Breeding for Flue-cured Tobacco (Nicotiana tabacum L.) Foliar Pest and Disease Resistance in Zimbabwe: A Review

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How to cite this article: Shava, J. G., Richardson-Kageler, S., Dari, S., Magama, F., & Rukuni, D. (2019). Breeding for Flue-cured Tobacco (Nicotiana tabacum L.) Foliar Pest and Disease Resistance in Zimbabwe: A Review. Agri Revs, 40(2):104-112.

Source of support: Nil
Conflict of interest: None
Submitted: 19/02/2019 Accepted: 06/04/2019

ABSTRACT

Since its introduction to Zimbabwean farmers in the early 20th century, flue-cured tobacco has grown to become one of the most profitable field crops to cultivate in the country. However, pests and diseases have been reported as some of the major contributors to yield and quality loss in the business of tobacco farming in Zimbabwe and across the world reducing the profitability of the tobacco business. This has resulted in large sums of financial resources being invested in research aimed at controlling pests and diseases in different crops. In Zimbabwe, millions of liters of pesticides have been pumped into the environment in an effort to control pests and diseases in flue-cured tobacco fields. There have also been efforts to incorporate inherent pest and disease resistance in the varieties of flue-cured tobacco developed in the country since the early 1940s. This paper is a review of the breeding efforts to incorporate pest and disease resistance in the elite flue-cured tobacco germplasm used to develop some of the popular varieties in Zimbabwe.

Keywords: Alternaria alternata, Black shank, Budworm, Flue-cured tobacco, Foliar diseases, Tobacco mosaic virus.

Agricultural Reviews (2019)

INTRODUCTION

The early tobacco farming industry in Zimbabwe was threatened by many challenges. One challenge of great importance involved diseases attacking the introduced and newly developed early varieties (Mbanga, 1991). Most of the early varieties had no resistance to any of the locally occurring diseases of tobacco. This scenario posed a major challenge to the successful cultivation of the crop by the pioneer farmers. The major diseases affecting the crop during these early years included, Tobacco mosaic virus (TMV), root-knot nematode [Meloidogyne javanica (Treub) Chitwood], Alternaria leaf spot [Alternaria alternata (Fr:Fr Keissl)], white mold [Sclerotinia sclerotiorum (Lib)de Bary], Angular leaf spot [Cercospora nicotianae (Ellis and Everh)], wildfire (Pseudomonas syringae pv. tabaci (Wolf and Foster) Young et al.) and Black shank (Phytophthora parasitica Dastur var. nicotianae (Breda de Haan) Tucker). TMV caused the greatest threat to the early inexperienced farmers who knew less about hygiene in the fields. As a result, as soon as the Trelawney Research Station in Zimbabwe was opened in the 1930s, work on developing TMV resistant varieties started ahead of research in resistance to other pests and diseases. This article is a review of all the work done in breeding for disease resistance in Zimbabwe since the inception of formal research in the crop. It is hoped that the review will extract some valuable insights in the possible sources of resistance to pests and diseases for use in current breeding efforts as well as give warnings to current breeders of past attempts in breeding efforts that yielded no meaningful gains for them to avoid them.

BREEDING FOR TOBACCO MOSAIC VIRUS (TMV) RESISTANCE

The first deliberate crosses aimed at developing segregating lines from which to select improved flue-cured tobacco lines were made during the 1940–1941 farming season in Trelawney (Tobacco Research Board, 1950). This flue-cured tobacco breeding effort in Zimbabwe was aimed at developing varieties with root-knot nematode and TMV (Fig. 1) resistance together with adaptation to local conditions (Tobacco Research Board, 1950). A batch of 42 lines coded M lines and divided into two groups depending on the original source of resistance to TMV were tested at Trelawney Research Station by Bolton and Stephen during the 1949–1950 season. The first group of M lines consisted of lines M1 to M6 whose source of TMV resistance was ‘Ambalema’, a Colombian variety of N. tabacum which has immunity to TMV death of the leaf tissue at the point of infection by the TMV. This indicated by a hypersensitive reaction that results in the...
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The Ambalema resistance to TMV was found to be controlled by two recessive genes in tobacco. Early breeding programs for resistance to TMV relied on the two sources of resistance namely N. glutinosa and ‘Ambalema’ through crossing variety introductions and locally developed lines. However, with time, resistance to TMV from Ambalema was dropped in preference to the dominant gene controlled TMV resistance from N. glutinosa.

