FACTORS AFFECTING ACORN PRODUCTION AND GERMINATION AND EARLY GROWTH OF SEEDLINGS AND SEEDLING SPROUTS

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ABSTRACT. Acorn production is extremely variable and unpredictable. Flowering is copious, but many climatic factors influence acorn development from initiation of flowers to acorn maturity. Acorns are consumed by birds, animals, insects, and microorganisms. The establishment of seedlings is more closely related to favorable site factors than to size of crops. A majority of oaks originate from advance reproduction that accumulates under the previous stands during several decades.

FOR THOUSANDS of years our major species of oaks have become successfully established from acorns. With this reproductive mechanism, the oaks have moved back and forth with the glacial periods of the North American continent. They have survived many climatic and geologic changes and many wildfire conflagrations, including the fires of Indians and the fires of pioneers. The oaks have also occupied new sites in competition with many other forest species. On many of the blight-killed chestnut sites in the eastern United States, the upland oaks have replaced dead chestnut trees *(Korstian and Stickel 1927; Woods and Shanks 1959).*

Our purpose in this paper is to discuss the factors that affect the production and germination of acorns, and the early growth of seedlings and seedling sprouts.

There are hundreds of published observations and scientific studies on these subjects. We have exercised our judgment to condense existing knowledge into general concepts. These concepts are presented to provide a framework of knowledge to guide practical decisions, as well as to identify some research needs. We have cited key papers that will lead the inquiring person into the details of anatomy, physiology, and growth and development of flowers, acorns, and seedlings. Much of this literature pertains either to the genus as a whole, or to additional species of oak other than the five upland species that are the subject of this symposium. Even within this group of five upland species, there are wide differences in the processes of sexual reproduction and early growth, and we must use caution in applying generalities to guide both practice and research.

FLOWER FORMATION

Acorns, the fruit of the oaks, develop from fertilized flowers, never from unfertilized flowers by such asexual methods as parthenogenesis and apomixis. All species of oak produce both male and female flowers on the same tree. Both staminate (male) and pistillate (female) flowers are formed every year in great abundance by practically every oak tree of flowering size and age; consequently, the year-to-year variability in size of acorn crops is not due to lack of flowering capability, nor to cyclic formation of flowers.

The pistillate flowers are located in the axils of the new leaves, whereas the staminate flowers develop on long slender catkins that are borne either in the axils of scale leaves of the current vegetative buds or in separate male buds *(Stairs 1964)*. Pollination is by wind and air currents.

Climatic factors are most important in controlling flower formation and development, and in the pollination of flowers. There are no important biotic factors that affect the formation of oak flowers. Various climatic factors, such as wind, late frost, prolonged rain, relative humidity, and temperature have been shown to affect the opening and closing of the anthers and the dissemination of pollen *(Sharp and Chisman 1961)*. A study of pistillate flowering and acorn development in Pennsylvania showed that good crops of white oak acorns were obtained when a warm 10-day period in late April was followed by a cool period in May *(Sharp and Sprague 1967)*. At present, there are no known ways to control flower formation and development or the pollination of flowers.

The ability to control these processes would be a valuable tool for the forest manager. Abundant flowering and high rates of pollination would insure more consistent acorn crops for reproduction and wildlife food. On the other hand, low flower production would leave larger food reserves for the growth of wood and other vegetative organs.

FRUIT FORMATION

Early ovule development begins approximately 1 month after pollination in the subgenus *Lepidobalanus* (white oaks), and approximately 13 months after pollination in the subgenus *Erythrobalanus* (red oaks). Although there is a major timing difference between the two groups before fertilization, the subsequent developmental stages of the embryo are relatively uniform from a cytological or morphological viewpoint. Therefore the major difference of interest is the time required for seed maturation. The white oak group matures seed in one growing season; the red oak group requires two growing seasons *(Stairs 1964)*.

The greatest loss in fruits occurs because of premature abscission. The highest rate of loss occurs during the period of pollination and fertilization *(Turkel, Rebuck, and Grove 1955)*, although abscission of immature acorns continues until maturity. We do not know the reasons for these abscissions, but we do know that trees with large crowns have about the same pattern of abscission as trees with small crowns *(Williamson 1966)*. Open-grown trees do not produce any more flowers and acorns than do trees with the same crown surface area in closed stands. However, the surface area of oak crowns in closed stands can be increased by thinning, because crown surface area for trees of a given age depends to a large degree on stand density. Limited evidence in Russia also suggests that increasing the growth rate of shoots by cultural practices such as thinning may increase fruit-bearing in the oaks *(Polozoya 1958)*.

