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BREEDING AND GENETICS

Merging of Plant Breeding and Pathology: A History of Cotton Breeding at Auburn

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ABSTRACT

Understanding the focus and history of a breeding program allows fellow researchers to build upon prior knowledge and helps determine the best expertise for specific objectives. To date, the cotton-breeding program at Auburn University has had a series of breeders that have worked directly with a plant pathologist. Homer Tisdale, the program's first breeder, was hired in 1913 with the goal of Fusarium wilt (FOV) resistance, a focus that was destined to become fundamental to the program. With the discovery of a "hot" field in Tallassee, Alabama, the program soon combined cotton variety testing and FOV screening tests. This led to the release of the most iconic variety of the program – Auburn 56 and characterizing of the relationship between root knot nematode and FOV. In 1965, the program shifted to a USDA cotton genetics project, led by R.L. Shepherd, who refined screening techniques and identified multiple sources of root knot nematode resistance. He released 40 cotton breeding lines, the most in the program's history, which ended in 1984 when the USDA lab was moved to Mississippi. In the late 1990's, breeder David Weaver joined a region-wide effort to investigate reniform nematode resistance. The current program, led by Jenny Koebernick, has a large emphasis on disease resistance. In 2019, attention shifted to identifying sources of resistance for the cotton leaf roll dwarf virus, collaborating directly with plant pathologists and entomologists. Overall, the greatest contribution of the program has been the synergy created between breeding and pathology that has helped advance cotton resistance to nematodes, fusarium wilt and bacterial blight.

Since cotton's establishment in the state of Alabama, growers have sought improved varieties in terms of disease and pest resistance to improve yield. To that end, the Alabama Agricultural Experiment Station (AAES) at Auburn, Alabama was created in 1883. With the goal to advance the state's agricultural and forestry industries, the station's objective for cotton improvement focused on disease resistance. With a rich history, this goal has often led to a tight collaboration between the plant breeder and pathologist, and at times, melding the two into one.

Since at least the early 1900s, the station's annual reports have had a particular focus on the root knot nematode and fusarium wilt (FOV) complex, discerning the epidemiology and concluding what currently available cotton lines exhibit resistance. Growers' experience with *Fusarium oxysporum* (Atk.) f. sp. *vasinfectum* Snyder & Hansen, identified and named by Auburn pathologist George Atkinson in 1892, in Alabama has been extensive. In 1895, individuals approached the United States Department of Agriculture (USDA) with pleas for help (Culp 1998). Extensive feeding by the nematode, *Meloidogyne incognita* Kofoid & White, contributes to this organism's infection and spread, linking the two in a disease cycle (Cauquil and Shepherd, 1970; Mai et al., 1987). The discovery of a "hot" bed of this pathogen in a field in Tallassee, Alabama in 1946 eventually led to the area being bought by Auburn University and designated as the Plant Breeding Unit (PBU) by 1951. An ideal location for testing resistance, by 1952 varieties were screened there with origins from across the region. Eventually, this nursery became the center of the breeding and research focus of the USDA's crop genetics lab.

1913 – 1955: The Homer Tisdale era

Figure 1: Homer Tisdale

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Homer Tisdale was hired in 1913 by the Alabama Polytechnic Institute (later changed to Auburn University) and AAES in Auburn to teach and breed cotton, corn, sweet potato, peanuts, and winter legumes. Until 1920, he was jointly employed by the Office of Cotton and Truck Crop Disease where he worked on breeding and distributing FOV resistant varieties of cotton, including known varieties such as Dixie, Dixie-Cook, and Dixie-Triumph (Ware, 1937). Annual reports dating back to 1922 consist of three-year averages of traits such as staple length across three regions of Alabama with the goal of providing growers with information on new varieties. By 1935, a three-year cotton variety study was initiated by the directive of the Division of Cotton & Other Fiber Crops & Diseases, spanning fourteen different locations in ten states. At the same time in 1936, the USDA started allocating funds to cotton improvement programs, and this convinced Tisdale to shift his priorities to focus solely on cotton. With the help of agronomist Jimmy Dick, Tisdale focused on FOV resistance and inheritance studies. Together, the pair released numerous Auburn-numbered varieties, sowing the seeds for the future cotton-breeding program. Many attributed Tisdale and others' selection efforts as the reason cotton could be grown economically in the Southeast (Ware, 1937). Soon, these cotton variety tests results were applicable across the entire region, reaching outside of Alabama. Here, experimental varieties were tested every year, requiring three years before being made public. Results were published annually in the station's reports, comparing agronomic characteristics from fiber quality and staple length to time of maturity against check varieties selected across the region.

