Wakeley's Early History of Southern Forest Genetics

Philip C. Wakeley and James P. Barnett

Philip C. Wakeley (deceased), Retired as a Research Scientist in 1964, U.S. Department of Agriculture, Forest Service, Southern Forest Experiment Station, New Orleans, LA 70113.

James P. Barnett, Retired Chief Silviculturist and Emeritus Scientist, U.S. Department of Agriculture, Forest Service, Southern Research Station, Pineville, LA 71360.

PREFACE

Hired as a researcher in 1924, Philip C. Wakeley led the U.S. Department of Agriculture Forest Service, Southern Forest Experiment Station's development of reforestation, tree improvement, and genetics across the South during his remarkable 40-year career. Wakeley's seminal *Planting the Southern Pines* (Wakeley 1954) was built on some of his earlier works (Wakeley 1929, 1935) and provided foresters with the tools and technology to reforest the South and remains one of the most-cited references of the Forest Service. Wakeley's studies helped convince foresters and managers of the potential to use genetics to improve the productivity of southern pine plantations, and he long served as the leader of southern forest tree improvement and genetics.

After his retirement, Wakeley documented the early history of some of the major forestry advances by the Station (Wakeley 1980, Wakeley and Barnett 2016). This documentation effort includes the following paper, originally presented by Wakeley at Louisiana State University's 24th Annual Forestry Symposium in 1975 (Wakeley 1975) and reproduced here in its entirety.[1] This paper is Wakeley's look back at the early development of the genetics of southern pines that now drive the productivity of Southern forests. An understanding of Wakeley's contributions is important as we observe the 100th anniversary of the founding of what is today the Forest Service's Southern Research Station. The contributions of Wakeley provide the basis for the amazing progress that occurred in improving forest productivity during the mid to late 20th century. As Carter and others (2015), paraphrasing Winston Churchill, said of Wakeley and his colleagues, "never in the history of forestry have so many benefited so much from the work of so few."

REFERENCES

Carter, M.C.; Kellison, R.C.; Wallinger, R.S. 2015. Forestry in the U.S. South: a history. Baton Rouge, LA: Louisiana State University Press. 448 p.

Wakeley, P.C. 1929. Planting southern pine. Leaflet No. 32. Washington, DC: U.S. Department of Agriculture Forest Service. 8 p.

Wakeley, P.C. 1935. Artificial reforestation in the southern pine region. Tech. Bull. 492. Washington, DC: U.S. Department of Agriculture Forest Service. 115 p.

Wakeley, P.C. 1954. Planting the southern pines. Agric. Monograph 18. Washington, DC: U.S. Department of Agriculture Forest Service. 233 p.

Wakeley, P.C. 1975. Southern forest genetics before 1951. In: Thielges, B.A., ed. Forest tree improvement—the third decade: proceedings of the 24th annual forestry symposium. Baton Rouge, LA: Louisiana State University, Division of Continuing Education: 3–12.

Wakeley, P.C. 1980. Silvicultural research—a perspective. In: Barnett, J.P., ed. Proceedings of the First Biennial Southern Silvicultural Research Conference. Gen. Tech. Rep. SO-34. New Orleans: U.S. Department of Agriculture Forest Service, Southern Forest Experiment Station: 1–5.

Wakeley, P.C.; Barnett, J.P. 2016. Early forestry research in the South: a personal history. Gen. Tech. Rep. SRS-137. Asheville, NC: U.S. Department of Agriculture Forest Service, Southern Research Station. 159 p. https://doi.org/10.2737/SRS-GTR-137.

[1] Wakeley's 1975 article is reproduced with the kind permission of D. Allen Rutherford, the Louisiana State University Agricultural Center, and the Louisiana State University School of Renewable Natural Resources.

