obtained, one each in July, August, and September of 1944, each successive sampling representing what appeared to be drier conditions than the preceding.

Finally, a substantial mixed sample of soil was obtained from each depth at each sampling point. The wilting percentage of each sample was determined in triplicate, using sunflowers as indicators. The wilting percentages as used in the calculations are averages, therefore, of the triplicate determinations.

Records of other environmental variables were obtained, beginning in April, 1945, when buds were just expanding, and continuing to mid-June, when all hardwoods were in full leaf. Instrument shelters of the Weather Bureau type were set up, one at the margin of a stand and another 40 feet inside. A hygrothermograph and maximum-minimum thermometers were operated in each shelter. Beside each shelter maximum-minimum thermometers were placed at the soil surface and suspended in pipe at depths of 4 and 15 inches in the soil. Evaporation rates were determined with Livingston atmometers in pairs at the margin and inside the stand. A black bulb atmometer was operated with each of the pairs of white ones.

Light intensity was measured in the 120-year stand between 12:00 A.M. and 1:00 P.M. (E.S.T.) in August when the sky was clear and when full sunlight was not less than 10,000 foot candles. Readings were made with Weston illuminometers simultaneously in the open, at the margin within the strip of reproducing pine, and in the interior of the forest. The latter readings were made at exactly 3-foot intervals along lines at right angles to the margin and extending 81 feet into the stands. All readings were taken at a height of 3 feet from the ground with the illuminometer in a horizontal plane. Additional light measurements were obtained with a pair of spherical thermocouples (Wilson, '43). These were attached about 18 inches apart to a portable stand, wired in series, and connected to a microammeter by a long cable.

Results

The depths of sampling were set arbitrarily at 6 and 15 inches because this seemed likely to include the majority of seedling roots and because most root growth is concentrated in this zone (Coile, '37). It was assumed that the samples from a depth of 6 inches would be representative of the A horizon and those from a depth of 15 inches would come from the upper part of the B horizon. This proved untrue, however, for the A horizon was found to vary in depth from less than an inch to over 15 inches. Since all the stands were on White Store Sandy Loam which has a sandy A horizon and a clay B horizon the water-holding capacities at the two depths would normally have been very different, as would the wilting percentages. The irregular depth of the A horizon, however, resulted in extremely variable soil textures in samples from the same level. The moisture content of a sample, therefore, gave no indication of the amount of water available for growth unless considered in relation to its permanent wilting percentage, and it became necessary to determine the permanent wilting percentage of the soil at each depth for every point of sampling. The available water was then expressed as the difference between the observed moisture content and the permanent wilting percentage. The results are summarized in table I, and the averages of all samplings are shown graphically in figure 2.

Examination of the data from the various samplings reveals that the soil was becoming drier as the season progressed, as indicated by the decreasing content of moisture available for growth. In general, at any given time and station there was more available water at 15 inches than at 6 inches, a fact related to both the lower water-holding capacity and the high root concentration near the surface. The averages of all samplings, as shown at the bottom of table I and in figure 2, indicate that the soil moisture content was lowest at the margins and increased toward both the open fields and the interior of the forests. This trend was most marked at the 15-inch depth and became more pronounced as the summer passed and the soil became drier. A statistical analysis [1]

[1] For which we are indebted to Professor F. X. Schumacher of the Duke School of Forestry.

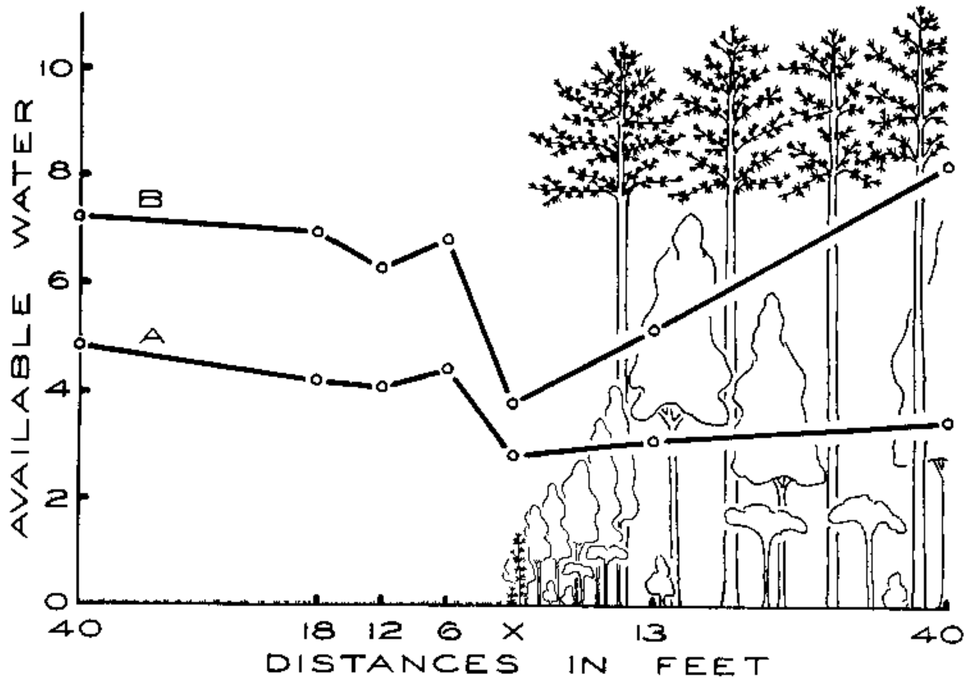

FIG. 2. Average available water in per cent of dry weight of soil at depths of 6 inches (A) and 15 inches (B) at the points indicated along five transects from open to interior of forest. X is in the marginal strip of young pine.

