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Tulip Breaking: Past, Present, and Future

This article focuses on the oldest recorded plant virus disease, tulip breaking, and reflects the authors' interests in molecular virology, the history of virology, and the broad influence of viruses upon societies and their culture. The potyvirus *Tulip breaking virus* (TBV) induces in the petals of its host tulips beautiful variegated color patterns that break the solid color of the uninfected tulips, hence the name "tulip breaking." The human passions of possession that these "broken tulips" induced in seventeenth century Holland generated an economic and social disorder with lasting cultural ramifications referred to as "tulipomania." Although the lure of the broken tulip persists in the twenty-first century, the molecular mechanisms governing the virus-induced color breaking in tulips remain little understood. Here, we review aspects of the historical impact of tulipomania, the biology of TBV, the pathways and regulation of plant pigment formation, and the potential mechanisms underlying virus-induced color breaking. The reader is cautioned that tulipomania, like tulip breaking, is still contagious.

Historical Impact: Madness in the Age of Reason

The seventeenth century is referred to by historians and philosophers as the Age of Reason (16). It is ironic that during this age of reason the populace of the Netherlands was driven to madness by the symptoms of a plant virus disease that never afflicted a single human host. The craze for the beautiful broken tulips (tulipomania) was by no means restricted to Holland; most of Europe succumbed. The love for the broken tulip is well expressed in the verse of the English poet Cowley (33):

> The tulip next appeared, all over gay,
> But wanton, full of pride, and full of play;
> The world can't show a dye but here has place;
> Nay, by new mixtures, she can change her face;
> Purple and gold are both beneath her care,
> The richest needlework she loves to wear;
> Her only study is to please the eye,
> And to outshine the rest in finery.
> –Abraham Cowley (1618-1667)

Fig. 1. ***Tulip Planting in Spring*** **by Pieter Brueghel, the Younger. Reproduced with permission from Scala/Art Resource, New York.**

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The greatest economic and cultural impacts of tulipomania were experienced in the Netherlands. The historical aspects of the disease reviewed in this article are drawn, therefore, from Dutch lore. Perhaps surprisingly, tulips did not originate in Holland, but in Turkey, where they were very popular. Tulips arrived in the Netherlands in the 1590s. The famous Dutch botanist Carolus Clusius is credited with planting some of the first tulips in Holland. Clusius served as chief horticulturist at the Hortus Botanicus at Leiden University. He purportedly obtained tulip seeds from his friend Ogier Ghislain de Busbecq, the Imperial Ambassador of Emperor Ferdinand I of Vienna to Suleiman the Magnificent of Turkey. Clusius bred and cataloged the tulips scientifically, and studied their potential medicinal properties. He carefully guarded his experiments. Among his treasures were some of the rare broken tulips with their spectacular patterns of color striations. These variegated tulips were highly coveted by all who viewed them, and because Clusius was most reluctant to sell them, they were frequently stolen for later profit. The thievery reached such proportions that Clusius abandoned his gardening in despair and gave his remaining bulbs to friends. Thus did his collection spread throughout the Netherlands (11,41).

Social and economic factors influencing the Dutch during the seventeenth century provided a fertile ground for the blossoming of tulipomania in the Netherlands. After decades of oppression by the Spanish, the Dutch had won their freedom and a sense of euphoria. A recent epidemic of bubonic plague had killed thousands, but the resulting labor shortage had the effect of increasing the wages of the survivors. Both factors generated an influx of available cash (40,44). However, the memories of plague and oppression left a sense of anxiety. It has been suggested that collecting earthly goods enhanced self-image and provided protection against the insecurities of the past (40). The beauty, rarity, unpredictability, and frailty of the broken tulip contributed to its rise as the object of collecting.

The cultivation of tulips became widespread in the Netherlands (Fig. 1). As the mania spread, the rare broken tulips increased dramatically in monetary value, and tulip collecting rapidly gave way to tulip profiteering. The madness peaked between 1634 and 1637. During this period, a single bulb of the rare broken tulip Semper Agustus sold for 3,000 guilders. The value of this sum in terms of goods was recorded in a pamphlet written in 1636 (Fig. 2) (5,11,41).

