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Vavilovian Mimicry: Nikolai Vavilov and His Little-Known Impact on Weed Science

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Nikolai Ivanovich Vavilov was an early 20th century Russian plant scientist who was killed by Joseph Stalin in 1943 for his adherence to basic genetic principles. Vavilov is well known within plant breeding and plant evolutionary biology circles, yet the science of Vavilov is just as important to the field of weed science. Specifically, Vavilov proposed that certain weeds adapted to weed control practices to survive in prehistorical agrarian societies. Most would refer to this adaption as crop mimicry, but the term "Vavilovian mimicry" is more apt. Vavilovian mimicry requires three factors: a model—the crop or desirable plant; a mimic—the weed; and an operator—the discriminating agent, possibly human, animal, or machine. In a modern context, it is proposed that weed adaptation to herbicide applications be included as a form of Vavilovian mimicry, with the acknowledgement that the operator is the herbicide. In this context, Vavilovian mimicry is the adaption of the weed mimic to be perceived by the operator as visually, physically, or biochemically indistinguishable from the crop model. This review will cover the history and legacy of Vavilov in a condensed version in the hope that weed scientists will hold this individual in high regard in our future endeavors and begin to acknowledge Vavilov as one of the first scientists to propose that weeds can mimic the attributes of crops.

Key words: Adaptation, crop mimicry, evolution, herbicide resistance, Nikolai Vavilov, Vavilovian mimicry.

In 2012 to 2013, at national scientific meetings I posed a question to numerous weed and agronomic scientist: "Are you familiar with the work of Nikolai Vavilov?" No one with whom I spoke could tell me who Nikolai Vavilov was—although many were familiar with Vavilov's nemesis Trofim Lysenko. After a short survey of weed science–related textbooks, the only citations of Vavilov were in Holzner and Numata (1982) and the works of Jack R. Harlan. Other prominent weed science textbooks such as Zimdahl (2007) and Radosevich et al. (1997) mention the work of Vavilov indirectly, but do not specifically mention Vavilov. To be fair, until a few years earlier I myself had never heard of Vavilov until I stumbled on to the book *The Murder of Nikolai Vavilov* (Pringle 2008). Pringle (2008) tells the story of one of the most brilliant biologists who ever existed, a story that few people have ever heard because in postczarist Russia, Joseph Stalin virtually exterminated legitimate science, replacing world-renowned scientists with working-class, self-taught pseudoscientists. As a plant breeder and plant geneticist and head of his All-Union Institute of Botany and Applied Cultures (other similar names are often listed as the name of the All-Union Institute headed by Vavilov), Vavilov was a leading world researcher in the field of plant breeding and genetics. If left to guide plant breeding research in the Soviet Union, modern-day Russia could be quite different. Instead, the work of Vavilov was discarded, and the world is poorer for it. Stalin and his crony pseudoscientists systematically intimidated, imprisoned, starved, and killed scientists, all for political control of scientific knowledge. Nikolai Vavilov died due to the harsh conditions of his imprisonment on January 26, 1943. He was imprisoned because being on the right side of science left him on the wrong side of Joseph Stalin.

The story of Nikolai Vavilov is important for numerous reasons. His story illustrates the dangerous mixture of politics and science that can pervert scientific research and stall technological advancement (Roll-Hansen 2005). His story is inspirational because throughout his persecution he remained dedicated to his country as a scientist, and even in the face of certain death in a Soviet prison he remained an inspiration to prisoners around him. The story of Vavilov illustrates the importance of free speech and expression in the scientific community. For the weed science community, it is the overlooked discoveries and theories of weed adaptation to cropping systems that need to be rediscovered and acknowledged.

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Figure 1. Nikolai Ivanovich Vavilov. November 25, 1887–January 26, 1943. (Image provided by N.I. Vavilov Research Institute of Plant Industry, St. Petersburg, Russia.)