From the TMV breeding program based on N. glutinosa, selections found acceptable for type coded M17 and M12 were evaluated in an agronomic trial with the hope of releasing them as commercial varieties later in the program. It was found that strains coded 7, 19, and 6 from the original M lines had resistance to tobacco mosaic virus (TMV). However, reports from a study by Chaplin (1970) suggested a negative correlation between TMV resistance and yield and quality in flue-cured tobacco and discouraged the Zimbabwean breeders. It had already been determined that hybrids were the only flue-cured tobaccos that could carry resistance to tobacco mosaic virus resistance without lowering the quality of the cured leaf (Raeber and Smeeton, 1971a). This meant that the results of this early breeding program for resistance to TMV were only going to be used in a hybrid with only one of the parents carrying the resistance gene. According to Raeber and Smeeton (1971c), TMV resistance from N. glutinosa is associated with unsatisfactory mottled upper leaves in the lines that possess it.

Lines with both TMV and wildfire resistance were tested in field evaluation trials during the 1970-71 season for the first time. The line WF14-30-5 which had TMV resistance from N. glutinosa and wildfire resistance from N. longiflora Cavanilles was evaluated with line WF2 which only had wildfire resistance. This trial also included Alternaria leaf spot resistant lines, A1 (22N) and A2 (22B) and the root-knot nematode resistant lines RK1 and RK2 from the root-knot nematode resistance breeding program involving N. tabacum (Raeber and Smeeton, 1971d). Because the line with TMV and wildfire resistance was found to be acceptable for nicotine content it was concluded that it was possible to develop flue-cured tobacco varieties carrying TMV resistance from N. glutinosa and wildfire resistance from N. longiflora with a good quality unlike what had been reported previously. A cross (‘Meadows Giant’ × ‘Burley 21’) × ‘Kutsaga 51’ was done and lines with resistance to both wildfire and TMV selected and evaluated for agronomic performance. TMV resistance in elite flue-cured tobacco varieties in Zimbabwe came from N. glutinosa through ‘Meadows Giant’ while wildfire resistance in the same elite flue-cured tobacco varieties came from N. longiflora through the burley variety called ‘Burley 21’ (Raeber and Smeeton, 1971a).

Two notable mutant lines with resistance to TMV and wildfire were isolated from the variety ‘Kutsaga Mammoth’ and were named ‘Kutsaga Mammoth B1’ and ‘Kutsaga Mammoth B2’ (Raeber and Smeeton, 1971b). These lines were, however, dropped because either it was difficult to make them pure breeding or that it was difficult to handle them for commercial production (Raeber and Smeeton, 1971b). White mold resistance was added to the TMV and wildfire resistant lines through double haploid breeding which gave birth to the lines DET10, AE48-18, and AE48-17 which were first evaluated in a multi-location trial during the 1976-77 season.

Because TMV was becoming a serious challenge in the tobacco farming sector due to the entry of many smallholder farmers, it was resolved to incorporate TMV resistance into all the parental lines during the late 1980s. The TMV resistance genes came from K 110 which was crossed to the lines KE1, RW, K326, STNCB, BAZ, and WZ. Another source of TMV was
AW3R which donated TMV resistance to the lines XM26, XS, XZ, ZAS, and ONC. All the TMV resistant varieties currently grown in Zimbabwe which include the ‘K RK26R’, ‘K RK72’, ‘K RK29’ and the ‘K RK70s’, originate from this program.

**Breeding for Alternaria (Alternaria alternata) and Frog Eye Leaf Spot (Cercospora nicotianae) Resistance**

Experiments to screen existing locally developed lines and introductions for Alternaria leaf spot (Alternaria alternata) and frog-eye leaf spot (Cercospora nicotianae) started during 1951-52 (Gildenhuys and Daulton, 1950). No material was found to possess resistance to these diseases during these early stages of screening (Bolton and Stephen, 1952). Early experimentation with *N. tabacum* and *N. rustica* for resistance to frog eye led these researchers to conclude that *N. tabacum* and *N. rustica* accessions available at the time in the country had resistance to the disease and that only *N. debneyi* Domin, *N. digluta*, and *N. repanda* Willdenow ex Lehmann had resistance under seedbed conditions.

There had been earlier reports claiming that ‘Beinhart 1000-1’, a Japanese variety, had Alternaria resistance. Experimental work found that ‘Beinhart 1000-1’ carried a partially dominant single factor for Alternaria resistance (Raebert and Smeeton, 1974b). Alternaria leaf spot resistance in ‘Beinhart 1000-1’ was found to be highly inheritable with a large proportion of the genetic variation being additive and hence fixable (Raebert and Smeeton, 1971d).