SOUTHERN FOREST GENETICS BEFORE 1951[2]

Philip C. Wakeley
U. S. Forest Service, Retired
Ithaca, New York

In this country, up to 1950, professional forest geneticists were few and far between, and their meagerly supported work attracted little serious attention. Between 1924 and 1950 their main efforts were devoted to hybridizing poplars in the Northeast, chestnut in the East, and pines at the former Eddy Tree Breeding Station (now the Institute of Forest Genetics) at Placerville, California. Beginning in the early 1900's, professional foresters established provenance tests of ponderosa pine and Douglas-fir in the West and of Scotch pine and Norway spruce in the Lake States and the Northeast, and published both the early results of these tests and a number of speculative articles on other phases of forest genetics. In 1928 Carlos G. Bates, of the Lake States Forest Experiment Station, seriously proposed to American foresters the development of what we now call seed orchards (Bates 1928), but his proposal bore no fruit for more than twenty years.

None of the above-mentioned professional forest geneticists or interested foresters worked in the Southern Pine Region. I can speak with some authority on what was done in the South before 1951, because, not to mince words, I did most of it myself until 1942, when Keith W. Dorman swung into action. My efforts were pretty amateurish, but they did lay a foundation for research on geographic sources of seed, derive some basic information on pine species characteristics and hybridization of pines, and identify and preserve some useful breeding stock.

Early hybridization studies

Chronologically, events up to 1951 were as follows.[3] I began work at the Southern Forest Experiment Station in 1924 with an interest in geographic variation carried over from college days and an interest in hybrids whetted by H. H. Chapman's published description of Sonderegger pine, the natural cross between longleaf and loblolly (Chapman 1922). During the latter 1920's my interest in hybrids was increased by correspondence and contact with the staff of the Eddy Tree Breeding Station. Genetics, however, was no part of my official assignment, which consisted of seed, nursery, and planting research.

In the spring of 1925, in North Carolina, I made my first field identification of, and collected official Forest Service specimens of, Sonderegger pine, thus very greatly extending its known range, previously limited (Sudworth 1927) to Louisiana and Texas.

On October 21, 1925, I conducted Lloyd Austin, the original Director of the Eddy Tree Breeding Station, over the Great Southern Lumber Company's big commercial pine nursery and the Southern Forest Experiment Station's one-year-old experimental plantations at Bogalusa, Louisiana. This, my first personal contact with a professional geneticist engaged in forest tree breeding, was a liberal education to me and greatly increased my interest in forest genetics and paved the way for years of correspondence with and, ultimately, two personal visits to, the Station (later the Institute) at Placerville. At a request of Austin's

[2] This article has been reproduced as originally published with the exception of the addition of the bold-faced headings to help organize the content, some inserted footnotes and figures to help the reader, and a few other minor technical edits.

[3] 1951 is significant because that was the year tree improvement and genetics became a funded part of the Station's research program; prior to then those topics were pursued only if individual rresearchers were interested.

during this 1925 visit I supplied the Eddy Tree Breeding Station, during the next few years, with some of the southern pine seed used in its later work.

Partly as a result of Austin's visit in 1925, and partly on the further initiative of the Southern Forest Experiment Station, the Station and other agencies tested nearly sixty species of exotic pines in Florida, Louisiana, and Texas, from 1927 through the early Thirties, but not a single species proved able to survive the climate of the Gulf Coast States (Wakeley 1935).

In the fall of 1925, on direct orders from Col. W. B. Greeley, then Chief of the U.S. Forest Service, I helped collect or procure loblolly pine seed from Louisiana, Texas, Georgia, and Arkansas for the first provenance test of any southern tree species. I planted the stock from these four seed lots on two one-half-acre blocks at Bogalusa in the winter of 1926-1927, and followed the test through for the next 35 years (Wakeley and Bercaw 1965). As noted later, this pioneer provenance test had far-reaching results. It is a tribute to Greeley's foresight that he ordered the test put in before many of the American articles on seed source and other phases of forest genetics appeared in print. It was sheer luck, however, that loblolly pine, the one species from which we could get seed from several sources in the extremely poor seed year of 1925, turned out to be the southern pine species with the greatest range of geographic variation in resistance to fusiform rust. It was also by luck, rather than from statistical competence, that I incorporated sufficient replication in the experimental design to show the significance of the differences that developed.