Nikolai Vavilov and His Nemesis Trofim Lysenko: Historical Context

It is impossible to discuss the science of Vavilov without first discussing the historical context in which Vavilov worked. Vavilov was born in 1887 and rose to prominence as a scientist in the mid-1920s to lead the All-Union Institute of Botany and Applied Cultures in the Soviet Union (Figure 1). Vavilov was well connected throughout the world with scientists such as William Bateson and Hermann Joseph Muller, and incorporated the work of non-Russian scientists into his work—including the work of Gregor Mendel, Charles Darwin, and Thomas Hunt Morgan (Crow 1993). Vavilov was in no way controversial in his scientific views. He was at the forefront in the mainstream of scientific thought in the area of genetics and plant breeding during his career. Vavilov served as vice president to the 1932 XI International Genetics Conference held in Ithaca, NY, and was elected president of the 1939 XII International Genetics Conference held in Edinburgh, Scotland. Vavilov saw value in integrating scientific ideas from throughout the world, while at the time the Soviet Union was becoming more isolated (Crow 1993). Vavilov had created a comprehensive plant breeding and genetics program to rival any other in the world and he did it by not being closed off to the world but by being open to all discoveries and ideas that all had to offer (Medvedev 1970). But in the Stalinist-led Soviet Union, scientists affiliated with persons outside the country were seen as possible conspirators against the government (Crow 1993; Medvedev 1970). Vavilov was frequently labeled a traitor and spy for foreign governments plotting to destroy the Soviet Union by not producing improved varieties of crops fast enough, thus prolonging famines and starvation.

Trofim Lysenko was a self-taught crop scientist who garnered attention as an opponent of Vavilov. Lysenko used political posturing, bold promises that could not be delivered upon, and absolute lies to destroy scientific research in the Soviet Union beginning in the 1930s (Crow 1993; Medvedev 1970; Roll-Hansen 2005). Lysenko dismissed the dominant scientific theories of the day proposed by Mendel, Darwin, and Morgan, such as basic heredity, chromosome theory, and the existence of mutations (Medvedev 1970). Lysenko and his Lysenkoists created theories based on Lamarckism, which stated that environmental factors experienced by an organism could be passed off to the offspring (Crow 1993). Building upon Lamarckism, Lysenkoists had to develop a new doctrine to replace mutation and chromosome theory. To Lysenko, the hereditary unit of a plant was the cell itself. Lysenko believed that by subjecting the cell to a given environment one could change the plant into a more fit variety or plant type (Crow 1993). Lysenko theorized that there were certain points in the life of a plant in which the environment was "assimilated" into a plant's heredity (Medvedev 1970). But at other periods in the life history, a plant would not be influenced by environmental stimuli. Lysenko proposed that the stress itself actually caused changes that would lead to greater stress tolerance in plants. As an illustration of this ignorance, Soyfer (1989) presents a picture dated 1948, which shows Lysenko boldly claiming he had even used this method to change *Triticum* spp. (wheat) into *Secale cereale* L. (rye). It must be noted that Lysenko's ideas fit well into political thought at the time, as the Communists held that if Communism created a better environment for the people then the people themselves would improve, and that these improvements would then be passed on to subsequent generations (Roll-Hansen 2005), the correlation being that Marxism improves the people just as the conditions in which a plant is grown change the plant and the subsequent plant generations. Interestingly, Mendelian genetics was seen as anticommunist in the Soviet Union at the time and the contention between Western and Soviet science over Mendelian genetics is an example of one of the first propaganda battles of the Cold War (Wolfe 2011).

The downfall of Nikolai Vavilov occurred throughout the 1930s, with the final blow from Trofim Lysenko occurring in 1935 to 1938, which led to Vavilov's eventual death in 1943 (Crow 1993; Medvedev 1970; Soyfer 1989). Until the mid-1930s, Vavilov had encouraged Lysenko to develop his theories and had done little to directly confront Lysenko publically about the lack of scientific justification for his research. But during this time, Lysenko began to aggressively name Vavilov as an enemy of his research and thus an enemy of the Soviet Union (Soyfer, 1989). Stalin, working through Lysenko, had eliminated all opposition and the Stalinist puppet Lysenko was named president of the Lenin Academy in 1938 (Roll-Hansen 2008). The Soviet government did not allow Vavilov to travel to Edinburgh, Scotland, to attend the 1939 XII International Conference of Genetics to serve in the honorable position as president. Vavilov was arrested while on a collecting expedition in Ukraine in 1940, imprisoned, and eventually died from the harsh conditions of Saratov prison in 1943. To illustrate how isolated Vavilov had become from his friends and colleagues throughout the world, notwithstanding the effect of the added complexity of World War II, it was initially thought that Vavilov died in 1942 not 1943 (Dozhansky 1947; Harland 1954; Hawkes 1990).

