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Competition results when the combined demands of plants for the essentials for growth are greater than the available supply. Competition in forests occurs whenever plants grow so close together as to result in a struggle for light above ground and for moisture and soil nutrients below ground. It causes the overtopping, suppressing, and crowding out of the weaker individuals by more vigorous and more aggressive trees.

Differences between individuals within a species in their response to competition results in an expression of dominance by the more aggressive trees. In mixed stands the most aggressive species usually become dominant. When they are able to maintain their competitive advantage and reproduce successfully they are usually considered as being relatively more tolerant than their associates. This gives rise to the concept that tolerance is "the capacity of a tree to develop and grow in the shade of and in competition with other trees."[2] It is "a general term for the relative ability of a species to survive a deficiency of an essential growth requirement, such as light, moisture, or nutrient supply."

The relative tolerance of the different species when in intense competition is very important in determining their respective roles in the natural succession of forest communities toward the climax type for a given climatic area.

Studies were begun at Duke University in 1932 to obtain additional evidence on the part played by the interacting factors of light and soil moisture in the competition, the expression of dominance, and the relative tolerance of loblolly pine (*Pinus taeda* L.) and its commonly associated species of angiosperms. Comparative studies were made of soil moisture and light intensity on seven sets of trenched and untrenched plots in loblolly pine, shortleaf pine, post oak–blackjack oak, white oak–black oak–red oak and red gum–yellow–poplar forest types.[3] The results showed that in closed stands in which light intensity was essentially the same a deficiency of soil moisture during the growing season was responsible for the death of pine seedlings one to two years old on the untrenched plots. The angiosperms, commonly present in the understory or sometimes newly germinated, usually persisted, although they sometimes died back and sprouted out again.

Trenching was followed by increases in the number of all species and in general luxuriance of the vegetation. Subsequent observations, however, indicated that after six to ten years the pine trees on the trenched plots became unthrifty and began to die. After a lapse of 10 to 15 years nearly all of the pines had died indicating that, apparently because of the relative intolerance of the pine trees to the shade of the overstory, a deficiency of light may have caused their ultimate death. This conclusion is supported by the results of a recent experiment suggesting that reduced light intensity is an important factor in the poor survival of pine seedlings under forest stands.[4]

These results are in accord with earlier research[5] which showed that at reduced light intensities hardwoods are photosynthetically more efficient than pines. This fact suggested that the lesser growth and smaller root systems of pine seedlings grown in the shade are likely to result in inadequate photosynthesis. Although under adequate light intensity pines can grow where moisture conditions are equal to or less than the needs of hardwoods, it appears that in shade they are unable to grow and develop successfully. In other words the survival and growth of pines require a light intensity high enough for them to produce sufficient food to develop root systems capable of absorbing the necessary water.

These considerations emphasize the interrelationship of the complex factors involved in competition and that not only the environmental factors of light intensity, soil moisture, and dissolved nutrients but also the relative photosynthetic efficiency and root habit and development are involved in relative tolerance.

In an effort to obtain additional evidence on the interactions and relative importance of these environmental factors another study was initiated in the Duke Forest in 1951. Sixty loblolly pine seedlings seven years old were selected from an even-aged stand of loblolly

[1]Presented at 12th Congress, International Union of Forest Research Organizations, Oxford, England, July 1956.

[2]Forestry Terminology. p. 85. Society of American Foresters. Washington, D. C. 1950.

[3]Korstian, C. F., and T. S. Coile. Plant competition in forest stands. Duke School Forestry Bul. 3. 125 pp. 1938.

[4]Kramer, P. J., H. J. Oosting, and C. F. Korstian. Survival of pine and hardwood seedlings in forest and open. Ecology 33:427-430. 1952.