The number of acorns produced by a tree also may be an inherent characteristic *(Irgens-Moller 1955; Sharp and Sprague 1967)*.

SIZE AND PERIODICITY OF CROPS

Numerous investigators have estimated the size of acorn crops from one to several years, and in all parts of the world where oak forests occur. Both timber and wildlife managers are intensely interested in the seed production of oaks, the timber manager because of the reproductive needs of the forest, and the wildlife manager for the store of food used by important game birds and animals.

It has been commonly observed by all of these investigators that acorn crops are extremely variable from tree to tree, from species to species, from location to location, and from year to year *(Beck and Olson 1968; Christisen 1955; Christisen and Korschgen 1955; Downs and McQuilken 1944; Gysel 1956; Minckler and Janes 1965; Tryon and Carvell 1962a, 1962b)*. The factors causing this variability are not known, though many attempts have been made to discover them *(Gysel 1958; Williamson 1966)*.

On a land-area basis, acorn crops vary from nearly zero to 250,000 or more acorns per acre. Many times the white oak group will produce heavily in a particular year, and the red oak group will have practically no yield, and vice versa *(Barrett 1931; Gysel 1956; Beck and Olson 1968)*. In mountainous terrain, the wide variability in microclimate due to elevation and aspect results in comparable variability in acorn production. There is need to develop an index of production that can be used to predict mast for animal food from both the white and red oak groups *(Gysel 1958)*. Since we do not have practical means for controlling the size of acorn crops, wildlife managers advocate the culture of mixed oak stands over a range of sites to minimize the likelihood of complete crop failure *(Christisen 1955; Collins 1961)*.

DESTRUCTION OF ACORNS

Acorns are consumed by birds, animals, insects, and microorganisms *(Korstian 1927)*. Two groups of insects, nut weevils and gall insects, cause the largest losses of acorns *(Barrett 1931; Beck and Olson 1968; Downs and McQuilken 1944)*. Brezner *(1960)* found that in Missouri the weevils of the genus *Curculio* were the principal agents of acorn depredation. Dorsey *(1967)* showed that the systemic insecticides Bidrin and phorate were effective in reducing acorn losses by the acorn weevil *(Curculio* spp.*)* when the insecticides were injected into the boles of the trees.

The percent of sound acorns capable of germination is closely related to size of crop *(Beck and Olson 1968; Korstian 1927; Minckler and Janes 1965)*. In poor years, nearly all acorns are consumed. The number of new seedlings added to the advanced regeneration each year is also directly related to size of the acorn crop.

In addition to consumption by organisms, acorns are destroyed by other means, such as freezing, drying out, burning in wildfires, and flooding. These destructive forces account for relatively large losses in poor crop years and relatively small losses in good crop years.

GERMINATION OF ACORNS

Sound, undamaged acorns have a germinative capacity between 75 and 95 percent *(USDA Forest Service 1948)*. Acorns of the white oak group germinate in the fall immediately after falling to the ground. Acorns of the red oak group overwinter on the ground and germinate the following spring. For germination to occur, the moisture content of acorns must not drop below 30 to 50 percent for white oaks, and 20 to 30 percent for red oaks *(Korstian 1927)*. Litter or soil cover affords protection against drying and is necessary for successful germination *(Barrett 1931; Korstian 1927)*. Germination is hypogeal, and under favorable conditions is generally complete in 3 to 5 weeks *(USDA Forest Service 1948)*.

In a West Virginia study, Carvell and Tryon *(1961)* found that, from equal numbers of red and white oak acorns, the number of white oak seedlings produced was five times as great as the number of red oaks. This situation appears to be the usual one, but the reason for the difference is not known. White oak acorns generally fall earlier than red oak acorns and are smaller than red oak acorns. Since the smaller white oak acorns germinate immediately and are covered by deeper leaf litter than are the red oaks, white oaks are probably afforded greater protection from damaging agents.