As a result of the soaring costs of the bulbs and the frailty of the flowers that rapidly withered, artists of the seventeenth century were commissioned to preserve the beauty of the broken tulips in paintings. For many, these artistic renderings of the tulips were more affordable than the tulips themselves (41). Thus did tulips provide sustenance to many artists, including master painters of the golden age of Dutch painting. The charming painting by Jan van den Hecke, shown in Figure 3, illustrates the artistic style and the broken tulips of this period. It is a recent acquisition of the Speed Art Museum in Louisville, KY, and is making its public debut after centuries in private collections. Representative paintings with broken tulips by more familiar artists are shown in Figures 4 and 5. Interestingly, although broken tulips are often referred to as Rembrandt tulips, Rembrandt rarely painted them. The designation refers instead to the golden age of Dutch painting.

Tulip breaking was highly unpredictable. Additionally, the broken tulips were purchased months before delivery, before the tulips could be examined for breaking, and before the future demand for the tulips was known with certainty (21,22,44). Thus, tulip investing evolved into a highly speculative futures market viewed as a form of gambling. The phenomenon became the target of moralists, satirical writers, painters, and cartoonists. Petrus Hondius (1578-1621), pastor of the congregation at Terneutzen in Zeeland, de-

	Guilders
Eight fat pigs	240
Four fat oxen	480
Twelve fat sheep	120
Twenty-four tons of wheat	448
Forty-eight tons of rye	558
Two hogsheads of wine	70
Four barrels of eight-guilder beer	32
Two tons of butter	192
A thousand pounds of cheese	120
A silver drinking cup	60
A pack of clothes	80
A bed with mattress and bedding	100
A ship	500
TOTAL	3,000

Fig. 2. Value of goods equal to the price of the rare broken tulip Semper Agustus, as recorded in a pamphlet written in 1636.

Fig. 3. *Flowers in a Glass Vase* by Jan van den Hecke, Flemish, 1625-1684. Oil on canvas. Bequest of Alice Speed Stoll to the Speed Art Museum, Louisville, KY. Reproduced with permission.

nounced the tulip trade early on in a 16,000 verse epic poem, a stanza of which is presented below (27).

> All these fools want is tulip bulbs
> Heads and hearts have but one wish
> Let's try and eat them; it will make us laugh
> To taste how bitter is that dish.
> –Hondius (1621).

Famous literature of the day included the novel *The Black Tulip* by Alexander Dumas, in which a quest for a fabled rare black tulip and the crash of a tulip market are described, and Jean de La Bruyere's (1645-1696) satire of tulipomania, *Les Caracteres* (30). A translated segment of the latter is presented (right).

> On Fashion (or Fads). One of the things that reveals our foolishness and pettiness is our slavery to fads regarding taste, life-style, health, and morals. Curiosity (or rather, faddishness) is not a desire for what is good or beautiful but for what is rare and unique: for what I have and nobody else has. It is not a love for what is perfect but for what is sought-after, for what is in fashion. It is not a hobby but an obsession, and often such a violent one that it does not yield (even) to (passions like) love or ambition—except for the insignificance of its object. It is not a passion for things that are rare and valuable in general, but only for a certain thing that is rare and as a consequence is in fashion.

Examples of paintings and engravings satirizing tulipomania are presented in Figures 6 to 8. In Jan Brueghel II's *Allegory upon the Tulip Mania* (Fig. 6), tulip traders are depicted as monkeys. The monkeys dining lavishly on the verandah ridicule the excesses of the traders (32). An engraved cartoon, Flora's Mallewagen (Flora's Chariot of Fools), by Chrispijn van de Passe, shown in Figure 7, was based on an allegorical painting of the same name by Hendrik Pot. In this cartoon, the goddess Flora, clutching bouquets of broken tulips, pilots a wind wagon headed to the sea and destruction. People from all trades are casting aside their tools and frantically attempting to jump on the doomed bandwagon. In the distance, a bird representing idle hope flies away. In another allegorical cartoon, Flora's Fools-Cap, engraved by Pieter Nolpe, tulip traders are shown gathered under a huge fool's cap as Flora is driven away on a donkey "for her whorish immorality" (Fig. 8).

In 1637, many tulipomaniacs realized that the madness could not last. Demand for broken tulips dissipated, selling escalated, prices plummeted, and speculators defaulted on their promissory notes. The bubble burst and left widespread bankruptcy in its wake. The seventeenth century tulip trade is viewed by economists as the first modern stock market. Tulipomania remains the paradigm of the economic bubble (20–22).