With prior experience devoted to cotton breeding and resistance, A.L. Smith transferred to Auburn in 1946 with a focus on the "hot" field at PBU. Together with Tisdale's cooperation, the pair began leading the cotton variety tests and eventually initiated the first FOV screening tests. Soon, every variety entered into the variety tests was being screened for FOV and nematode resistance, allowing for further comparisons in the region. By 1950, the team had priorities for improving fiber strength, wilt resistance inheritance, resistance to root knot nematode, and bacterial blight resistance. By 1952 the FOV screening test became region-wide. In the same year, the most iconic variety from Tisdale's program, and arguably of Auburn's entire history, was released, Auburn 56. With Dick and Tisdale's efforts, it was developed between 1935 and 1946, and revealed its worth under testing at the PBU (Smith, 1964). It became the number one variety grown in the nation due to its increased resistance to FOV and root knot nematode. The program was unable to produce enough seed to keep up with demand, prompting the creation of the Alabama Crop Improvement Foundation Seed company. The program's next decade was dedicated to the improvement of this variety, but Tisdale passed away in 1955 after 42 years of service.

Auburn 56

With over a decade of development, Dick and Tisdale's renowned variety owes its origins to a wilt-resistant Cook selection made near Loachapoka, AL in 1908, a variety line initially bred and coined by McQueen Smith Farming Co. in Prattville, AL. Several additional crosses with Cook varieties and open-pollinated seed derived from a single plant row contributed to a variety that was subsequently developed between 1935 and 1953 (Smith, 1964; Culp, 1998). Upon the Plant Breeding Unit's founding in 1946, this variety proved its worth with its outstanding FOV and nematode resistance. Moreover, in 24 Eastern Regional Cotton Variety Tests from 1960 to 1962, Auburn 56 had the top lint yield of 892 kg ha^{-1} when compared with five other top varieties while remaining comparable in boll weight, fiber strength and micronaire units (Smith, 1964). Additional *Verticillium alboatrum* Reinke & Berth tolerance added value to this variety's worth as a source of genes (Smith, 1964). Auburn 56 went on to be extensively used in germplasm and variety development. In fact, the majority of all future Auburn germplasm lines were developed with some ancestry dating back to Auburn 56 (Table 1). It went on to be used in other successful programs across the region, including germplasm lines produced by the Pee Dee Experiment Station in Florence, SC (Culp, 1998), the Coastal Plain Experiment Station in Tifton, Georgia, and the Delta & Pine Land Co., in Scott, MS (Ramey, 1966).

Table 1. List of cotton breeding material released by the Auburn, AL, cotton breeding program.