At Bogalusa in 1926-1927, in addition to the loblolly seedsource stock, I planted 330 naturally-occurring Sonderegger pines culled from the Great Southern Lumber Company's longleaf pine nursery beds. The initial survival of these hybrid seedlings was good, and their early growth was rapid, but they soon showed them selves subject to the ills of both parent species—the brown spot needle blight affecting longleaf, and the rabbit-damage, tip-moth infestation, and fusiform-rust infection affecting loblolly. This Sonderegger pine test plot was the forerunner of others that I established near

This photo was used in early publications to illustrate the importance of genetic variation in loblolly pine.

Alexandria, Louisiana in the mid-30's and of much more extensive Sonderegger pine plantations established by the Southern Institute of Forest Genetics in the 50's. The various plantations yielded some basic information on inheritance, but Sonderegger pine has proved of little practical use except occasionally as an understock in establishing grafted longleaf pine seed orchards.

From 1928 through 1935 I selected and recorded, in 25 acres of experimental plantations at Bogalusa, southern pines of out standing form, growth-rate, and resistance to disease. Periodic remeasurements of the selected trees and of adjacent medium-quality and inferior trees, through 30 years in plantation, eventually yielded considerable basic data on growth rate and patterns of growth, made possible the selection of several trees of superior form and growth rate (and of others of aberrant form) for future breeding experiments, and in particular brought to light several longleaf pines with a strongly inherited resistance to brown spot needle blight in the juvenile stage (Derr and Melder 1970, Wakeley 1968, Wakeley 1971).

Longleaf x slash pine hybridization

In 1928 and again in 1929 I attempted to verify H. H. Chapman's assumption of the longleaf X loblolly parentage of Sonderegger pine (Chapman 1922) by crossing the assumed parents artificially by the technique then in use at Placerville. Both attempts failed, but in 1929 I did make a successful and fully authenticated artificial cross upon longleaf with slash pine pollen. The cross yielded about four dozen seeds, which I shared equally with the Eddy Tree Breeding Station. Because of inadequate nursery facilities in 1931, I got only two seedlings from my share of the seed; both are shown in figure 8 on page 1252 of the 1937 Yearbook of Agriculture (Schreiner 1938). (Both were later lost in plantation, one to brown-spot infection and the other to wind-breakage at a rust canker, though extensive production since 1950 has proved this hybrid less susceptible to brown spot than the longleaf parent and less susceptible to rust than the slash pine parent.) As of March 1975 (W. B. Critchfield, personal communication), 13 of the hybrids from the original 1929 controlled pollination are still alive in the Placerville arboretum.

Some botanist—Blakeslee?—produced an authenticated interspecific hybrid of two pines in the Northeast about 1911, a cross that my limited personal library has not enabled me to document. The Eddy Tree Breeding Station made successful controlled crosses of knobcone X Monterey pine in 1927. My controlled hybridization of longleaf X slash in 1929 appears to have been the first artificial cross of any southern pines, and only the third controlled hybridization of pines ever carried out.

Philip Wakeley checking the condition of the bud in a rapidly growing longleaf pine seedling in 1938. (USDA Forest Service photo taken by J.D. Guthrie in October 1938)

In 1931 I made successful controlled back-crosses on Sonderegger pine with pollen of both its parent species. This ended my hybridizing of southern pines until the U.S. Forest Service embarked on its present program of forest genetics research in 1950-1951, but familiarity with the back-crosses later helped me unravel the puzzle of a "hybrid swarm" discovered in a mixed longleaf-loblolly stand in western Louisiana.

The great expansion of the U.S. Forest Service planting program during Civilian Conservation Corps days increased the need for information concerning geographic sources of seed. In the winter of 1935-1936 I established a second provenance test, involving eight sources of longleaf, nine sources of slash, and two sources each of loblolly and shortleaf. The seedlings, far from comparable within species, were obtained where we could find them from beds in nurseries with acceptable records of seed origin, and were planted in one locality only. This test yielded no useful results.