The establishment of oak seedlings in West Virginia was found to be more closely related to favorable site factors than to size of acorn crops *(Tryon and Carvell 1958, 1962a, 1962b)*. However, this relationship varies widely for the different species of oaks and regions of the country.

EARLY GROWTH OF SEEDLINGS AND SEEDLING SPROUTS

The principal factors that influence the development of oak seedlings are light intensity and soil moisture *(Bourdeau 1954; Kozlowski 1949)*. The five upland oak species under discussion in this symposium are intermediate in shade tolerance and reach maximum rates of photosynthesis at lower light intensities than intolerant species such as the southern pines *(Kramer and Decker 1944)*. As a result, these oaks can compete favorably in a broad range of light climates if soil moisture is adequate. The exclusion from poor sites of the oak species normally found on good sites (northern red, scarlet, and white oaks) is because of insufficient drought resistance of the better oaks. The exclusion from good sites of poor-site oaks such as blackjack oak is explained by the low shade tolerance and slow rate of growth of blackjack oak.

Merz and Boyce *(1958)* found that 88 percent of the oak reproduction became established prior to both light and heavy harvest cuts. The amount and distribution of oak reproduction found in the harvest cuts is not necessarily related to the cutting intensities. A majority of oaks in the new stands grow from seedling sprouts that have accumulated over several decades prior to the harvest cut. The major oak species in these areas was white oak. Some of the red oaks, mostly northern red and scarlet oak, do not persist as advanced reproduction for more than a few years.

McGee *(1967)* found abundant oak regeneration under eight mixed oak stands in the Southern Appalachians prior to installing a study of cutting intensity. He observed a dynamic fluctuation in the advance regeneration as seed germinated, seedlings lived a few years, died, and were replaced by new ones.

There is a high mortality of newly established oak seedlings on all sites. Death is highest in the first 6 years of the seedling's life. Few seedlings survive the first year without dying back and sprouting at least once. Some seedlings (mostly white oak) survive under dense canopies for periods up to 50 or more years by a repeated process of sprouting and dying *(Merz and Boyce 1956; Merz and Boyce 1958; Minckler and Janes 1965)*. This survival is made possible by the large number of buds that occur on new seedlings and subsequently develop near the ground line of the long-surviving individuals. Near the base of new shoots a large number of buds is formed in the axils of rudimentary leaves. These leaves look like tiny hairs. The buds in the leaf axils, which may remain in suppression for many years, and the three buds in the axils of each cotyledon *(Kurmes and Boyce 1964)*, form a reservoir of buds for repeated sprouting of shoots.

When the top of a young seedling dies back, one or more of the suppressed buds grow. These buds are often below the soil surface, and are protected from damage. Such characteristics make it possible for oak seedlings to survive after the tops are destroyed by animals, insects, disease, logging, and fire. In this manner, seedling sprouts of oaks accumulate beneath the canopies of existing stands *(Liming and Johnston 1944)*.

Various forms of partial cuts prior to final cuts have been recommended to regenerate the oaks from current seed crops, but there are no certain ways to manage stands of oak for the abundant production of acorns. Methods of management have been developed to favor the accumulation of advanced oak regeneration. These methods are discussed in other symposium papers.

Literature Cited

Barrett, L. I.
1931. Influence of forest litter on the germination and early survival of chestnut oak, *Quercus montana* Willd. Ecology 12: 476-484.

Beck, D. E., and D. F. Olson, Jr.
1968. Seed production in southern Appalachian oak stands. USDA Forest Serv. Res. Note SE-91. 7 pp. SE. Forest Exp. Sta.

Bourdeau, P. F.
1954. Oak seedling ecology determining segregation of species in Piedmont oak-hickory forests. Ecol. Monog. 24: 297-320.

Brezner, Jerome.
1960. Biology, ecology, and taxonomy of insects infesting acorns. Mo. Agr. Exp. Sta. Res. Bull. 726. 40 pp.

Carvell, K. L., and E. H. Tryon.
1961. The effect of environmental factors on the abundance of oak regeneration beneath mature oak stands. Forest Sci. 7: 98-105.

Christisen, D. M.
1955. Yield of seed by oaks in the Missouri Ozarks. J. Forestry 53: 439-441.