[5]Kramer, P. J., and J. P. Decker. Relation between light intensity and rate of photosynthesis of loblolly pine and certain hardwoods. Plant Physiol. 19: 350-358. 1944.

pine and hardwoods. The hardwoods included a variety of species indigenous to mesic upland sites of the North Carolina Piedmont Plateau. The experimental area represented a high quality site as indicated by an abundance of yellow-poplar (*Liriodendron tulipifera* L.).

Twenty pines were randomly selected for each of the following treatments:

1. Both crown and root competition was greatly reduced by killing all woody plants within 33 inches of the pines with Ammate (ammonium sulfamate).

2. Crown competition was greatly reduced by tying back all woody plants capable of shading the pines, leaving root competition undisturbed.

3. The pines in this group were allowed to compete with the associated species above and below ground. They served as the control for treatments 1 and 2.

Height and diameter growth was recorded for four succeeding growing seasons. Growth analyses for the first two growing seasons indicated that the unreleased control pines grew significantly less than those in treatments 1 and 2. There was, however, no significant difference between the growth of the pines under treatments 1 and 2. At that time treatment 1 was modified by poisoning all woody plants within 12.5 feet of the pines.

The accompanying table includes the adjusted treatment means of height and diameter growth for the four years. Adjusted means indicate the treatment means which would have been obtained had the group means been the same at the beginning of the experiment.

Because of the high site quality of the area which probably had an adequate amount of mineral nutrients required for the growth of forest trees, the root competition in this experiment represents mainly that for available soil moisture.

TABLE 1.—ADJUSTED TREATMENT MEANS OF HEIGHT AND DIAMETER GROWTH FOR FOUR YEARS

Treatment	Height: Adjusted mean growth	Height: Average difference between adjusted treatment means	Diameter: Adjusted mean growth 1 inch above ground	Diameter: Average difference between adjusted treatment means
	Inches	*Inches*	*Inches*	*Inches*
1. Hardwoods poisoned	98.7	Treatment 1 minus Treatment 2 14.2*	2.34	Treatment 1 minus Treatment 2 0.67*
2. Hardwoods tied back	84.5	Treatment 1 minus Treatment 3 37.8**	1.67	Treatment 1 minus Treatment 3 1.40**
3. Control	60.9	Treatment 2 minus Treatment 3 23.6**	0.94	Treatment 2 minus Treatment 3 0.73**

*Significant at 5 percent level.
**Significant at 1 percent level.

Average light intensity available to the crowns of the experimental pines was measured on a clear day between 10:30 A.M. and 3:00 P.M. It was expressed as a percentage of the light intensity measured in an open field during the same period. The calculated values for treatments 1 and 2 were the same; namely, 73 percent of full sunlight and that for the untreated control was 35 percent. Since there was no significant difference in the intensity of light available to the pines in groups 1 and 2, the differences in average growth of the treatment groups can be attributed to differences in available soil moisture. Thus the trees in group 1 grew significantly more than those in group 2 because they had access to more available soil moisture during the growing season.

The difference in light intensity apparently accounts for the variation in growth of groups 2 and 3. The pines within group 2 were exposed to twice the intensity of light available to those in the control.

The combined effect of deficient light and soil moisture is reflected in the growth and general appearance of the treated and control pines. Most of the treated pines appeared healthy and vigorous. They had well developed leaders and long crowns composed of first to fourth order branches. The dark green needles pointed upward, forming an acute angle with the stems.

Most of the control pines had an unthrifty chlorotic appearance. Many of them were completely overtopped by competing hardwoods. Three control pines died during the last growing season. It is interesting to note that all three dead pines had been exposed to the lowest light intensity within the control group.

The present experiment further emphasizes the importance of both light and soil moisture as vital factors in the growth and development of loblolly pine when in competition with hardwoods. Either deficient soil moisture or inadequate light intensity can become a limiting factor and the interacting combination of both usually prevents the survival of this species under such conditions. Thus the death of the intolerant pine permits the more tolerant and commonly slower growing hardwoods ultimately to dominate the stand and become the climax in the natural succession.