Released material	Year	Pedigree	Reference
Cook 144 Auburn	≤ 1930s	Unknown	Tisdale and Dick, 1945
Cook 144-7	≤ 1941	Unknown	Anonymous, 1941
Cook wilt-resistant	≤ 1941	Unknown	Anonymous, 1941
Deltapine wilt-resistant Auburn	≤ 1944	Unknown	Tisdale and Dick, 1945
Auburn 061	≤ 1944	Unknown	Tisdale and Dick, 1945
Cook 144-10	1945	Unknown	Tisdale and Dick, 1946
Auburn 770	1946	Unknown	Tisdale and Dick, 1947
Auburn 108	1946	Unknown	Tisdale and Dick, 1947
Auburn 10168	1946	Unknown	Tisdale and Dick, 1947
Auburn 770-322	1946	Unknown	Tisdale and Smith, 1947
CSS9-48	1948	Unknown	Tisdale and Smith, 1949
CSS9	1948	Unknown	Tisdale and Smith, 1949
CSS11	1948	Unknown	Tisdale and Smith, 1949
CSS-491-2	1949	Plains x Stoneville 20; Plains x Stoneville 20 x Empire	Chapman, 1961
Plains	1949	Stoneville 2B; Clevewilt x Stoneville 2B	Chapman, 1961; Ramey, 1966
Auburn 56	1952	Coker 100 Wilt, Coker 100, Cook 307	Chapman, 1961; Ramey, 1966; Smith, 1964
81	≤ 1953	Unknown	Tisdale and Smith, 1956
Auburn 56-23	≤ 1955	Unknown	Tisdale and Smith, 1956
Auburn 9531-2	≤ 1955	Unknown	Tisdale and Smith, 1956
Auburn 81-2	≤ 1955	Unknown	Tisdale and Smith, 1956
Plains S.L.	≤ 1955	Unknown	Tisdale and Smith, 1956
492	1956	Unknown	Smith and Chapman, 1957
543 (A1517 x E-3)	1957	Unknown	Chapman and Smith, 1958; Chapman, 1961
H-257-23	1957	Unknown	Chapman and Smith, 1958
H-257-33	1957	Unknown	Chapman and Smith, 1958
491-2	1957	Unknown	Chapman and Smith, 1958
257-97	1958	Unknown	Chapman and Smith, 1959
257-98	1958	Unknown	Chapman and Smith, 1959
541	1958	Unknown	Chapman and Smith, 1959
543	1958	Unknown	Chapman and Smith, 1959
257-58-3	1959	Unknown	Chapman, 1960
CSS (G)	1959	Unknown	Chapman, 1960
A-56-B	1961	Unknown	Chapman, 1962
5914-BBR-A56	1961	Unknown	Chapman, 1962
Auburn M	1962	A selection of Auburn 56	Johnson, 1973; Ramey, 1966; Chapman, 1963
Auburn 56-SL	1962	Unknown	Chapman, 1963
Auburn 56-B	1962	Unknown	Chapman, 1963
4912-BBR	1962	Unknown	Chapman, 1963
4912 SL	1962	Unknown	Chapman, 1963
Auburn BR1	1971	Auburn 56, K4E	Kappelman, 1972
Auburn BR2	1971	Auburn 56, K4E	Kappelman, 1972
A6-688-BE	1972	Unknown	Johnson, 1973
A6-741-AE	1972	Unknown	Johnson, 1973
79N	Unknown	Tamcot SP 21	Kappelman, 1983b
Auburn 623 RNR	1974	Clevewilt 6-3-5, Mexico Wild	Shepherd, 1974
Auburn 566 RNR	1979	Coker 201 , Auburn 623 RNR	Shepherd, 1979
Auburn 612 RNR	1979	Auburn 56, Auburn 623 RNR	Shepherd, 1979
Auburn 634 RNR	1979	Auburn 56, Auburn 623 RNR	Shepherd, 1979

Table 1. (continued).