During the 1964-65 season, the line ‘Beinhart 1000-1’ possessing resistance to Alternaria leaf spot was tested for resistance to the disease under Zimbabwean conditions in a trial that included ‘Florida 22’ (which had been classified as tolerant to Alternaria in the USA), ‘K51’ (V340), the highly Alternaria leaf spot susceptible ‘Yellow Mammoth’, and the F1 cross of ‘Beinhart 1000-1’ × ‘K51’. The results of the study showed that the F1 involving ‘Beinhart 1000-1’ had intermediate resistance to Alternaria leaf spot suggesting additive gene action for Alternaria leaf spot resistance. It was also ascertained that the F1 had broad leaf venation and the “upright” habit of leaf insertion characteristics of ‘Beinhart 1000-1’ meaning that these traits were dominant (Raebert and Schweppenhauser, 1965b).

At this point it was concluded that “a combination of resistance from ‘Beinhart 1000-1’, Alternaria tolerance from ‘Florida 22’ acting as a buffer and the yield and quality characteristics from ‘K51’ should constitute the major breeding objective of a resistant variety suitable for Zimbabwean conditions” (Raebert and Smeeton, 1970). This assertion guided flue-cured tobacco variety development in Zimbabwe throughout the coming five decades and it appears as if it will shape the future of the variety development programs of the country. Breeding efforts for resistance to Alternaria leaf spot at the time continued and during the 1969-70 season, Alternaria leaf spot resistant lines identified as Alternaria line 123 and Alternaria line 23 were tested under “variety trials” for the first time together with ‘Kutsaga Mammoth’ (Raebert and Smeeton, 1970). Other promising lines coded 10, 56, 72, and 80 were identified but 56 and 72 had the best quality.

The first lines possessing Alternaria leaf spot resistance to be evaluated for agronomic performance were 22N and 22B in the 1970-71 seasons. Line 22B showed acceptable qualities except that it had lower nicotine content. It was concluded that the line would be considered for commercial release if low nicotine broadleaf types of tobacco became acceptable to the market (Raebert and Smeeton, 1971d). Line 22N needed further improvement for many traits and was shelved for further improvement. *Nicotiana tormentosiformis* Goodspeed which had also been thought to possess Alternaria leaf spot resistance was screened for resistance to the disease and was found not to possess any resistance.

A triple cross (‘Beinhart 1000-1’ × ‘Florida 22’) × ‘Kutsaga 51’ was constituted and from the segregants of this cross, line A56N-1 was found promising for resistance to Alternaria leaf spot and other quality traits (Raebert and Smeeton, 1973a). A56N-1 is later flowering than the then-popular variety ‘Kutsaga 51’ (Raebert and Smeeton, 1973b). Its resistance derived from ‘Beinhart 1000-1’ had the best Alternaria resistance and can be used as a source of resistance to the disease in future breeding programs. Future flue-cured tobacco breeding programs in Zimbabwe should consider using this line as a source of Alternaria leaf spot resistance. In an effort to confer multiple disease resistance into flue-cured tobacco lines, a cross DETW5 × 22S2–48 was made and resultant lines coded AW were developed for further evaluations. This is most likely the cross from which the high Alternaria leaf spot resistant lines, AW6S and AW3R, currently in use in Zimbabwe originated.

**Breeding for White Mold (Sclerotinia sclerotiorum) Resistance**

The same 1952-53 season saw the launch of a breeding program to develop flue-cured tobacco varieties with resistance to a fungal foliar disease, white mold (S. sclerotiorum). The studies showed that white mold resistance in the available flue-cured tobacco germplasm was simply inherited. Interspecific hybrids including crosses of *N. tabacum* crossed to *N. sylvestris* Spaggazzini and Comes, *Nicotiana digluta*, N. longiflora, and N. glauca Graham were constituted and these crosses suggested quantitative white mold resistance in the species evaluated (Stephen, 1953).

A backcross breeding programme involving H76 and a selection from the then recently locally selected line from the original American Hicks variety called ‘Hicks 148’; and another breeding scheme involving a selection from another exotic variety ‘White Gold’, called ‘White Gold 225’ and H76, with H76 as the recurrent white mold resistant parent, were initiated and gave some white mold resistant lines. The line H76 is a white mold resistant line in a BC$_3$S$_2$ stage made in Taiwan between a Japanese variety ‘Kuofan’ and another
American variety Hicks as the recurrent parent. During the 1964-65 season, Raeber and Schweppenhauser (1965a) tested 365 lines with ‘Kuofan’ white mold resistance and 3 lines (WK11, WK 35, WK39) with \( N. \text{digluta} \) white mold resistance.