of the data showed that the amount of available water at a depth of 6 inches was significantly greater in the fields at 6, 18, and 40 feet from the margin than it was at the margins, but that it was not significantly greater inside the margins than at the margins. At a depth of 15 inches the content of available water was significantly greater at 40 feet outside and 35 feet inside the margins than at the margins.

The data show, then, that on the average the surface soil in the north and northwestern margins of these forests is at least as dry, in terms of available water, as in the interior of the stands and significantly drier than in adjacent open fields, while the soil at a depth of 15 inches is drier at the margins than either inside or outside of the stands.

The instrumental records, obtained over a period of two and a half months, showed no consistent marked differences between the interior and margin of the stand. As the season advanced and hardwood leaves expanded there were progressive changes in humidity, light, and temperatures of air and soil which were of interest in themselves, but there were no differences apparent in the data which could be used to explain the survival of pine at the margins of forest stands.

Light values as measured with Weston illuminometers held in the horizontal plane were highly variable from place to place but conclusively and consistently different for forest, margin, and open. Light values obtained at the margin averaged 16.9 per cent of full sunlight and values in the interior averaged 5.9 per cent. This indicates that, when the forest trees are in full leaf, seedlings at the north or northwestern margin may receive 2.8 times as much light as those in the forest. Actually the difference is probably somewhat greater since a tilting

TABLE I. *Average values for available water at each sampling and at each sampling point. Distances from the margin (X) in feet are indicated by O for open and I for interior of forest.*

	Depth inches	O-40	O-18	O-12	O-6	X	I-13	I-35
Transect 1								
July	6	11.6	9.2	10.1	12.0	6.8	8.8	8.8
	15	1.3	11.2	5.2	6.4	6.2	12.2	10.7
Aug.	6	3.4	3.0	9.6	7.3	3.6	4.8	3.2
	15	7.0	5.1	5.2	7.7	3.9	7.7	10.0
Sept.	6	0.1	1.0	4.0	1.6	0.3	1.6	1.7
	15	1.1	5.4	3.6	4.4	1.6	3.6	0
Transect 2								
July	6	9.5	8.3	8.6	8.0	8.4	7.2	6.2
	15	9.2	8.1	8.0	7.7	7.3	10.8	18.1
Aug.	6	4.1	3.0	4.3	4.7	3.7	2.8	1.9
	15	6.3	6.3	5.6	5.4	8.0	8.9	16.1
Sept.	6	0.7	1.2	0.9	1.2	1.2	0.7	1.0
	15	11.7	2.8	2.8	2.1	1.0	2.2	4.8
Transect 3								
July	6	13.7	6.3	2.6	4.1	4.1	5.1	9.4
	15	5.9	7.7	9.5	11.3	6.0	3.9	5.1
Aug.	6	6.8	0	2.2	2.2	0.5	0	4.2
	15	3.6	8.3	6.4	6.5	2.4	1.1	3.9
Sept.	6	0	0.2	1.4	1.3	0	0	0
	15	1.3	5.0	4.2	8.7	0.4	0	3.0
Transect 4								
July	6	4.2	7.7	6.0	6.5	4.6	0.4	2.4
	15	0	0.9	18.9	20.2	4.8	6.3	12.8
Aug.	6	3.3	6.2	4.1	4.7	3.0	2.1	1.2
	15	11.2	13.1	2.3	7.0	4.1	6.5	12.9
Sept.	6	1.3	2.0	0	0.7	0	1.5	0.1
	15	11.8	10.0	4.8	4.6	1.0	5.0	10.8
Transect 5								
July	6	6.6	6.3	3.9	6.5	5.1	5.6	4.8
	15	13.3	7.7	6.4	6.9	4.9	3.4	6.7
Aug.	6	4.5	5.7	2.3	4.8	0.7	3.7	3.9
	15	12.2	6.9	6.4	1.7	4.0	4.1	5.2
Sept.	6	2.9	2.9	1.2	0.6	0	1.9	2.7
	15	12.4	5.5	5.0	1.6	0.9	1.3	2.4
Average of all samplings	6	4.85	4.20	4.08	4.41	2.80	3.08	3.43
	15	7.22	6.93	6.28	6.81	3.77	5.13	8.17

Standard error of difference between any 2 averages at 6 in. depth = 0.650. Standard error of difference between any 2 averages at 15 in. depth = 1.658.

of the instrument toward the open gave much higher readings because of reflected light. The records of the spherical thermocouples undoubtedly come nearer to indicating total effective light because light from all directions, reflected and direct, is involved in the readings. A fast-shifting light fleck is not apparent in the readings and when one sphere is in a strongly lighted spot the other may not be. Thus readings from the thermocouples are not as widely variable as those from a photoelectric cell. The thermocouples, because they measure light from all directions, gave slightly lower values than the illuminometers (15.7 and 5.1 per cent for margin and interior, respectively) but indicated that the effective light at the margin is three times that of the interior. This value seems most acceptable for it includes reflected light from the open as well as the shading effect of the forest and marginal shrubs.