Trofim Lysenko is seen today as the poster child for pseudoscience (Roll-Hansen 2005). Lysenko was a puppet of the Stalin regime who couched scientific ideas in political rhetoric in order to destroy opposition. Science requires free and open exchange of ideas and scientists should never fear reprisal for truthful reporting of their work. Lysenko's actions and his impact on Vavilov and Soviet science in general should be a historical lesson that the scientific community never forgets.

The Centers of Origin of Cultivated Plants: The Legacy of Nikolai Vavilov

Much of the work of Nikolai Vavilov has been compiled into a single text, *Origin and Geography of Cultivated Plants*, comprising 25 separate manuscripts. The compilation of the Russian version of these manuscripts was published in 1987 on the 100th anniversary of Vavilov's birth. The English version was published in 1992. As a matter of convenience, this manuscript is cited as "Vavilov 1992, page number" to allow for ease of reference to this book.

> By knowing the past, looking at elements from which crops developed and gathering cultivated plants in the ancient centers of agriculture, we hope to learn soon how to control the historic processes and how to change cultivated plants and domesticated animals in a manner reflecting the interests of our modern times.
>
> —Nikolai Vavilov (Vavilov 1992, p. 173)

Nikolai Vavilov's greatest contribution to science was his identification of the centers of origins of many modern crops (Hawkes 1990). Vavilov recognized, building off the previous work of Alphonse de Candolle, that centers of origin represent the areas of greatest genetic diversity. As stated, "the region of maximum variation, usually including a number of endemic forms and characteristics as well, can usually also be considered as the center of type formation" (Vavilov 1992, p. 32).

Consider the center of origin of the *Triticum aestivum* L. (soft wheat), referred to as *Triticum vulgare* L. by Vavilov. According to Vavilov, the maximum area of variation of *T. aestivum* is centered in southwestern Asia, specifically within Afghanistan, Pakistan, and northwestern India. Vavilov described many wild types and landraces of *Triticum* spp., which were previously unreported (Vavilov 1992, p. 36). In describing the *T. aestivum* of Afghanistan, Vavilov noted the greatest diversity in the Hindu Kush mountain region surrounding the city of Kabul (Vavilov 1992, p. 36). He also described similar regions of maximum diversity for *Triticum compactum* Host (clubbed wheat) and *Triticum sphaerococcum* Percival (Indian dwarf wheat) in the region of these three modern-day countries. Within these species, Vavilov focused on the variation that occurred within a given species in the centers of origin that he developed into his seminal work, *The Law of Homologous Series in Variation* (Vavilov 1922). Vavilov's law of homologous series of variation attempted to define the polymorphic nature of many of the world's crops, including *Triticum* spp., *Hordeum vulgare* L. (barley), *Avena sativa* L. (oat), *S. cereale*, *Brassica* spp., and *Cucurbita* spp. In this work, Vavilov defined species-specific characteristics that could vary within a species. The most impressive of these was Vavilov's reporting of 3,000 different types of *T. vulgare* that, according to Vavilov, were "perfectly recognizable morphologically" and did not include those bred from Western Europe (Vavilov 1922). It is difficult to fathom the knowledge needed to separate 3,000 different plant types of *T. vulgare*, as well as the time and energy it took to make such a classification, notwithstanding the time it took Vavilov to make the collections and the distance he had to travel.