Christisen, D. M., and L. J. Korschgen.
1955. Acorn yields and wildlife usage in Missouri. Trans. N. Amer. Wildlife Conf. 20: 335-357.

Collins, J. O.
1961. Ten-year acorn mast production study in Louisiana. La. Wildlife and Fisheries Comn., New Orleans.

Dorsey, C. K.
1967. Experiments to control acorn weevils with systemic insecticides. Forest Sci. 13: 390-396.

Downs, A. A., and W. E. McQuilken.
1944. Seed production of southern Appalachian oaks. J. Forestry 42: 913-920.

Gysel, L. W.
1956. Measurement of acorn crops. Forest Sci. 2: 305-313.

Gysel, L. W.
1958. Prediction of acorn crops. Forest Sci. 4: 239-245.

Irgens-Moller, H.
1955. Forest tree genetics research: *Quercus* L. Econ. Bot. 9: 53-71.

Korstian, C. F.
1927. Factors controlling germination and early survival in oaks. Yale Univ. School Forestry Bull. 19. 115 pp.

Korstian, C. F., and P. W. Stickel.
1927. The natural replacement of blight-killed chestnut in the hardwood forests of the Northeast. J. Agr. Res. 34: 631-648.

Kozlowski, T. T.
1949. Light and water in relation to growth and competition of Piedmont forest tree species. Ecol. Monog. 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: 350-358.

Kurmes, E. A., and S. G. Boyce.
1964. Genetically paired oak seedlings. J. Forestry 62: 637-638.

Liming. F. G., and J. P. Johnston.
1944. Reproduction in oak-hickory forest stands of the Missouri Ozarks. J. Forestry 42: 175-180.

McGee, C. E.
1967. Regeneration in southern Appalachian oak stands. USDA Forest Serv. Res. Note SE-72. 6 pp. SE. Forest Exp. Sta.

Merz, R. W., and S. G. Boyce.
1956. Age of oak "seedlings." J. Forestry 54: 774-775.

Merz, R. W., and S. G. Boyce.
1958. Reproduction of upland hardwoods in southeastern Ohio. Central States Forest Exp. Sta. Tech. Paper 155. 24 pp.

Minckler, L. S., and Donald Janes.
1965. Pin oak acorn production on normal and flooded areas. Mo. Agr. Exp. Sta. Res. Bull. 898. 15 pp.

Polozoya, L. Ya.
1958. Growth of oak shoots in relation to fruit-bearing processes. Soobshcheniya Instituta Lesa, Akademiya Nauk SSSR No. 9: 3-17. Trans. TT-69-53022. Indian Nat. Sci. Doc. Center, New Delhi.

Sharp, W. M., and H. H. Chisman.
1961. Flowering and fruiting in the white oaks. I. Staminate flowering through pollen dispersal. Ecology 42: 365-372.

Sharp, W. M., and V. G. Sprague.
1967. Flowering and fruiting in the white oaks. II. Pistillate flowering, acorn development, weather and yields. Ecology 48: 243-251.

Stairs, G. R.
1964. Microsporogenesis and embryogenesis in Quercus. Bot. Gaz. 125: 115-121.

Tryon, E. H., and K. L. Carvell.
1958. Regeneration under oak stands. West Va. Univ. Agr. Exp. Sta. Bull. 424. 22 pp.

Tryon, E. H., and K. L. Carvell.
1962a. Acorn production and damage. West Va. Univ. Agr. Exp. Sta. Bull. 466T. 18 pp.

Tryon, E. H., and K. L. Carvell.
1962b. Comparison of acorn production and damage on sites with abundant and with sparse oak regeneration. West Va. Univ. Agr. Exp. Sta. Current Rep. 36. 7 pp.

Turkel, H. S., A. L. Rebuck, and A. R. Grove, Jr.
1955. Floral morphology of white oak. Pa. Agr. Exp. Sta. Bull. 593. 14 pp.

USDA Forest Service.
1948. Woody-plant seed manual. U. S. Dep. Agr. Misc. Publ. 654, 416 pp.

Williamson, M. J.
1966. Premature abscissions and white oak acorn crops. Forest Sci. 12: 19-21.

Woods, F. W., and R. E. Shanks.
1959. Natural replacement of chestnut by other species in the Great Smoky Mountains National Park. Ecology 40: 349-361.