The Virus: An Artistic Agent

The potyvirus *Tulip breaking virus* (TBV) is the most commonly cited causal agent of classical or Rembrandt tulip breaking (24). Clusius in 1576 was one of the first to describe a "viral" flower color-

Fig. 4. *Flower Vase in a Window Niche* by Ambrosius Bosschaert II (1573-1621). Oil on wood. Mauritshuis, the Hague. Reproduced with permission from Scala/Art Resource, New York.

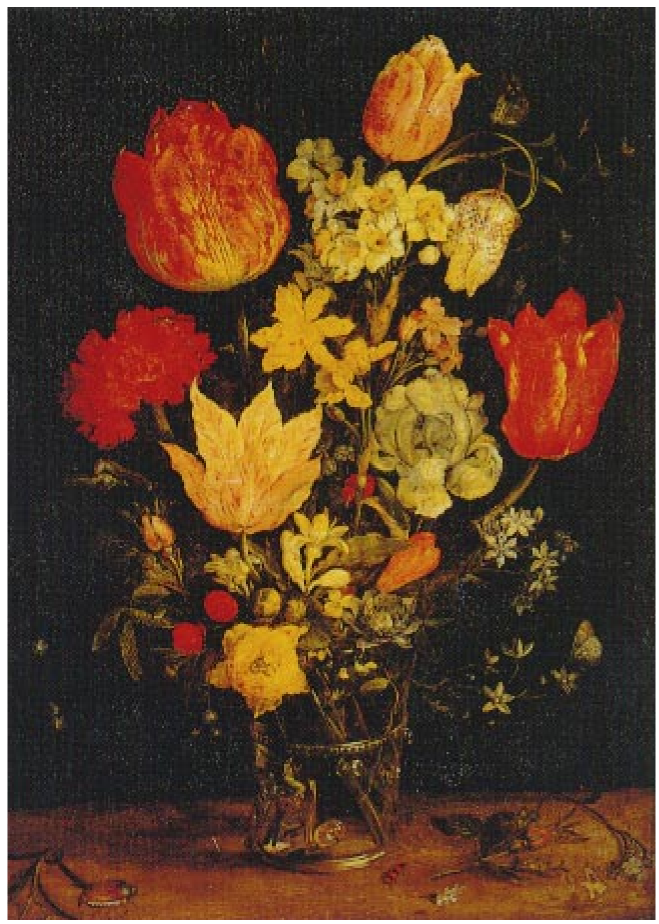

Fig. 5. *A Vase of Flowers* by Jan Brueghel I (1568-1625). Reproduced with permission from Scala/Art Resource, New York.

breaking in tulips. He noted in his report that tulip plants that exhibited flower color variegation in striped and flamed patterns also showed weakening leading to eventual loss of the varieties (49).

As far back as 1637, color breaking in tulips was demonstrated to be transmissible from bulbs of variegated tulips to bulbs of uniformly colored tulips by grafting (15,41). Of course, these ancestral plant pathologists did not realize that their grafting owed its success to a transmissible disease agent. It was not until the experiments of Cayley and of McKay in the late 1930s (15) that transmissibility was linked to a virus.

Although variations in the intensity and distribution of color-breaking patterns were recognized early on, there have been some arguments over the years as to the cause. Some authors attributed the diversity to differences in host genotypes and virus strains, whereas others concluded that other potyviruses serologically and biologically distinct from TBV could also induce flower breaking (7,12,35).

Dekker et al. (12) characterized five viruses that cause color breaking in tulips and concluded (based on host range, serology, potyvirus-specific PCR, and sequence analysis) that they are distinct potyviruses. These viruses are: TBV (synonyms: lily mosaic virus, lily streak virus, and tulip mosaic virus), *Tulip band-breaking virus* (TBBV), tulip top-breaking virus (TTBV), *Rembrandt tulip-breaking virus* (ReTBV), and *Lily mottle virus* (LMoV). All, except TTBV, are listed in the *7th Report of the International Committee on the Taxonomy of Viruses* (ICTV) as approved members of the genus *Potyvirus,* in the family *Potyviridae* (46). TTBV, apparently a strain of the potyvirus *Turnip mosaic virus*, is considered by ICTV as a tentative member of the genus (18).