Vavilov described the southwestern Asia region of modern-day Turkey, Syria, Iran, Iraq, Pakistan, Afghanistan, and the Caucasus regions of Georgia, Armenia, and Azerbaijan as containing "a wealth of varieties and races" (Vavilov 1992, p. 39). He encouraged plant breeders to "search for new types of soft wheat in the mountain areas of southwestern Asia" because "all the enormous variety of spring and winter types … are represented here" (Vavilov 1992, p. 39). Vavilov made similar lengthy excursions to discover the centers of origin of *Triticum durum* L. (hard wheat) and *Triticum monococcum* L. (Einkorn wheat). It is no wonder that an obituary written of Vavilov states that he had "a mind that never slept and a body which for its capacity for enduring physical hardships can seldom have been matched" (Harland 1954; Hawkes 1990). It should be noted that while the general principle of centers of evolutionary origin remains a general principle of biology, Vavilov's distinct areas of plant evolution have been challenged (Simmonds 1995). Without discounting his work, biologists simply recognize that centers of origin are more diffuse and evolutionary processes more complex than thought by Vavilov and that the centers of origin theory simply does not apply to all species (McCoy and Heck 1976; Simmonds 1995). While this scenario of maximum diversity within centers of origin is true for *S. cereale* and other species, it is not an absolute as other evolutionary processes can influence species diversity and evolution (McCoy and Heck 1976).

In attempting to locate the centers of origin of *S. cereale*, Vavilov and others came to the conclusion that *S. cereale* had a polyphyletic origin (Vavilov 1992, pp. 57–58). Multiple possible origins were attributed to the existence of weedy *S. cereale* in other grains. Thus, weedy plants seemed to have the potential to serve as the origin of modern-day cultivated species. As stated by Vavilov, "Many presently cultivated plants originated from weeds infesting the crops of more ancient cultivated species" (Vavilov 1992, p. 18). Vavilov found the greatest diversity of *S. cereale* in modern-day Afghanistan, Georgia, Turkey, and Iran (Vavilov 1992, p. 79). To illustrate the diversity of *S. cereale*, Vavilov wrote of 18 separate varieties of *S. cereale* found in Afghanistan. But in these areas, *S. cereale* was a weed of *Triticum* spp. and *H. vulgare*. In Turkish, the common name for *S. cereale* translates to "the plant that torments the wheat and barley" (Vavilov 1992, p. 84). Vavilov wrote of Afghan farmers who would sweep the *S. cereale* spikes from the fields with brooms in the hope it would not return the next season (Vavilov 1992, p. 83) as well as a second practice that allowed the *S. cereale* spikes to rise above the wheat canopy, at which point they could be safely "mowed" and removed (Vavilov 1992, p. 86). Those who implemented this practice were exempt from taxes.

Other research has further substantiated Vavilov's theory that *S. cereale* first arose as a weed in *Triticum* spp. Sakamoto (1982) reported a wide distribution of wild ancestral species of *S. cereale*—*Secale segetale* (Zhuk.) Roschev. and *Secale afghanicum* (Vav.) Rochev.—from the Mediterranean throughout the Middle East whose distribution overlapped that of the wild ancestors of *Triticum* spp.. Sakamoto (1982) further substantiated the distribution and weedy nature with personal observations of *S. cereale* varieties observed as a major weed in northern Afghanistan in *Triticum* spp. fields. Five principal weedy *Secale* species have described throughout the Middle East with various adaptations and weedy characteristics: *Secale montanum* Guss. Emend. Sencer, *Secale ancestrale* Zhuk., *S. segetale*, *Secale dighoricum* (Vav.) Roschev., and *S. afghanicum* (Sakamoto 1982; Stutz, 1972). Sencer and Hawkes (1980), referencing morphological, ecological, archaeological, and cytology data, confirmed that *S. cereale* evolved from *S. montanum* as a weed of *Triticum* spp. and *H. vulgare* fields. Two characteristics, nonshattering rachis and increased caryopsis size, led to both the unconscious and conscious selection and eventual evolution of *S. cereale* as a desirable crop (Sencer and Hawkes 1980). Specifically, Sencer and Hawkes (1980) named the high-elevation area of eastern Turkey between Lake Van and Mount Ararat as the most likely location of *S. cereale* evolution as a species and the location at which its transition from a wild to weedy species occurred. Becoming a weed and seed contaminant of *Triticum* spp. and *H. vulgare*, *S.*

cereale could spread, adapt, and eventually overtake desirable grains in other high-elevation areas where it was more adapted.