Variations due to day length

Meanwhile, however, upon promise to the Southern Forest Experiment Station of a special allotment of $25,000 for provenance tests, I undertook, with seed from the exceptionally good 1935 seed crop, an ambitious, region-wide source-of-seed study of the same four principal southern pines. The allotment failed to materialize, but the Southern Station enlisted the help of voluntary cooperators in several different agencies throughout the South and launched the study without the special funds.

This region-wide study fared badly from the start. Cooperators supplied longleaf seed from 11 sources, slash seed from 10, loblolly seed from 11, and shortleaf from 10, but choice of sources depended less upon effective sampling of species ranges than upon where cooperators could be found. For each species, it was planned to plant stock of all sources at or near the point of origin of each and every seed lot but, in general, the cooperators were unable to contribute enough seed for this purpose. To make matters worse, nursery production of several lots of stock fell below expectations, fewer plantations were established than had been planned, and some of the plantings that were made were improperly executed or inadequately recorded. Finally, the Southern Station's own plantation for the study near Alexandria, Louisiana (which was the only one containing all 42 lots of seed collected) was destroyed by fire during World War II. For all immediate practical purposes, therefore, the study was a failure.

It did, however, have two important indirect results. First, the shortleaf pine seedbed producing the stock for the Alexandria plantation gave us our first insight into the remarkable north to south variation of this species in response to differences in day length during the growing season—a phenomenon to be even more strikingly demonstrated later on in loblolly pine (Perry and Wang 1957). Second, it enabled us to avoid the gross mistakes of 1935 through 1937 when we established the much more effective Southwide Pine Seed Source Study, with seed from the 1951 and 1955 crops (Kaufman 1971, Snyder et al. 1967, Wells and Wakeley 1966, 1970a and b).

High gum yield selections of longleaf pine

In 1935, T. A. Liefeld of the Southern Station began one of the few genetics studies in which I had no part. He collected wind-pollinated cones from two groups of longleaf pines near Lake City, Florida, one group having gum yields from slightly above average to two-thirds of average, and the other having yields from slightly above to fifty percent above average. Seedlings from the two lots of seed were planted on the Olustee Experimental Forest a year later. Micro-chipping of 17 progeny of the lowyielding and 17 progeny of the high-ielding mother trees showed significantly better gum yield from the progeny of the high-yielders (Mergen 1953), indicating the strong genetic control of gum yield in longleaf pine.

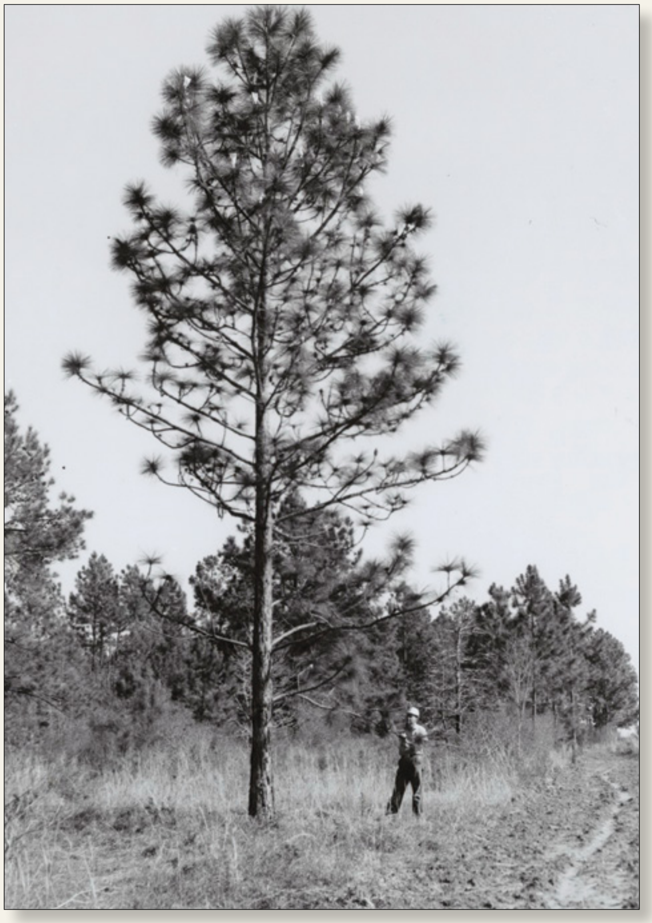
In the spring of 1936 the Forestry Division of the Tennessee Valley Authority began another project in which I had no part. This was the breeding of walnuts, hickories, chestnuts, oaks, honey locusts, black locusts, and persimmons to combine high productivity and quality of nuts, acorns, or other fruits with desirable timber qualities (Schreiner 1938). Also in 1936, the Appalachian (now the Southeastern) Forest Experiment Station began a study of inheritance in pine by planting seedlings from wind-pollinated seed from 122 individual loblolly seed trees, but without obtaining any conclusive results.