The virions of TBV, like other members of the genus *Potyvirus*, are flexuous filaments with helical symmetry (Fig. 9) and contain a nonsegmented positive sense RNA genome (25). TBV is worldwide in distribution, and its natural hosts are limited to two genera in the Liliaceae, *Tulipa* and *Lilium*. (48). The host ranges of TBBV and ReTBV, like TBV, are also limited to genera in the Liliaceae. TTBV and LMoV, on the other hand, were found to infect several experimental hosts, including *Nicotiana clevelandii*, *N. benthamiana*, *Chenopodium quinoa*, and *Tetragonium expansa* (12). As is typical of potyvirus infections, cylindrical inclusions (pinwheels) were found in thin sections of TBV-infected cells of both tulip and lily (48).

The potyviruses infecting tulip are transmitted by several species of aphids in a nonpersistent manner. The aphid vectors include *Myzus persicae, Aphis gossypii, A. fabae, Macrosiphum euphorbiae*, *Dysaphis tulipae*, and *Aulocorthum circumflexum*; TBV transmission in the field was correlated with the occurrence of *Macrosiphum euphorbiae* and *Dysaphis tulipae* (24).

Symptoms of tulip breaking have been described as stripes, streaks, feathering, or flames of different colors on petals (Fig. 10). The symptoms vary with the flower variety and age at the time of infection. The color variation is related to local accumulation of pigments in the upper epidermal layer. The lighter colors appear as irregular streaks or fine feathering. Dark breaking occurs when the color in the epidermal cells intensifies in small dark streaks or elongated flecks. The flame pattern characteristic of early Rembrandt tulips appears as narrow or broad streaks of color in the center portion of the petal. Flames may also occur near petal edges. The original flamed plants contained two-

Fig. 7. Flora's Mallewagen by Chrispijn van de Passe (1594-1670). Reproduced from *The Book of Tulips,* T. Lodewijt, 1979, with permission from The Vendome Press, New York.

Fig. 8. Flora's Fools-Cap engraved by Peter Nolpe. Reproduced from *The Book of Tulips,* T. Lodewijt, 1979, with permission from The Vendome Press, New York.

Fig. 6. *Allegory Upon the Tulip Mania* by Jan Breughel II (1601-1678). Reproduced from *The Book of Tulips,* T. Lodewijt, 1979, with permission from The Vendome Press, New York.

Fig. 9. Negatively stained virions of *Tulip breaking virus*. The particles are filamentous, usually flexuous, 750 to 775 nm long and 14 nm wide. Reproduced from http://www.ncbi.nlm.nih.gov/ICTVdb/WIntkey/Images/a1.gif

tone mixes of red, yellow, purple, and white. These same colors may be found in genetically bred Rembrandt "look-alikes" of today, which resemble the virus-infected tulips of the 1600s. Although virus-induced flower breaking may sometimes be confused with genetic variegation, it is not the only effect of potyviruses on tulips: virus infection also reduces flower size, pollen production, and seed set (6).

In addition to the potyviruses discussed here, several other viruses, including the nepovirus *Arabis mosaic virus*, the carlavirus *Lily symptomless virus*, the cucumovirus *Cucumber mosaic virus*, and the potexvirus *Potato virus X*, have been reported to cause minor flower-breaking symptoms in tulip (e.g., flecks, narrow dark or light streaks). The floral and foliar symptoms induced by these viruses, however, are distinct from those caused by TBV (3,13,39,47). Highly specific and sensitive serological and nucleic acid-based methods are available for definitive identification of these viruses.

Fig. 10. Flower-breaking symptoms in *Tulip breaking virus*–infected tulips (Madame Spoor). Light and dark breaking symptoms can be observed. Reproduced from Brunt et al. (9).

Fig. 11. Rembrandt look-alikes tulip mixture. Reproduced with permission from the 1999 Fall Planting catalog, Dutch Gardens, Adelphia, New York.