One can imagine how the world's major grain crops came to be as humans moved from hunter–gatherer to agrarian societies. Hunter–gatherer societies underwent three distinct stages in the domestication of cultivated plants: gathering, cultivation, and domestication (Weiss et al. 2006). For grains, the two main characteristics that would have led to cultivation are enlarged grains and seeds that do not dehisce via nonshattering rachis (Weiss et al., 2006). Harvesting by panicle or spike removal would have selected for nondehiscent seed, whereas harvesting by beating or thrashing could have preserved dehiscent seed characteristics or even selected for increased dehiscent characteristics (De Wet and Harlan 1975). Change from gathering to cultivating societies was likely a slow process with starts and stops until domestication was achieved (Murphy 2007). To quote De Wet and Harlan (1975), ''Suffice it to say that domestication is a continuous process, not an event.'' Regardless, the key factor germane to this discussion is that ancient peoples would have purposefully selected the crops they wanted to domesticate, such as *Triticum* spp. and *H. vulgare* in southwestern Asia and the Caucasus. And in the domestication of these species, enlarged grain and nondehiscence would have been some of the first characteristics selected.

But *S. cereale* did not arise as result of gatherer preference and selection of desirable characteristics; rather the crop origin of modern *S. cereale* arose as a weed of the desirable cereals (Vavilov 1992). To eliminate the contaminating *Secale* spp. ancestors, ancient peoples would have had to develop a keen visual understanding of how to differentiate the ancient *Secale* spp. from desirable cereals. Eliminating desirable species would have been unacceptable because one would be reducing a likely fragile food supply. Thus, *S. cereale* evolved by initially mimicking the visual appearance of *Triticum* spp. and *H. vulgare*. Once grain ears were produced, *Secale* spp. would be selected for nondehiscence in the harvest process. As for the origin of *S. cereale*, Vavilov was able to describe a weed species that evolved with the desirable crop to become the desirable crop itself.

> If the above facts are taken into consideration, the history of the origin of cultivated rye becomes straightforward and very simple. The ancient crops of winter wheat and winter barley, when transferred from south toward the north, east and west brought with it rye in the form of a weed. When cultivated under more severe conditions with colder winters and on poor, podsolic soils, rye began to overpower the weaker wheat and barley types.'' (Vavilov 1992, p. 88).

Thus, in the context of understanding the evolutionary history of crops, Vavilov describes key concepts related to weed science—weed transport via seed contamination and increased weed competition under nonoptimum crop growth conditions. But possibly more importantly, Vavilov describes the ability of a weed species to evolve to appear phenotypically similar to the desirable crop, evolve to tolerate management practices applied to the desirable crop, or both—a process that should be known as Vavilovian mimicry (Pasteur 1982).

Vavilov and the Theory of Plant Mimicry

> All these examples illustrate the amazing hereditary variability of the species of cultivated plants as well as of weedy species, and the role of an unconscious selection during their formation.
> —Nikolai Vavilov (1992, p. 439)

> The borderline between crops and weeds is often tenuous and may be only a matter of opinion ….One man's weed is another man's crop.
> —Jack R. Harlan (Harlan 1982)

To any weed scientist the idea that weeds can adapt to agricultural practices is obvious. Weed adaptation and changes in weed species composition as influenced by crop and weed management practices are well known (e.g., Shaw 1964; Skroch et al., 1975). From herbicide-resistant weeds to the study of diverse weed ecotypes, it is known that weeds adapt. What is often not considered, however, or at least to a similar extent, is the long-term evolutionary consequences of such adaptation as was seen with the evolution of *S. cereale* (Ellstrand et al. 2010; Harlan 1965). Vavilov recognized that certain weed species adapted so well to human activity over the course of their evolutionary history that humans lose their ability to discriminate between the desirable species and the weeds. In early agriculture, physical removal of weeds required the ability to discriminate between desirable crops and weeds. It is a phenotypic adaptation process whereby a discriminating organism or implement can no longer distinguish between the crop and weed. This tactic of plant adaptation is referred to as "crop mimicry" (Barrett 1983), or, in order to give homage to the legacy of Nikolai Vavilov, "Vavilovian mimicry" (Pasteur 1982).