\( N. \text{digluta} \) white mold resistance is known for its hypersensitive reactions at the point of infection. The Japanese variety ‘Kuofan’ has two recessive loci for white mold resistance (Raeber et al., 1968). All the tested lines had been lastly crossed to White Gold to improve their quality after four generations of crossing them to ‘Hicks’. The ‘Kuofan’ lines had no undesirable genetic factors for yield and quality and six of these lines were recommended for multi-location evaluation. The \( N. \text{digluta} \) lines were discarded on the basis of poor quality. Selections 145 and 296 of the 395 lines tested during the 1964-65 season were named ‘Kutsaga E1’ and ‘Kutsaga E2’ respectively (Raeber et al., 1968). ‘Kutsaga E1’ is an orange cured leaf style flue-cured tobacco standard currently in 2017 in Zimbabwe.

‘American 287’ (V422) a Russian variety from the Tobacco Research Station of Krasnoder, was reported by Ternosky in 1966 to carry a dominant gene for “immunity” to TMV and white mold from \( N. \text{glutinosa} \) (Raeber and Smeeton, 1973c). Tests at Kutsaga in Zimbabwe showed that the line produced pronounced hypersensitivity lesions under favorable white mold infection conditions in the greenhouse but not in the fields (Raeber and Smeeton, 1973d). ‘Kutsaga 51’ was a very popular variety with growers during the 1960s when it was put on open release. Its weakness was that it was susceptible to white mold. Work to incorporate white mold resistance originally from \( N. \text{glutinosa} \) through ‘American 287’ into this variety began and a selection coded 92-58-1a-6 was found to be acceptable and similar to ‘K51’. This line was released as a commercial variety named ‘Kutsaga 51E’ in 1974 (Raeber and Smeeton, 1974a).

Further studies on white mold resistance in tobacco showed that the line TB22 (V629) has white mold resistance from \( N. \text{tomentosiformis} \) while the variety ‘Hicks’ (VS10) has resistance to white mold from \( N. \text{glutinosa} \). It was, however, shown that resistance from these two tobacco species is the same single dominant resistance gene after close analysis (Raeber and Smeeton, 1974b).

**Breeding for Angular leaf spot (Cercospora nicotianae) Resistance**

Breeding for Angular leaf spot (\( C. \text{nicotianae} \)) (Fig. 2) in flue-cured tobacco started during the late 1950s when some strains of \( N. \text{tabacum} \), and \( N. \text{rustica} \) showed resistance to the disease during screening tests. Other wild relatives of \( N. \text{tabacum} \) which showed resistance to the disease during these early tests were \( N. \text{alata} \) Link and Otto, \( N. \text{arentsii} \) Goodspeed, \( N. \text{occidentalis} \) Wheeler, \( N. \text{syvlestris} \) Spagazzini & Comes, \( N. \text{digluta} \), \( N. \text{repanda} \) Wildenow ex Lehmann, \( N. \text{plumbaginifolia} \) Viviani, \( N. \text{trigonophylla} \) Dunal, \( N. \text{bigelovii} \) (Torrey)Watson, \( N. \text{nightiana} \) Goodspeed, \( N. \text{rotundifolia} \) Lindley and \( N. \text{nudicaulis} \) Watson (Gildenhuys and Stephen, 1957).

Advanced wildfire resistant lines coded TW lines which came from the crosses involving ‘Meadows Giant’ × ‘K51’ and ‘Burley 21’ were also tested for Angular leaf spot resistance and showed a wide variation during the 1974–1975 season. One of these lines coded TW441 was crossed to ‘K51E’ and used to make a white mold and wildfire resistant dihaploid lines called DETW lines from the F1 cross. The lines were screened for Angular leaf spot resistance together with other lines from different programs. The screening program showed that ‘Meadows Giant’, AR63-1, and ‘Kutsaga ME’ had better resistance to Angular leaf spot than all the other lines (Raeber and Smeeton, 1975). The line coded \( S_4 \) WZ24-3.
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Breeding for wildfire (Pseudomonas syringae pv. Tabaci) resistance