In 1924 Dr. Ernst J. Schreiner, in cooperation with the New York Botanic Garden, began hybridizing poplars for the Oxford Paper Company. Later, he was appointed Forest Geneticist at the Northeastern Forest Experiment Station, where he was assigned the preparation of an article on Improvement of Forest Trees for the 1937 Yearbook of Agriculture. He toured the United States and Canada, visiting genetics installations and interviewing other forest geneticists and a few interested foresters, to verify and expand the manuscript of this article. He interviewed me in New Orleans on December 10, 1936.

He included in the article (Schreiner 1938) the only photograph ever published of my 1929 longleaf X slash pine hybrids, together with notes on the provenance tests I had established up to that time. He also included, and credited to me, some suggestions on "the outstanding technical and practical problems that remain to be solved." In view of the direction that southern tree improvement research and practice have taken since 1951, I derive considerable satisfaction from having made valid suggestions as early as 1936.

Brown spot disease resistant longleaf pine

In December 1937, Dr. Paul V. Siggers, while examining an unsprayed seedbed in an abandoned nursery, discovered a 2-year-old longleaf pine seedling with practically complete resistance to brown spot needle blight. It looked like a green whisk-broom standing on end among the thousands of almost completely brown or completely defoliated seedlings around it. He obtained it from the nursery operator and he and I planted it on the J. K. Johnson Tract near Alexandria, Louisiana. This



This longleaf pine was found in an abandoned nursery bed, was resistant to brown-spot needle disease, and was planted on the Palustris Experimental Forest. Control pollinated seeds from it were used in tree improvement studies to establish brown-spot resistant material in genetically improved seed sources. The tree was killed by a southern pine beetle infestation in the early 1980s, but its parentage lives on in many other established seed sources. (USDA Forest Service photo taken by R.W. Neelands in January 1961)

tree, now known familiarly as "Father Abraham," survived and grew well, and has since been shown by exhaustive tests to transmit its brown-spot resistance to its progeny. It has therefore become a key tree in the important program of breeding for disease resistance in longleaf pine (Derr and Melder 1970).

Selection for high gum yield in slash pine

In 1942, Keith W. Dorman and co-workers began the first comprehensive and adequately supported program of breeding superior trees within one species of southern pine. They did it by selecting slash pines of exceptionally high gum yield in the vicinity of Lake City, Florida. The selection was on a comprehensive scale which was rigorous, exacting, and well-recorded, and this resulted in the discovery of twelve trees each of which produced two or more times as much gum as average trees of comparable size (Mergen and Pomeroy 1954).