Released material	Year	Pedigree	Reference
Auburn 72 OK-4	1982	K4E, Auburn okra-leaf, Hopicala	Kappelman, 1983a
Auburn 72 OK-8	1982	Auburn 56, K4E, BC4, Auburn okra-leaf	Kappelman, 1983a
Auburn 72 OK-14	1982	Auburn 56, K4E, BC4, Auburn okra-leaf	Kappelman, 1983a
Auburn 73B-1	1982	K4E, Auburn 56-5, 79N	Kappelman, 1983b
Auburn 73B-2	1982	K4E, Auburn 56-5, 79N	Kappelman, 1983b
Auburn 73B-5	1982	K4E, Auburn 56-5, 79N	Kappelman, 1983b
Auburn 73B-12	1982	K4E, Auburn 56-5, 79N	Kappelman, 1983b
Aub Ne 213	1982	Stoneville 213 x nectariless	Sheperd, 1982a; Shepherd, 1987
Aub Ne-16	1982	Deltapine 16 x nectariless	Shepherd, 1982a
Aub Ne-56	1982	Auburn 56 x nectariless	Shepherd, 1982a
Aub Ne-149	1982	Triple Hybrid 149 x nectariless	Shepherd, 1982a
Aub Ne-165	1982	Pee Dee 2165 x nectariless	Shepherd, 1982a
Aub Ne-201	1982	Coker 201 x nectariless	Shepherd, 1982a
Aub Ne-277	1982	Delcott 277 x nectariless	Shepherd, 1982a
Aub Ne-310	1982	Coker 310 x nectariless	Shepherd, 1982a
Aub Fg-16	1982	Deltapine 16 x frego bract	Shepherd, 1982b
Aub Fg-56	1982	Auburn 56 x frego bract	Shepherd, 1982b
Aub Fg-149	1982	Triple Hybrid 149 x frego bract	Shepherd, 1982b
Aub Fg-165	1982	Pee Dee 2165 x frego bract	Shepherd, 1982b
Aub Fg-201	1982	Coker 201 x frego bract	Shepherd, 1982b
Aub Fg-213	1982	Stoneville 213 x frego bract	Shepherd, 1982b
Aub Fg-277	1982	Delcott 277 x frego bract	Shepherd, 1982b
Aub Fg-310	1982	Coker 310 x frego bract	Shepherd, 1982b
Auburn BR Ok4	1986	Auburn BR1, Auburn 56	Shepherd and Kappelman, 1987a
Auburn BR Ok5	1986	Auburn BR1, Auburn 56	Shepherd and Kappelman, 1987a
Auburn BR Ok6	1986	Auburn BR1, Auburn 56	Shepherd and Kappelman, 1987a
Auburn BR Ok7	1986	Auburn BR1, Auburn 56	Shepherd and Kappelman, 1987a
Aub BR3	1986	Deltapine 16, Auburn 56, 79N	Shepherd and Kappelman, 1987b
Aub BR4	1986	Deltapine 16, Auburn 56, 79N, Pee Dee 0109	Shepherd and Kappelman, 1987b
Aub BR5	1986	Deltapine 16, Auburn 56, 79N, Dixie King II	Shepherd and Kappelman, 1987b
Aub BR6	1986	Deltapine 16, Auburn 56, 79N, Deltapine 26	Shepherd and Kappelman, 1987b
Aub BR7	1986	Deltapine 16, Auburn 56, 79N, McNair 511	Shepherd and Kappelman, 1987b
Aub BR8	1986	Deltapine 16, Auburn 56, 79N, Coker 310	Shepherd and Kappelman, 1987b
Aub BR9	1986	Deltapine 16, Auburn 56, 79N, Acala SJ-2	Shepherd and Kappelman, 1987b
Aub BR10	1986	Deltapine 16, Auburn 56, 79N, Delcot 277	Shepherd and Kappelman, 1987b
Aub 82 RNR Ne	1986	Auburn 634 RNR, Aub Ne 213	Shepherd, 1987
Aub 244 RNR	1986	Aub 634 RNR, Stoneville 213	Shepherd, 1987
Aub 299 RNR	1986	Aub 634 RNR, Stoneville 213	Shepherd, 1987
Hybrids			
Hybrid 9531	≤ 1944	Unknown	Tisdale and Dick, 1945
Hybrid 1282	1948	Unknown	Tisdale and Smith, 1949
Hybrid 12206	1948	Unknown	Tisdale and Smith, 1949
Hybrid 81-16	≤ 1950	Unknown	Tisdale and Smith, 1953
Hyb. P X 56	≤ 1952	Unknown	Tisdale and Smith, 1953
Hybrid 56-24	≤ 1952	Unknown	Tisdale and Smith, 1953
Hybrid 257-202	≤ 1952	Unknown	Tisdale and Smith, 1953
Hybrid 9531-601	≤ 1952	Unknown	Tisdale and Smith, 1953

1955 – 1964: The A.L. Smith era

After Tisdale's passing, Smith, now employed by both the USDA and as an adjunct faculty member at Auburn, took over the cotton breeding and research program focusing on a range of FOV research including soil fumigation, fertility requirements, and resistance inheritance. He was instrumental in the development of the FOV screening test in 1946 which eventually led to the identification and understanding of the FOV-root knot nematode complex. This provided the knowledge for breeding nematode resistance and through it, led to FOV resistance as well.