Early tests for resistance to wildfire (Pseudomonas syringae pv. tabaci) among the available cultivars and lines indicated that 'Virginia Gold', 'Yellow Mammoth', and '1-5' were the least susceptible to the disease. In further efforts to incorporate for resistance to wildfire in flue-cured tobacco, locally bred 'Burley 21', 'Meadows Giant', 'Virginia Gold', and 'Delcrest' were evaluated for resistance to the disease. This study showed that Burley 21 was the practical source of wildfire resistance since its resistance to the disease showed additive gene action (Raebel and Schweppenhauser, 1964b). 'Burley 21' wildfire resistance came from a wild species Nicotiana longiflora by introgression. It was also proposed that higher levels of tolerance to wildfire could be incorporated in the resistant selections to act as a buffer against possible emergence of new forms of the pathogen capable of overcoming the 'Burley 21' based resistance. It was decided that further breeding efforts for resistance to wildfire in Zimbabwe were to be based on the double cross ('Meadows Giant' × 'Burley 21') × ('Virginia Gold' × 'Burley 21') (Raebel and Schweppenhauser, 1964a). Resistance to wildfire present in the current elite flue-cured tobacco in Zimbabwe emanated for this cross decided by Raebel and Schweppenhauser in 1964. Later on, in a burley breeding program, Raebel and Smeeton (1970) reported linkage between the genes controlling wildfire resistance and those controlling TMV resistance.

The line STNCB2-28 which had shown excellent resistance to root-knot nematode lacked wildfire resistance, and a program to incorporate wildfire resistance to the line was initiated. Lyle (1993) developed the RW lines in a program aimed at incorporating wildfire resistance into STNCB2-28 and the RW lines are currently used in breeding programs of flue-cured tobacco at Kutsaga Research Station in Zimbabwe.

Breeding for Granville wilt (Ralstonia solanacearum) resistance

Local selections and some introductions were tested for resistance to Granville wilt during the 1960s. Studies carried out in the 1965–1966 season with many selections showed that lines G70 and G77 were promising for resistance to Granville wilt (Raebel and Schweppenhauser, 1966). Consequently, the future breeding efforts on breeding for resistance to Granville wilt included the line G70 since it was not prone to producing “sponge” tobacco in addition to disease resistance (Raebel and Schweppenhauser, 1964b). Tests carried out during the 1984 season showed that the line STNCB2-45-16-14 has excellent Granville wilt resistance just like NC89, 'Speight G28', and 'Coker 48' (Raebel and Smeeton, 1984). This line is a sister line to STNCB2-28 which is known for its resistance to root-knot nematodes.

Further breeding efforts for resistance to Granville wilt led to the development of the XCRN lines which sought to incorporate Black Shank and Granville wilt resistance in flue-cured tobacco during the early 1990s. The other lines developed during the 1990s period for Granville wilt resistance were PD, SC, and XAG lines. XAG lines were developed to combine the root-knot nematode, Angular leaf spot, Alternaria leaf spot and monogenic Black shank resistance of XM lines with the high bacterial wilt resistance and polygenic black shank (0 and 1) resistance of the South African variety LK 30/40/60 (Du Toit et al., 1999).

Breeding for resistance to blue mold (Peronospora tabacina d. B. Adam)

Although no cases of blue mold (P. tabacina) had been reported in the country, the early tobacco breeders decided to breed varieties resistant to the disease which is occasionally prevalent in the United States of America as a precaution in case the disease occurs in Zimbabwe. During the 1962–1963 season, 49 Australian lines, a line called Bel 61-10 from the USA and 'Hicks' were screened for blue mold resistance by Raebel and Schweppenhauser and they discovered that some Australian lines had blue mold resistance (Raebel and Schweppenhauser, 1963). This work, however, did not continue to the release of a blue mold resistant variety locally. In the event that blue mold becomes a threat to tobacco farming in Zimbabwe, screening can be started with the remnant seed of lines used by Raebel and Schweppenhauser in 1963 (Raebel and Schweppenhauser, 1963).

Breeding for bushy top and rosette virus in tobacco

The program to breed for resistance to bushy top (Fig. 3) and rosette virus in Zimbabwe started as a greenhouse experiment screening local lines and introductions for resistance to these two viral diseases (Raebel and Schweppenhauser, 1965a). These lines included a German variety called 'Virgin A Mutante' (VAM), the original Hicks (V393) from Japan, a local selection from 'Hicks' (V393) called 'Hicks 148', 'SCR', 'Robusta', and 'Vinica'. Further tests incorporating wild species of tobacco were conducted and four selections from varieties, 'Ungarischer Riese', 'Molovata', 'Fodya', and 'Paesana' showed tolerance to both bushy top and rosette viruses (Raebel and Schweppenhauser, 1965b).
Work to improve the local tobacco germplasm for resistance to the two diseases was discontinued until the late 2000s when it was revived. However, today there is still no variety with resistance to either Bushytop or Rossette virus in Zimbabwe.