Vegetative propagation of the selected high-yielders proved impracticable, but controlled cross-pollinations of high-yielders and similar controlled crosses of "check" trees of merely average yield resulted in a small plantation, by courtesy sometimes dubbed "the first southern pine seed orchard," on the Olustee Experimental Forest. The plantation is, of course, properly a progeny test. Ultimately, it demonstrated the strong inheritance of high gum yield in slash pine and gave impetus to the selection and breeding of southern pines for other economically important characteristics. About 1948 Dorman, who had transferred from the Southern to the Southeastern Forest Experiment Station, began selection and breeding for some of these other traits, with progeny tests at Calloway Gardens, near Hamilton, Georgia.

Pine seed source studies

Meanwhile, in 1944, I had published the results of the fifteenth-year remeasurement of the original loblolly seed-source study at Bogalusa, Louisiana. They showed that the growth of the "local" Livingston Parish, Louisiana, stock was significantly better than that of the Texas, Georgia, and Arkansas stocks, and that the Georgia stock was very significantly more susceptible to fusiform rust than were the three stocks of more westerly origin (Wakeley 1944). These findings attracted little attention at the time, both because everyone was preoccupied with World War II and, more specifically, because during the War forest planting was at a low ebb.

In 1949, however, when World War II was over and the pulp and paper industry was beginning to plant the southern pines on an unprecedented scale, Gaylord Container Corporation personnel helped me thin the loblolly seed-source plantation by removing every other tree in each row. Stacking the wood separately by geographic source of seed, showed significant differences in volume production from source to source. The trees from the Arkansas source, for example, had produced only 40 percent as much pulpwood per acre as those from the Louisiana source. Enlarged photographs showing the differences in tree heights and in volumes of stacked pulpwood (Wakeley 1954) when exhibited at a meeting of the Southern Pine Pulpwood Association, blew the question of geographic sources of southern pine seed wide open. Following the meeting, several pulp and paper companies cancelled large orders for seedlings that they had previously placed with State forest nurseries, because the States could not certify the geographic sources of the seed they had sown. Thenceforward, practically all forestry agencies in the South kept much better records of seed sources.

In 1948, Chronica Botanica Company published the English version of Bertil Lindquist's Genetics in Swedish Forestry Practice (Lindquist 1948). Although severely criticized by several professional forest geneticists both here and in Sweden, it was a strikingly illustrated and very persuasive little book. It was widely read by Federal, State, and industrial foresters, administrators, and executives, and apparently contributed greatly to an increased interest in, and to an outburst of enthusiasm and financial support for, forest genetics research and applied tree improvement throughout the United States, much of it along the lines suggested by Bates in 1928.

In the South, a very practical manifestation of this awakened interest was the organization, early in 1951, of the Committee on Southern Forest Tree Improvement. Several influential foresters, at least three of whom had attended the 1949 World Forestry Congress in Finland and had been impressed by recent northern European advances in forest genetics, joined forces in getting the Committee started, and its membership has always been broadly representative of forestry agencies and interests throughout the South. Through its active subcommittees, its own regular meetings, its arranging of region-wide general conferences, its sponsoring of more than thirty publications, and a brisk inter-member personal correspondence, the Committee has been an important stimulus to research and practice and an invaluable clearing-house for plans and information. In particular, it strongly supported the pioneering efforts of Dr. Bruce Zobel, Dr. Thomas O. Perry, and Dr. Keith W. Dorman in establishing grafted southern pine seed orchards through State, University, and pulpwood-industry cooperation (Kaufman 1971).

Although I was a charter member of the Committee, and served as Chairman of its Subcommittee on Geographic Source of Seed until my retirement from the U. S. Forest Service in 1964, I must turn the story over at this point to younger men who are still actively engaged in forest genetics research and tree improvement practice. They are far better qualified than I am to supply up-to-date information, guidelines, and directions to those who need them.

Wakeley's concluding thoughts

I should like, however, to conclude with two comments.

First, between 1953 and 1973--the latest year for which figures have been published -- the area of southern pine seed orchards increased from the acre or so of Dorman's purely nominal seed orchard on the Olustee Experimental Forest to 7,250 acres. These orchards are already so productive that several States and industrial concerns are sowing many (and in some instances all) of their nursery beds with genetically improved orchard seed. For a mere two decades this is a stupendous accomplishment.