There are three key players in Vavilovian mimicry: (1) the model—the crop or desirable plant that is being imitated; (2) the mimic—the plant that is imitating the model; and (3) the operator—the discriminating entity that distinguishes between the model and the mimic (Vane-Wright 1980; Wiens 1982). The majority of documented mimicry cases involve insects or animals (Williamson 1982). Insects and animals have the ability to move and disperse into the background or among the model species (Williamson 1982). Dispersion increases the difficulty of the operator to distinguish the mimic. Plants are both sessile and tend to aggregate, both traits that are disadvantageous for mimicry. Williamson (1982) suggested that plants can bypass these characteristics by discontinuous flowering and by utilizing seed mimicry to increase dispersal with the model seed by the operator.

There are several different types of mimicry. True mimicry, or Vavilovian mimicry in the case of weed species as defined above, is simply the inability of an operator to distinguish between the model and the mimic. Crypsis is a form of mimicry in which the operator is unable to distinguish between the mimic and the background, e.g., an insect camouflaged in the bark of a tree (Endler 1981). Crypsis could also include a vining plant that climbs a model plant with both having similar leaf characteristics, thus making it more difficult for the operator to distinguish between the two until flowering or fruiting. Other definitions of mimicry distinguish between how the mimicry affects the evolution or population dynamics of the mimic and whether the model is a single species or multiple species (Endler 1981). For weed science, true Vavilovian mimicry and crypsis are the most important forms of mimicry, with other forms most applicable to insects or animals.

A question arises: Who or what is the operator? In the eyes of Vavilov the operators were ancient farmers within the areas of evolutionary origin of our modern-day major cereal grains. However, these ancient mimetic practices are no longer in place (Barrett 1983). One can imagine these ancient farmers removed undesirable plants by hand or with rudimentary tools, learning to distinguish based on the subtle visual differences between leaf fold, leaf coloration, or overall growth habit. But over time these differences may have become less apparent, leading to decreased discrimination and allowing visually similar biotypes to survive. Such a mimetic system is what could have given rise to weedy *S. cereale*. But it is important also to understand that the transition of wild to weedy in the domestication of *S. cereale* is an extreme case and that although wild plants can become weedy, very few actually become domesticated desirable plants.

It is unknown how these mimetic systems developed, considering that the practices that led to development of *S. cereale* have been lost to history. Therefore, modern-day mimetic systems are needed to support this theory. A modern example of Vavilovian mimicry is the selection of *Echinochloa crus-galli* (L.) Beauv. subsp. *oryzicola* in rice (Barrett and Wilson 1981; Harlan 1982). *Echinochloa crus-galli* (barnyardgrass) is so biotypically diverse that it is often referred to as the barnyardgrass complex due to the large number of subspecies (Barrett and Wilson 1981; Danquah 2002; Schlichting and Levin 1986). *Echinochloa crus-galli* subsp. *oryzicola* is more upright in growth and has a white midrib similar to cultivated rice (Gould 1991). *Echinochloa crus-galli* subsp. *oryzicola* adaptation to rice production has limited its ability to exist as a weed in other environments where seasonal drought can limit its fitness compared to *E. crus-galli* subsp. *crus-galli*.