Discussion

Having established that the available soil moisture at the margins of these stands is not significantly different from that in the interior, or that it is possibly even lower, it follows that the differential survival of pine reproduction at the margins and in the stands is related to some factor other than water. This factor apparently is light intensity. It appears that pine seedlings can survive periods of low available soil moisture and even compete successfully with hardwoods provided that they are not too heavily shaded. Chapman ('45) reported that loblolly pine seedlings growing under the shade of a forest stand in Louisiana always die sooner or later. He stated that the immediate cause of their death is fire or drought, but seedlings growing in full sun or partial shade were found to be much more resistant to both fire and drought than those growing in full shade. In view of these observations it seems reasonable to regard light as a limiting factor in the establishment of pine seedlings under dense forest stands. Full sunlight is not necessary for survival because, as previously stated, the margins studied had northerly exposures and were shaded to some extent most of the day. Furthermore, Korstian and Coile ('38) found that loblolly and shortleaf pine seedlings survived for several years in the shade on their trenched plots.

It is probable that shading produces its effects by reducing the size and rate of growth of root systems. Coile ('40) reported that loblolly pine seedlings grown in open fields have much deeper and better branched root systems than those grown in forests. Shirley ('45) reported that growth of northern pines increases with light intensity up to 100 per cent of full sunlight and that root development is in proportion to top development in all light intensities. It is likely that the lesser growth and smaller root systems of pine seedlings in the shade are the result of inadequate photosynthesis, for loblolly pine has been shown to attain maximum photosynthesis only in full sunlight (Kramer and Decker, '44).

The recent trend toward emphasizing soil moisture rather than light as the most significant factor in tolerance originated with Fricke ('04), who drew his conclusions from trenched plots in Scotch pine stands in Germany. Several other European investigators expanded his observations but came to conflicting conclusions. In America the trenched-plot experiments of Toumey and Kienholz ('31) showed that shade intolerant species, such as white pine, became established and grew well, at least for several years, under a forest canopy if protected from root competition by trenching. Recently Lutz ('45) rechecked one of Toumey's plots after 13 years without treatment. Toumey (l.c.) had reported that 8 years after trenching, the rate of height growth of white pine was declining. He explained the decline on the basis of increased root competition among the pines within the plots. In 1943 Lutz found that all of these pines were dead and that hemlock had increased in numbers and size. Lutz stated "If the moisture supply was too low for pine it is difficult to believe that it was sufficient for hemlock. Yet the pine died and the hemlock flourished." He concluded "that radiation intensity was too low for the relatively shade-intolerant white pine but was favorable for the shade-tolerant hemlock."

Korstian and Coile's trenched plots in the Duke Forest are already beginning to show similar effects although they have not been untouched equally long. Many of the pines which survived in the plots during the early treatment and observation are now dead. Those remaining are spindly, unthrifty, and obviously on the decline. Hardwoods, on the other hand, are increasing in the plots as is normal in pine forests here. Obviously there is sufficient water available for growth of hardwoods. Since the pines can survive under equal or inferior moisture conditions provided that the light intensity is high enough, it follows that in the shade they are unable to obtain sufficient water for successful growth. Survival and growth of pines require a light intensity which is high enough for them to produce enough food to develop root systems capable of absorbing the necessary water.

Summary

Seedlings of several species of pine often become established along the margins of forests in the Piedmont although they rarely become established within a stand.

Sampling of the soil along transects from open fields across these margins into the interior of stands of shortleaf pine showed that available water at the margins is as low as within the stands. Measurements of various atmospheric factors indicate no environmental differences between margin and interior of the forest which are likely to be significant with respect to establishment of pine except in value of light intensity, which is much higher at the margin.

More successful establishment of shortleaf pine at the margin of a forest than in the interior cannot be ascribed to more favorable moisture conditions but it probably is related to the higher light intensity. It is known that certain other equally intolerant pines require full sunlight for maximum photosynthesis and that they develop more extensive root systems in the open than under forest stands. Thus, the pines at the margin, which are probably able to manufacture more food and therefore to develop more extensive root systems, can survive drought better than those in the forest. This leads to the conclusion that light is probably more significantly controlling than soil moisture in the complex of factors limiting the establishment of shortleaf pine seedlings under forest stands. This conclusion probably also applies to loblolly pine.

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