The Rembrandt Tulip Look-alikes

The beautiful virus-infected tulips are no longer available commercially as a result of the unpredictability of the flower patterns and the subtle reductions in the overall fitness of the infected plants. The Dutch hybridizers (specialists who breed flowers with specific characteristics) were able to mimic the exotic virus-induced patterns in healthy plants. Today, Rembrandt tulip look-alikes (Fig. 11) such as the red-and-white Union Jack and Spring Green (Fig. 12), are readily available to the home gardener. It should be mentioned here that the process of creating new tulip varieties, called hybridizing, is one that requires both skill and patience. It may take as long as 15 and sometimes 25 years before a new tulip variety can be brought to market. Hybridizing is a traditional craft practiced in Holland today much as it has been for centuries. Although hybridizing per se appears to be a simple process—flowers are mated artificially by rubbing the pollen of the stamen of one blossom against the pistil of another (Fig. 13)—the expertise begins with the hybridizer's close knowledge of the thousands of species and cultivars available to serve as parents. The hybridizer must make decisions based on weighing how different properties of color, flowering period, resistance to disease, and other traits might be combined to yield the qualities and novelty he or she seeks. The judgment and competence of the hybridizer are qualities that cannot yet be matched, even with all the modern advances in genetics and gene transfer technology.

Fig. 12. Tulip cultivar Spring Green, a representative of Rembrandt tulip. Courtesy of C. E. Kosmas, M.D., Ph.D. (*personal communication*).

Fig. 13. Tulip hybridizing. Photograph depicts the artificial hybridizing process, which involves rubbing the pollen of the stamen of one blossom against the pistil of another. Courtesy of Netherlands Flower Bulb Information Center (David Caras, *personal communication*).

Hybridizers look for parents among three sources: cultivars, species, and sports. Cultivars are those types of flowers that have been previously created by the hybridizer's hand. Species refers to flower varieties as they are found in nature. Sports are natural mutations. All of today's double-flowering and Parrot tulip varieties, for example, can be traced to various mutations (Figs. 14 and 15). To help preserve the gene pool for future hybridizers, the Dutch flower bulb industry has long subsidized and supported the Hortus Bulborum in Limmen, the Netherlands, which is liter-

Fig. 14. Tulip cultivar Nizza, a representative of double late tulips. Courtesy of C. E. Kosmas, M.D., Ph.D. (*personal communication*).

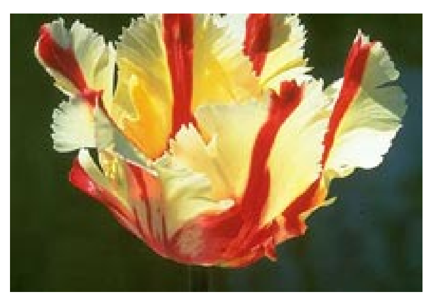

Fig. 15. Tulip cultivar Flaming Parrot, a representative of Parrot tulips. Courtesy of C. E. Kosmas, M.D., Ph.D. (*personal communication*).

ally a living museum of bulb flowers. This outdoor flower field includes varieties that, for one reason or another, are no longer commercially cultivated. Cultivars in the museum date back as far as 1595, each marked with a plaque to identify the flower and the year of its introduction. The museum is a popular tourist attraction in spring and is actively used by commercial hybridizers (D. Caras, *personal communication*).

Molecular Basis of Virus-Induced Flower Breaking

Flower color is largely determined by the differential accumulation of plant pigments called anthocyanins. A large spectrum of anthocyanins exhibiting different colors exists, but no one plant is capable of producing the full spectrum. Thus, color potential varies among plant species. The biochemistry and enzymology of the pathway leading to anthocyanin production is well understood, and virtually all the genes that encode the enzymes of biosynthesis have been isolated (26). A generalized pathway based on studies of petunia is shown in Figure 16. Expression of the genes for the various enzymes involved in the pathway is regulated at the level of transcription by a large group of transcription factors (38). Alterations in the regulatory elements or mutations in the genes encoding the enzymes can result in blocks in the pathway and thus the accumulation of intermediates that often yield different colors.

The first application of gene technology to modify flower color led to the creation of an orange pelargonidin-producing petunia variety. This was achieved by expressing the dihydro-flavonol-4-reductase gene (DFR; Fig. 16) from maize in a suitable petunia line and crossing different transgenic petunia lines containing the maize DFR gene with elite breeding material (37).