Second, although interspecific hybrids have as yet played a negligible part in the southern pine tree improvement program, two of them, the longleaf X slash pine cross and the shortleaf X slash cross, have characteristics both of disease-resistance and of growth that make them very promising for use in many localities where incidence of fusiform rust is high. From studies of my own and co-workers (Wakeley et al. 1966, Harold J. Derr, personal communication) I feel confident that, with proper care, either of these hybrids can be mass-produced in orchards at somewhat but not excessively greater cost than the pure species already corning from our present orchards. With several "second generation" purespecies orchards already in the making, it seems to me that the time is ripe for a pilot-plant attempt at orchard production of at least one hybrid southern pine.

LITERATURE CITED

Bates, C. G. 1928. Tree "seed farms." J. For. 26:969-976.

Chapman, H. H. 1922. A new hybrid pine (Pinus palustris X Pinus taeda). J. For. 20:729-734.

Derr, H.J., and T. W. Melder. 1970. Brown-spot resistance in longleaf pine. For. Sci. 16:204-209.

Kaufman, C. M. 1971. The Southern Forest Tree Improvement Committee, 1951-1971. South. For. Tree Improv. Comm. Publ. #32. 31 p.

Lindquist, B. 1948. Genetics in Swedish forestry practice. Chronica Botanica Co., Waltham, Mass. 173 p.

Mergen, F. 1953. Gum yields in longleaf pine are inherited. Southeast. For. Expt. Sta. Res. Note #29. 2 p.

Mergen, F., and K. B. Pomeroy. 1954. Tree improvement research at the Lake City, Florida, Research Center: A project analysis. Southeast. For. Expt. Sta. Paper 45. 59 p.

Perry, T. O., and C. W. Wang. 1957. Second Progress Report, Cooperative Forest Genetics Research Program. Univ. Fla. School of For. Rep. 4. 28 p.

Schreiner, E. J. 1937. Improvement of forest trees. U.S. Dept. Agr. 1937 Yearb. (p. 1242-1279).

Snyder, E. B., P. C. Wakeley, and O. O. Wells. 1967. Slash pine provenance tests. J. For. 65:414-420.

Sudworth, G. B. 1927. Check list of the forest trees of the United States, their names and ranges. U.S. Dept. Agr. Misc. Circ. 92. 295 p.

Wakeley, P. C. 1935. Artificial reforestation in the Southern Pine Region. U.S. Dept Agr. Tech. Bul. 492. 115 p.

Wakeley, P. C. 1944. Geographic source of loblolly pine seed. J. For. 42:23-32.

Wakeley, P. C. 1954. Planting the southern pines. U.S. Dept. Agr. Agr. Monog. 18. 233 p.

Wakeley, P. C. 1968. Rust susceptibility in longleaf pine associated with brown-spot resistance and early commencement of height growth. For. Sci. 14:323-324.

Wakeley, P. C. 1971. Relation of thirtieth-year to earlier dimensions of southern pines. For. Sci. 17:200-209.

Wakeley, P. C. and T. E. Bercaw. 1965. Loblolly pine provenance test at age 35. J. For. 63:165-174.

Wakeley, P. C., O. O. Wells, and T. E. Campbell. 1966. Mass production of shortleaf X slash pine hybrids by pollinating unbagged female flowers. Joint Proc., 2nd Genet. Workshop SAF, and 7th Lake States For. Tree Improv. Conf. USFS Res. Pap. NC-6. p. 78-79.

Wells, O. O., and P. C. Wakeley. 1966. Geographic variation in survival, growth, and fusiform-rust infection of planted loblolly pine. For. Sci. Monogr. 11. 40 p.

Wells, O. O. and P. C. Wakeley. 1970 a. Variation in longleaf pine from several geographic sources. For. Sci. 16:28-42.

Wells, O. O. and P. C. Wakeley. 1970 b. Variation in shortleaf pine from several geographic sources. For. Sci. 16:415-423