Breeding for Potato Virus Y (PVY) and Necrotic Virus Y (NVY) Systems

The realization that PVY and NVY were potentially devastating viral diseases threatening the success of the new tobacco industry in Zimbabwe started quite early prompting the early breeders to explore the potential of developing varieties resistant to these diseases. Breeding for PVY and NVY resistance in flue-cured tobacco in Zimbabwe started during the 1964-65 season with the evaluation for resistance to the two viral diseases on Virgin-A-Mutante (V391) and N. sylvestris (W22). ‘VAM’ is an x-ray induced mutation in the German variety Virgin A (Raeber and Schweppenhauser, 1963). Studies by Dr. G. Koelle at Forchleim Station in Germany had shown that ‘VAM’ has a single recessive locus for virus Y resistance (Raeber and Schweppenhauser, 1965a). On the other hand, N. sylvestris is one of the progenitors of the species N. tabacum and had been said to have necrotic virus Y resistance. However, in these early tests of the virus resistance in Zimbabwe, N. sylvestris was found to be susceptible to necrotic virus Y and ‘VAM’ appeared to have what the early breeders referred to as “immunity” to the local strains of necrotic virus Y (Raeber and Schweppenhauser, 1963).

Based on Koch’s postulates, results suggested that ‘VAM’ may not be able to act as a carrier of the necrotic virus Y pathogen. Because of this observation, there was a proposal, then, that a test be done through a hybridization program and cytological examinations to determine whether or not the mutation that gave birth to the ‘VAM’ line involved a deletion of a chromosome or not (Raeber and Schweppenhauser, 1963). If a chromosome was deleted during mutagenesis, then, it was pointed out that it would be difficult to combine the resistance in it with fully satisfactory agronomic and manufacturing properties of tobacco. This, therefore, suggests the possible futility in the use of ‘VAM’ in current PVY resistance breeding programs in Zimbabwe as a source of PVY resistance as the products may not be liked by the industry because of lack of good manufacturing and agronomic properties.

After this initial work involving ‘VAM’ and N. sylvestris, further screening among selections from ‘K51’, ‘SCR’, ‘Vinica’, ‘Robusta’, ‘Havana IIC’ (V418), ‘Havana IIC’ (V419) with strains of PVY from Mazoe, Acturus, Kutsaga and Harare West yielded some resistant selections which were crossed to K51 and further tested. A cross of ‘K51’ × ‘VAM’ was made and resistant selections with narrow leaves isolated. In the same trial after many generations of selfing, it was suspected that there may be an association between NVY resistance and budworm susceptibility. The nature of the association was not clear but thought to involve linkage or pleiotropism (Raeber and Smeeton, 1974a). Current work on breeding for PVY resistance in Zimbabwe has to consider this early observation in order for varieties with resistance to budworm to be produced in addition to PVY resistance. A German line SCR was also reported to have necrotic virus Y resistance. During the 1990s period, lines coded UM were developed from the cross ‘TN90’ × ‘KM10’ and showed some resistance to PVY. This program was, however, discontinued because of high staff turnover.
Breeding for Black Shank (Phytophthora nicotianae) Resistance
Breeding work to incorporate Black Shank (P. nicotianae) resistance in flue-cured tobacco in Zimbabwe started during the 1990s. The efforts to incorporate Black Shank resistance in the local elite tobacco germplasm resulted in the development of the lines PD, SC, XAG, and XCRN lines (Du Toit et al., 1990). However, these lines have not yet been utilized probably because the disease has not been considered serious in the country. There are, however, reports of incidences of the Black Shank in Hurungwe and Headlands.

Breeding for Anthracnose (Colletotrichum destructivum O’Gara) Resistance
Anthracnose (Colletotrichum destructivum) was first reported in Zimbabwe in 1953 and work on improving flue-cured tobacco resistance to Anthracnose started during the 1954-1955 season (Gildenhuys and Stephen, 1955). Many species which included N. sylvestris, N. repanda, N. glauca, N. alata, N. suaveolens Lehmann, and N. digluta showed moderate resistance to the disease after a screening process in the field (Gildenhuys and Stephen, 1956).

Reconstitution of Multiple Disease Resistance during the 1990s
Breeding efforts during the 1990s focused on making root-knot nematode resistance the basic trait of every variety released in the country. All the lines bred during this period came from recurrent breeding schemes which included a root-knot nematode anchor line. Examples of the products of these schemes are the populations coded XM, XS, XZ, and ONC which all have the root-knot nematode resistant line STNCB2-28 in their original crosses (Du Toit et al., 1999). The overall objective of these breeding programs was to develop lines with resistance to all the major disease of tobacco. The XS, XZ, and ONC lines all have resistance to wildfire (0 and 1), Angular leaf spot (0 and 2), white mold, Alternaria leaf spot, and root-knot nematodes. On the other hand, XCRN lines have resistance to wildfire (0 and 1), white mold, Granville wilt, and black shank.