Development of a blue rose, tulip, or carnation by molecular breeding is more challenging. The simultaneous presence of three factors is required in order to obtain blue flower colors: the synthesis of 3′,5′-hydroxylated anthocyanins (delphinidins); the presence of flavonol co-pigments; and a relatively high vacuolar pH. Progress has recently been made in isolating "blue genes" from petunia that may help in the creation of such a blue rose, tulip, or carnation. The enzymes required for the synthesis of delphinidins (flavonoid-3′,5′-hydroxylase; Fig. 16) and flavonols (flavonol synthase) are well characterized, which has allowed the corresponding genes to be cloned by standard methods. The major difficulty in the process is cloning the genes that control vacuolar pH (*ph* genes). Mutation studies in petunia have identified six genes (*ph1-ph6*) that control intracellular pH in flower petals and, hence, the color of the flower (37).

The painterly pathology of the potyviruses that induce color breaking in tulips reflects their ability to interfere with the accumulation of anthocyanins in the tulip flower petals. It should be reiterated here that, in addition to anthocyanin accumulation, there are other factors that determine flower color, including vacuolar pH, cell shape, and co-pigmentation (38).

It is not known whether the flower-breaking patterns in TBV-infected tulip plants reflect virus distribution in the petals. Flower breaking, in general, is considered a good diagnostic feature for infection with viruses that induce mosaic symptoms (34). It is possible that the broken sectors represent virus-infected tissues, whereas the normal areas are derived from virus-free cells. *Tobacco mosaic virus* (TMV) has been reported to be detectable only in the white sectors seen within the normal pink-colored tobacco flowers (34). This is reminiscent of the development of mosaic patterns in leaves (i.e., color-breaking patterns are laid down in the floral apex and are dependent on flower ontology); thus color breaking in tobacco petals may develop only in flowers that are smaller than a certain size when infected (34). The finding that tulip plants inoculated with TBV less than 11 days before blooming did not exhibit color breaking symptoms is consistent with this hypothesis (52). From a preliminary examination of broken and normal petal tissues from various plant species infected with several different viruses, Matthews (34) concluded that the absence of color was due to the absence of particular pigments rather than to a change in pH within the vacuole.

The generation of broken flowers may also be explained by the phenomenon of gene silencing. Gene silencing is a common phenomenon in transgenic plants that affects transgenes and endogenous genes. Transgenes are transcriptionally silenced if