Another historic case of Vavilovian mimicry is that of a contaminant plant with *Vicia sativa* L. (common vetch) contaminating *Lens esculenta* L. (lentils) as described by Rowlands (1959). What puzzled scientists at the time was that the vetch-like contaminant was morphologically similar to *V. sativa* but produced a flat seed seemingly identical to *L. esculenta* rather than the more spherical-rounded seed produced by *V. sativa*. While it seems obvious in hindsight that the vetch-like contaminant was actually *V. sativa* that was a Vavilovian seed mimic of *L. esculenta* selected for due to the inability to separate flat *Vicia sativa* seed from *L. esculenta*, to researchers at the time this was a controversial topic. Dmitriev (1952) had reported, citing Lysenko (1950), that the flat-seeded, lentil-like *V. sativa* was actually lentil that had been converted to *V. sativa* but retained its flat-seeded characteristic. Such was the power that Lysenkoism pseudoscience held over Soviet plant science at the time. Rowlands (1959) described extensive testing to refute the idea presented by Dmitriev (1952) with the primary evidence being that the flat-seeded seeded *V. sativa* was completely incompatible with *L. esculenta*. But when the flat-seeded *V. sativa* was crossed with rounded, the sphericalseeded types yielded a classic Mendelian 3 : 1 pattern in the F2 generation, with rounded seed being dominant over flat seed.

As described by Rowlands (1959), V.S. Dmitriev was another crony of Lysenko bent on promoting the pseudoscientific agenda of Stalin. Dmitriev (1951) also had described how *S. cereale* could be converted to weedy *Bromus secalinus* L. (cheat)—actually claiming that Russian scientists could convert one species into another! Rather than employing Occam's razor, that the simplest explanation is the most likely explanation, which in this case is that *B. secalinus* is a common weed in *S. cereale* and separation of seed is difficult, Dmitriev continued to promote such pseudoscientific beliefs.

In all fairness, I was unable to obtain English translations of any of Dmitriev's work and instead had to rely on secondary-source interpretation of Dmitriev's work, primarily Rowland (1959) in this case. Other work clearly substantiates the theory promoted by Lyseknoists that they could convert one species into another (see Medvedev 1970; Soyfer 1989).

Examples of Vavilovian Mimicry in Weed Science

Flat-seeded *V. sativa* represents a subset of Vavilovian mimicry known as seed mimicry. Harlan (1982) states, ''Seed mimicry is, perhaps, more common than vegetative mimicry. Here the weed need not fool the farmer's eye; it needs only to fool a machine or winnowing process.'' *Cardiospermum halicacabum* L. (balloonvine) has a similar seed size and shape to *Glycine max* L. (Merr.)(soybean) and is often referenced as a seed mimic due to the inability to separate the two seed mechanically (Johnston et al. 1979).

In classifying a weed adaptation mechanism as a true Vavilovian mimic, how one defines the operator is a key factor. To illustrate this, consider the following two possible mimetic systems: mowing adaptation and herbicide resistance. *Poa annua* L. (annual bluegrass) has two possible subspecies: *Poa annua* subsp. *annua* (L.) Timm. and *Poa annua* subsp. *reptans* (Hausskn.) Timm. (McElroy et al. 2002). *Poa annua* subsp. *annua* is considered to be a winter annual with germination in the late summer or autumn and flowering and eventual death in late spring to summer. *Poa annua* subsp. *reptans* is considered to be a perennial species that is more adapted to close mowing of golf course putting greens. La Mantia and Huff (2011) have theorized that *Poa annua* subsp. *reptans* develops due to an epigenetic adaptation mechanism and *Poa annua* subsp. *reptans* will revert back to subsp. *annua* over several generations if mow pressure is removed. In this case, the model is the desirable turfgrass, in most cases *Agrostis palustris* L. (creeping bentgrass), and the mimic is *Poa annua* subsp. *reptans*. The operators in this case are humans and the turfgrass mower. *Poa annua* subsp. *reptans* maintains higher turfgrass quality under golf course putting green conditions than subsp. *annua* presumably due to increased mowing tolerance. *Poa annua* subsp. *reptans* is often allowed to survive under golf course putting green conditions with no further control practices employed due to the improved turfgrass characteristics over than *Poa annua* subsp. annua. Due to increases in visual quality and tolerance to mowing, *Poa annua* subsp. *reptans* can be classified as a Vavilovian mimic as it has developed desirable characteristics similar to the desirable *A. palustris* crop.