Breeding for Budworm Resistance
Budworm damage affects mainly the yield, quality and marketability of cured leaf (Sahayaraj and Asha, 2010; Devi and George, 2010; Sharma et al., 2017; ). There was no direct effort to breed for budworm (Fig. 4) resistance in tobacco in Zimbabwe. All the information about budworm tolerance in varieties came as a result of research efforts directed at improving the resistance of breeding material to PVY (Raebert and Smeeton, 1974a). These studies showed that all PVY susceptible entries were less susceptible to budworms and that the genes controlling budworm susceptibility in the variety ‘VAM’ were recessive. These studies also showed that virus Y resistance in ‘VAM’ is controlled by a single recessive gene. This means that breeding for resistance to PVY resistance from ‘VAM’ should always be accompanied by selfing so as not to lose the gene. This virus Y resistance gene in ‘VAM’ was also found to have some pleiotropic effect on budworm resistance (Raebert and Smeeton, 1974a).

The Tayu and Yutq Populations
In line with the overall objective of developing varieties with multiple disease resistance, the TAYU and YUTQ populations

Fig. 4: Budworm damage on a tobacco crop. Yield and quality are negatively affected by budworm attack
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were constituted. Lines from YUTQ populations had resistance to root-knot nematodes, Angular leaf spot, wildfire (0 and 1), Alternaria leaf spot, Frog eye, and white mold resistance (Nyoka and Du Toit, 2004). The TAYU population was developed for resistance to root-knot nematodes, Angular leaf spot, wildfire (0 and 1), Alternaria leaf spot, frog-eye leaf spot and white mold (Nyoka and Du Toit, 2004).

CONCLUSION AND RECOMMENDATIONS

There have been concerted efforts to breed for resistance to all the foliar pests and diseases in flue-cured tobacco (Fig. 5). The majority of the early flue-cured tobacco breeding programs in Zimbabwe relied on variety introductions from the USA. Breeding for disease resistance formed the bulk of the work carried out over the past 50 years of tobacco variety development and improvement in Zimbabwe. Most of the flue-cured tobacco disease resistance present in the elite germplasm used in the current varieties originated from other species of tobacco through interspecific hybridization and introgression through backcross breeding. It is also concluded that the Zimbabwean flue-cured tobacco germplasm possesses resistance genes to the majority of flue-cured tobacco diseases. For future pests and disease resistance breeding efforts, it is recommended that breeders use the already concentrated resistance genes to reduce on the time needed to gain resistance to specific pests and diseases and the associated costs.

ACKNOWLEDGMENTS

Authors would like to thank the Tobacco Research Board for supporting this review work and giving access to their library and other documents.

REFERENCES

Bolton, A. And Stephen, R. C. (1952). Breeding for resistance to Cercospora nicotianae (Frogeye). Tobacco Research Board Annual Report: 1951-1952.

Chaplin J. F. (1970). Associations among disease resistance, agronomic characteristics and chemical constituents in flue-cured tobacco. Agronomy Journal 62: 87-91.

Devi, G. and George J. (2010). Predatory nematodes as biocontrol agent against plant-parasitic nematode - A review. Agricultural Reviews, 39(1) 2018: 55-61.

Du Toit, M., Bailey L. L., Jack A. M. and Molam, M. (1990). Breeding for Black shank disease resistance. Tobacco Research Board, Annual Report: 1989-1990.

Du Toit, M., Bailey L. L., Jack A. M. and Molam, M. (1999). Breeding for root-knot and disease resistance. Tobacco Research Board, Annual Report: 1998-1999.

Gildenhuys, P. J. and Daulton, R. A. C. (1950). Variety tests on different soils. Tobacco Research Board Annual Report, 1949-1950.

Gildenhuys, P. J. and Stephen, R. C. (1956). Breeding for Anthracnose resistance. Tobacco Research Board of Southern Rhodesia Annual Report: 1955-1956.

Gildenhuys, P. J. and Stephen, R. C. (1957). Breeding for Angular leaf spot resistance. Tobacco Research Board of Southern Rhodesia Annual Report: 1956-1957.

Lyle, J. C. F. (1993). Breeding for wildfire (1) resistance. Tobacco Research Board, Annual Report: 1992-1993.

Mbanga, T. (1991). Tobacco: A Century of Gold. ZIL Publications (Pvt) Ltd.