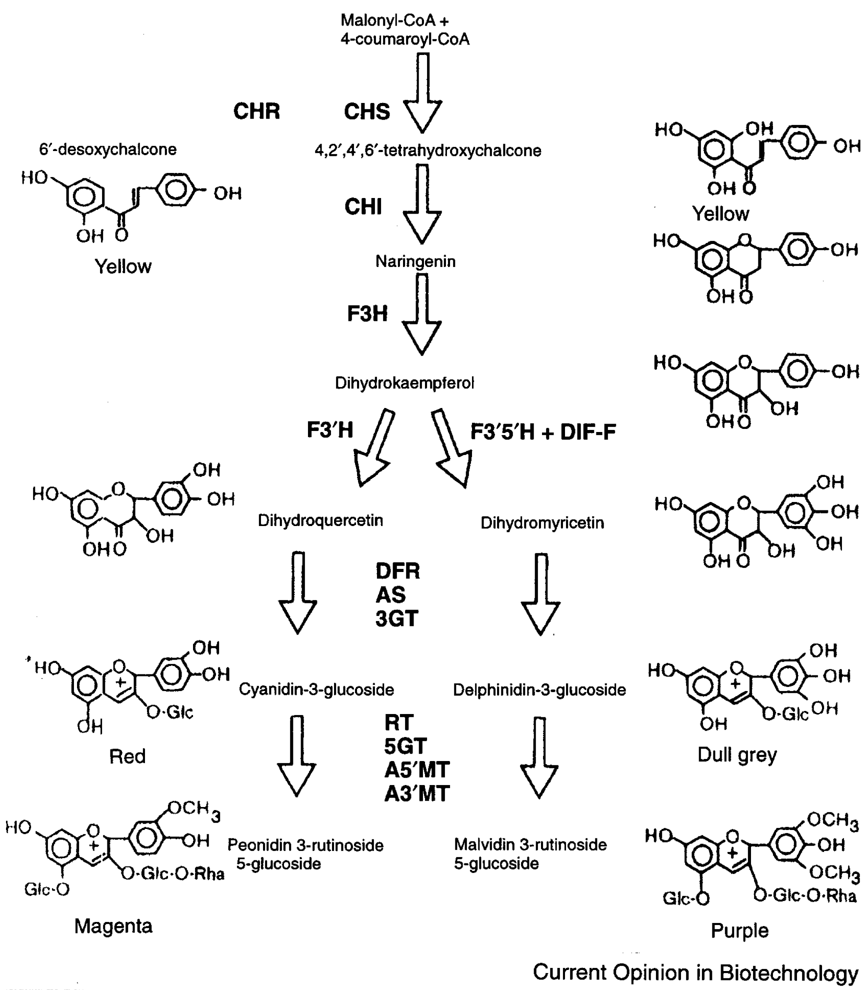

Fig. 16. Anthocyanin biosynthesis pathway in petunia. Enzymes are printed in bold capitals. CHR = chalcone reductase, AS = anthocyanidin synthase, A3′MT = anthocyanin 3′ methyltransferase, A5′MT = anthocyanin 5′ methyltransferase, CHI = chalcone flavanone isomerase, CHS = chalcone synthase, DFR = dihydroflavonol 4-reductase, DIF-F = cytochrome b5 specific to F3′5′H, F3H = flavanone 3-hydroxylase, F3′H = flavonoid 3′-hydroxylase, F3′5′H = flavonoid 3′,5′-hydroxylase, 3GT = 3′-glucosyltransferase, RT = rhamnosyltransferase, 5GT = 5-glucosyl transferase. Figure reproduced from Current Opinion in Biotechnology, 10, Mol et al., Novel coloured flowers, 198-201, Copyright 1999, with permission from Elsevier Science.

the promoter is inactivated, which may be correlated with DNA methylation. If RNA is produced but does not accumulate, transgenes are posttranscriptionally silenced. The expression of endogenous genes can also be posttranscriptionally silenced (degradation of RNA after transcription) by introduced sense transgenes when these genes are sufficiently homologous to their endogenous counterparts (14,19).

Cosuppression (posttranscriptional gene silencing; PTGS) was first discovered when attempts were made to overexpress the chalcone synthase gene (*chs*, a key enzyme in the anthocyanin biosynthesis pathway; Fig. 16) in transgenic petunia. In addition to the expected deep purple color, completely white flowers and those with a variegated pigmentation phenotype were also produced (45). The findings that viruses can both initiate and be the targets of PTGS suggest that PTGS is a manifestation of a universal antivirus defense mechanism in plants (1,43). RNA viruses are able to induce PTGS of nuclear genes (or transgenes) in a homology-dependent manner or PTGS-like degradation of the invading viral RNAs (RNA transcripts in the case of DNA viruses), even in the absence of homologous nuclear genes (10,43). The recovery phenomenon observed in nepovirus-infected plants and in some other virus-infected plants has been shown to correspond to post-transcriptional decrease of viral RNA. It is probable that the process of gene silencing has evolved as a response to selection pressures by pathogenic viruses. This idea is supported by the finding that many plant viruses encode proteins that can suppress PTGS as a counter-defensive strategy (2,8,29,50).

It is not known how virus infection induces PTGS of anthocyanin pathway structural and/or regulatory genes and as a result leads to flower color breaking. Although the exact mechanism by which PTGS operates has yet to be elucidated, the first cellular component of the RNA-silencing pathway to be cloned was determined to be homologous to an RNA-dependent RNA polymerase (RdRP) isolated from plants. Several current models for gene silencing include RdRP as a central player in the RNA silencing pathway, indicating the requirement of novel RNA synthesis (14). Double-stranded RNA has also been implicated as an initiator of PTGS in plant systems (51). The recent identification of a small antisense RNA species of a uniform length that is associated with several instances of RNA silencing in both transgenic and nontransgenic plants predicts that it may comprise a specificity determinant and a component of the systemic signal for PTGS (14,23).