Aiding Smith after Tisdale's passing was L.J. Chapman, an assistant in agronomy who worked with Smith to conduct the cotton variety tests and write annual reports. During this collaboration, several Auburn hybrids were developed and released between 1957 and 1963 (Table 1), expanding a program that was growing increasingly distinguished. In a 1963 Auburn press release, Smith is noted for producing a hairless cotton leaf. By identifying a variety with only a few leaf hairs, he was able to follow a backcross procedure to remove the hair. To illustrate this, he described finding 24,295 hairs on the experimental strain "All-in-one" and a range of 521 to 523 on "DeltaSmooth 723". He later incorporated this trait into Auburn 56 and developed versions consisting of smoothleaf, nectarless, glandless, high lint percent and high fiber quality. Smith's tenure of the breeding program came to an end in 1964 when he passed away on the job from a heart attack.

Eventually, Jimmy Dick left to work at Coker's Pedigreed Seed Company, later transferring to become the Director of the Cotton Breeding Program at the Delta Branch Experiment Station in Stoneville, Mississippi. Earl B. Minton took his place and served as the research plant pathologist at the USDA from 1952 to 1964. He continued the collaboration with Tisdale, and then Smith, and finally received his PhD at Auburn in 1964. He went on to publish several papers investigating the FOV-root knot nematode complex. Together with his brother and USDA assistant nematologist, Norman Minton, they concluded that FOV was only a problem when coupled with the damaging actions of nematode feeding and wounding (Minton and Minton, 1966).

1964-1990 – The Shepherd-Kappelman era

Raymond Shepherd began his PhD at Auburn University in 1960 under the guidance of a forage breeder, Wiley C. Johnson, Jr., focusing on screening and breeding for resistance to the root knot nematode in white clover. By 1965 he had graduated and was appointed the leader of the USDA Genetics and Breeding Investigations Project. Shepherd applied his dissertation work to develop and refine screening techniques that were fundamental in numerous crops as well as cotton. He cultivated breeding stocks from wild *G. barbadense* that, at the time, had much higher resistance to root knot nematode than previously available varieties. His efforts demonstrated that progress could be made in selecting for resistance and laid the foundation for his future career.

Following a similar path of its predecessors, the USDA project at Auburn consisted of both a plant breeder, Shepherd, and a pathologist, A.J. Kappelman. They both contributed to several released Auburn varieties – including Auburn BR1 and Auburn BR2 – that exhibited high bacterial blight resistance not exhibited by Auburn 56, as well as improved yield and fiber quality (Kappelman, 1972).

Shepherd's host-plant resistance breeding program team released the largest number of cotton germplasm breeding stocks in the history of the program. In 1979 he released three lines with higher resistance to the root knot nematode-FOV complex than anything else at the time: Auburn 566RNR, Auburn 612RNR, and Auburn 634RNR (Shepherd, 1979a). Further increasing its worth, Auburn 634RNR was specifically screened against 35 isolates of root knot nematode in four races from ten countries, finding a world-wide value for this line (Shepherd, 1981). Eight frego bract lines and eight nectarless lines were released in 1981, particular traits aimed at resisting certain diseases and insects (Shepherd, 1982a; Shepherd, 1982b). An additional eight germplasm lines and four more okra-leaf lines resistant to bacterial blight were released in 1986 (Shepherd and Kappelman, 1987a; Shepherd and Kappelman, 1987b). Okra leaf is a characteristic that is believed to reduce boll rot by opening up the plant canopy, increasing air flow, and confers resistance to white fly and pink bollworm, as well as contributing to an earlier maturation time (Andries et al. 1969). Likewise, frego bract is a trait believed to support insect management by aiding in accumulation of insecticides toxic to pests (Parrott et al. 1973). All of these provided material for other breeding programs to use and build upon.

Shepherd successfully incorporated different sources of resistant upland germplasms that produced an additive effect of higher levels of resistance.

Numerous researchers had attempted this since between 1895 and 1965 with failing results. Furthermore, he and colleagues demonstrated that root knot nematode exacerbated the severity of cotton seedling diseases (Cauquil and Shepherd, 1970). His program also determined that selection for resistance against root knot nematode was better characterized by measuring nematode egg production on affected plants than measuring root galling alone (Shepherd, 1978; Shepherd, 1979b).