Nyoka, B. I. and Du Toit, M. (2004). Breeding for multiple disease resistance in the TAYU population by recurrent selection. Tobacco Research Board, Annual Report: 2003-2004.

Raeber, J. G. and Schweppenhauser, M. A. (1963). Breeding for resistance to Blue mold (Perenospora tabacina). Tobacco Research Board, Annual Report: 1962-1963.

Raeber, J. G. and Schweppenhauser, M. A. (1964a). Breeding for resistance to wildfire. Tobacco Research Board, Annual Report: 1963-1964.

Raeber, J. G. and Schweppenhauser, M. A. (1964b). Preliminary variety test. Tobacco Research Board, Annual Report: 1963-64.

Raeber, J. G. and Schweppenhauser, M. A. (1965a). Breeding for resistance to Bushy-top and Rosette virus diseases. Tobacco Research Board, Annual Report: 1964-1965.

Raeber, J. G. and Schweppenhauser, M. A. (1965b). Varietal reactions to Bushy-top and Rosette virus under greenhouse conditions. Tobacco Research Board, Annual Report: 1964-1965.

Raeber, J. G. and Schweppenhauser, M. A. (1966). Breeding for resistance to Granville wilt (Pseudomonas solanacearum). Tobacco Research Board, Annual Report: 1965-1966.
Breeding for Flue-cured Tobacco (Nicotiana tabacum L) Foliar Pest and Disease Resistance in Zimbabwe

Raeber, J. G., Schweppenhauser M. A. and Smeeton, B. (1968). Agronomic evaluation of Alternaria resistant narrow leaf lines. Tobacco Research Board, Annual Report: 1967-1968.

Raeber, J. G. and Smeeton, B. (1970). Breeding for resistance to wildfire and TMV. Tobacco Research Board, Annual Report: 1969-1970.

Raeber, J. G. and Smeeton, B. (1971a). Variety Trials. Tobacco Research Board, Annual Report: 1970-1971.

Raeber, J. G. and Smeeton, B. (1971b). Agronomic trial of mammoth type lines with wildfire and TMV resistance. Tobacco Research Board, Annual Report: 1970-1971.

Raeber, J. G. and Smeeton, B. (1971c). Variety trials. Tobacco Research Board, Annual Report: 1969-1970.

Raeber, J. G. and Smeeton, B. (1971d). Variety Trials. Tobacco Research Board, Annual Report: 1969-1970.

Raeber, J. G. and Smeeton, B. (1973a). Agronomic trial of Alternaria resistant narrow leaf lines. Tobacco Research Board, Annual Report: 1972-1973.

Raeber, J. G. and Smeeton, B. (1973b). Agronomic trial of Alternaria resistant narrow leaf lines. Tobacco Research Board, Annual Report: 1972-1973.

Raeber, J. G. and Smeeton, B. (1973c). Agronomic trial of white mould resistant narrow leaf lines. Tobacco Research Board, Annual Report: 1972-1973.

Raeber, J. G. and Smeeton, B. (1973d). Co-operative trials of mammoth strains. Tobacco Research Board, Annual Report: 1972-1973.

Raeber, J. G. and Smeeton, B. (1974a). Varietal susceptibility to natural infestation with budworm. Tobacco Research Board, Annual Report: 1963-1964.

Raeber, J. G. and Smeeton, B. (1974b). Inheritance of tolerance to Alternaria in tobacco. Tobacco Research Board, Annual Report: 1973-1974.

Raeber, J. G. and Smeeton, B. (1975). Breeding for resistance to Alternaria. Tobacco Research Board, Annual Report: 1974-75.

Raeber, J. G. and Smeeton, B. (1978). Agronomic trial of Alternaria resistant narrow leaf lines. Tobacco Research Board, Annual Report: 1977-1978.

Raeber, J. G. and Smeeton, B. (1984). Co-operative cultivar trials of standard and mammoth cultivars/lines. Tobacco Research Board, Annual Report: 1983-1984.

Sahayaraj, K. and Asha A. (2010). Biological Control Potential Evaluation of Rhinocoris Kumarii Ambrose and Livingstone (Hemiptera: Reduviidae) on Aphis Craccivora (Koch.) (Hemiptera: Aphididae). Indian J. Agric. Res., 44 (4):281-287.

Sharma R., Ram L. and Devi R. (2017). Efficacy of white muscardine fungus (Beauveria bassiana) on rice hispa (Dicladospa armigera) Indian J. Agric. Res., 51(3):296-298

Stephen, R. C. (1953). Variety improvement. Tobacco Research Board, Annual Report: 1952-1953.

Tobacco Research Board. (1950). Annual Report.