Based on present information on PTGS, we propose the following model as a possible explanation of virus-induced color breaking: as a consequence of putative protein–protein interactions or sequence similarities (e.g., conserved DNA-binding motifs), viral gene products may interfere/outcompete with the endogenous activators/suppressors that regulate expression of the anthocyanin biosynthesis pathway. This eventually leads to down-regulation/overexpression of one or more of the genes that control flower color. Overexpression would in turn trigger cosuppression or PTGS. The size of broken sectors observed may thus reflect both the time in development when cosuppression was triggered and the rapidity with which the signal can move through plasmodesmata (28). Alternatively, virus infection may alter flower color by interfering with anthocyanin glutathionation and active transport to the vacuole or with the pH of the vacuole (37).

Outlook

Viruses are commonly viewed as evil bearers of plagues that destroy people, their crops, and their livestock. Nevertheless, viruses are not altogether nasty. Dubos (15) refers to TBV as a “benevolent virus,” the overall effects of which could be beneficial to the community and even to the infected host. More recently, Lederberg (31) pointed out that “microbes have a shared interest in their host’s survival: a dead host is a dead-end for most invaders too. Domesticating the host is the better long-term strategy for pathogens.” Most certainly, TBV was responsible for the domestication of the TBV-infected tulip. Because the symptoms of TBV made tulips novel and beautiful, TBV infection led to the widespread cultivation of virus-infected tulips in the seventeenth century. Additionally, although TBV does weaken its host, the potential benefits of infection might outweigh the negatives. It is well known that flower color plays a major role in the attraction of pollinators (26,38). The new color patterns induced in the infected tulip could result in the attraction of more or different pollinators. It has been suggested that a change in pollinators could lead to genetic isolation of the novel plant and subsequent speciation (42). Flower color also has been shown to affect seed dispersal and predator avoidance. Additionally, because many plant pigments absorb UV light, variations in flower color can affect the sensitivity of the host DNA to damage from the strong UV light that plants encounter in the field. Thus, TBV could play a positive role in both the short-term survival and ultimate evolution of its host.

Virus-induced color breaking provides an easily scored phenotype and an ideal system to study virus–host interactions. With the considerable progress made in understanding the molecular basis of petal coloration, and with the availability of infectious full-length cDNA clones of many of the viruses that cause flower color breaking, the host and viral determinants of this phenomenon can be dissected.

The intimate interaction between viruses and RNA silencing in plants is being exploited to create a novel technology for functional genomics in plants. Virus-induced gene silencing (VIGS) is an exciting new technology based on the observation that gene expression in plants can be suppressed in a sequence-specific manner by infection with virus vectors carrying fragments of the host genes to be silenced. A number of endogenous genes and transgenes have been targeted successfully by VIGS (4). Development of VIG vectors for use to dissect the color-breaking mechanism in tulip appears feasible and could benefit from recent discoveries that VIGS and PTGS are related to antivirus defense in plants. Potyviruses, however, may not provide strong VIGS vectors because they have been shown to generate strong repressors of PTGS (4). Although the potyvirus–host systems studied to date are very limited and generalizations may be premature, the TBV–tulip system offers potential for deeper insights into the pathways of flower color determination, as well as viral pathogenesis and defense mechanisms. Perhaps TBV itself will guide us to a faster process for creating virus-free, treasured Rembrandt tulips.

Our reverence for the tulip and the passion for novel tulips extends into the twenty-first century. We hear it in the jazz of Duke Ellington’s “Tulip or Turnip” (17), and we experience its economic impact. The worldwide retail trade in cut flowers was over 2.5 billion U.S. dollars annually in 1995, and the value of cut tulips in the Dutch auction that year was 170 million U.S. dollars (53). We have seen a recent resurgence of interest in tulipomania. Two new books relating the historical aspects of this social disorder have appeared (11,41). Additionally, the Chicago Botanical Gardens is hosting an indoor exhibition entitled “TulipMania: Five Centuries of Mystery and Madness”. There are even rumors that Steven Spielberg is working on a film based on the new novel, *Tulip Fever,* set in the midst of seventeenth century tulipomania (36). Tulipomania lives.

Acknowledgments

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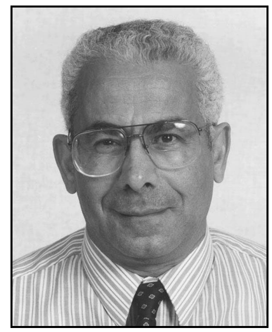

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