In a report detailing the overall progress breeders have made towards FOV resistant germplasm, Kappelman (1980) noted the challenges of doing so when genes tied to resistance may also be linked with less than desired agronomic and fiber characteristics. The breeding program at Auburn was brought to a halt in 1984 when the USDA lab was moved to Mississippi State, MS. However, they continued to coordinate and release additional cotton germplasms with potential disease and insect resistance. Shepherd earned the Joint Cotton Breeding Policy Committee's Cotton Genetics Award in 1986 and eventually retired from the USDA in 1990.

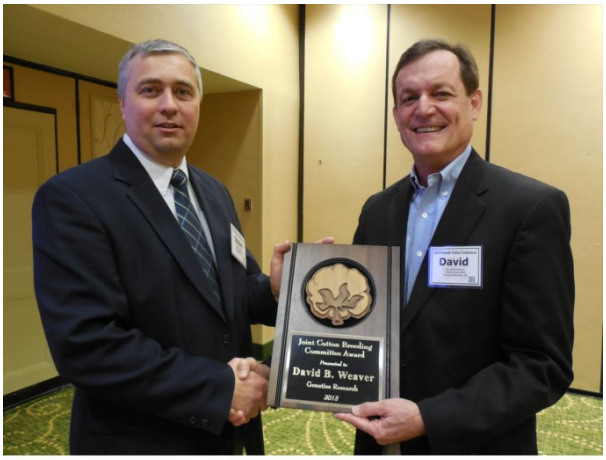
COTTON GENETICS AWARD: C.W. Manning (l.) cotton breeder with Stoneville Pedigreed Seed Company, Stoneville, MS., presents plaque for 1987 Cotton Genetics Award recipient Dr. Raymond Shepherd, an agronomist at the USDA-ARS Crop Science Research Laboratory, Starkville, MS.

Figure 2: Dr. Raymond Shepherd (right) receiving the cotton genetics award.

1990 – 2016

In 1981, David Weaver was hired at Auburn University as a soybean breeder back when acreage of soybean was at its peak of around 2 million acres (NASS, 2020). By the late 1990's, the support for soybean commodities had dwindled and Weaver was approached by Cotton Incorporated to consider his expertise for cotton breeding. Breeding for any row crop is a major task and taking on an additional one was quite a challenge. However, Weaver did have a MS in cotton breeding and was willing to accept the task. The first step was determining which objectives and practices could be applicable across both crops. His soybean program had a large emphasis in disease and nematode resistance, so he saw that as an opportunity to expand into cotton. Weaver initially concentrated on cultivar development and investigating breeding strategies before shifting focus to reniform nematode resistance.

He paired with Kathy Lawrence, Auburn research nematologist, to study the rising incidence of cotton yield loss to reniform nematodes, *Rotylenchulus reniformis* Linford & Oliveira. A large portion of the cotton germplasm collection was screened with no real resistance being found (Weaver et al., 2007). As a concentrated effort across multiple public programs, including the USDA, resistance was found in *G. longicalyx* J.B. Hutch & B.J.S. Lee and *G. barbadense* L. (Robinson et al., 2008). Weaver was awarded the Joint Cotton Breeding Policy Committee's Cotton Genetics Award in 2015 and retired in 2016.



Dr. David B. Weaver, a cotton breeder who has dedicated his career conducting plant breeding research and educating generations of undergraduate and graduate students at Auburn University, is the recipient of the 2015 Cotton Genetics Research Award.

Figure 3: David Weaver (right) receiving the 2015 Cotton Genetics Research Award.

In 2016, Jenny Koebernick was hired as the cotton and soybean breeder for Auburn. Her background is in cotton breeding and like Weaver, aligns the program to be applicable across both crops when able. Koebernick's goals include continuation of the historically close association of plant breeding with the pathology department, including taking over the PBU FOV nursery. In 2018, the polerovirus Cotton Leaf Roll Dwarf Virus (CLRDV) transmitted by the cotton aphid (*aphis gossypii*) was discovered in Alabama and will be a major objective for Koe-

bernick's breeding program moving forward. She is instrumental in helping form a team of Auburn research scientists as well as USDA and other land grant universities to address the virus from a multi-disciplinary approach.

In conclusion, Auburn has had a rich history of breeding for disease resistance with major contributions in FOV, root knot nematode, and bacterial blight. Moving forward the program continues to collaborate closely with pathologists and now entomologists as searching for both CLRDV and cotton aphid resistance will be primary objectives.

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