Quite possibly the most prominent mimetic system in modern agriculture is that of de novo herbicide-resistant weed development due to selection pressure created by continuous herbicide use. Selection for herbicide resistant weeds is a historical problem with the vast majority of herbicide modes of action experiencing at least one evolved herbicide-resistant weed species. Acknowledging that herbicide-resistant weeds are a historical problem for all herbicide modes of action, in the past 10 years, however, glyphosate-resistant weed species have arisen as a preeminent problem primarily because of the mass adoption of glyphosate-resistant crops. As pointed out by Barrett (1983) however, the ''model'' does not have to be present in such a system, as is the case with *Conyza canadensis* (L.) Cronq. (horseweed) that was treated in a burndown scenario prior to spring crop planting (VanGessel 2001). But while the model was not present in this case, herbicide applications were made in preparation for the model. With chemical selection via herbicides, selection becomes molecular differentiation. Mimicry moves away from visual characteristics distinguished by humans, grazing animals, or machinery to mimicry at the biochemical level. One could argue that chemical-assisted selection of *Amaranthus palmeri* S. Watts. (Palmer amaranth) in glyphosate-resistant crops should be classified as a mimetic system, considering the model was present at the time of selection and the mimic is simply adapting the primary operator, in this case glyphosate applied by humans (Culpepper et al. 2006; Norsworthy et al. 2008). It is the opinion of the author however, that de novo herbicide resistance should be classified as Vavilovian mimicry. Weed management systems changed dramatically in the 20th century, moving from primary physical weed control methods utilized throughout human history to chemically assisted weed control. Although adaptations to herbicide applications are not based on changes of physically identifiable attributes, changes are based upon quantifiable physiological and molecular changes that mimic the biological processes of plants tolerant to a given herbicide. To put it simply, a herbicide-resistant plant may not look different to us, but it certainly ‘‘looks different’’ to the herbicide.

These examples illustrate the difficulty of excluding or including certain weed adaptation scenarios based on the provided definition of Vavilovian mimicry. Alternatively, it is proposed that Vavilovian mimicry of weed species be defined broadly as ‘‘natural selection associated with agricultural practices’’ (de Wet and Harlan 1975). A broader definition would include seemingly all weed adaptation scenarios in anthropogenic systems, including herbicide resistance development.

Vavilovian Mimicry and the Future of Weed Science

Today we live in an era of rapid weed adaptation to herbicides. Herbicide-resistanct weed species are being discovered at an alarming pace due to usage of herbicides in diverse crop and noncrop areas and due to the broad adoption of genetically modified crops primarily resistant to glyphosate. Just as *S. cereale* arose from the inability of farmers to differentiate these species from *Triticum* spp. and *H. vulgare*, so the herbicides applied eventually lose their ability to differentiate between the desirable crop and the weed they once could control. Both are processes of human selection as part of our food production process. By and large the weed science community is focused on herbicide resistance adaptation and less focused on how plant species could be adapting to management practices in other ways. Such a focus is to be expected, as herbicide resistance is the biggest problem facing chemical-based weed control, which is the predominant means of weed management in much of the world. There is a possibility, however, that weeds are adapting to tillage practices, plasticulture, mowing, burning, fertility practices, irrigation practices, or any other management practice and such adaptations are not being seen simply because these areas do not receive the same degree of attention given to herbicide resistance.

The major lesson weed scientists should take from Vavilov is that weeds will continue to adapt to the actions of humans. Weeds have the ability to adapt to herbicide treatments regardless the number of herbicide resistance traits that are ‘‘stacked’’ into a genome. ‘‘Evolution occurs in space and time’’ (Vavilov 1992, p. 130). When herbicides are applied on enough acreage over a long enough time scale, herbicide-resistant weeds will be selected for.

But Vavilov also teaches us that weeds can evolve beneficial uses for humans based on changing societal needs. If you need convincing, perhaps you should consider including some *Portulaca oleracea* L. (common purslane) or *Taraxacum officinale* F.H. Wigg (common dandelion) in your next fresh salad (Lizarazo et al. 2010; Smith and Figueiredo 2010), or think about trying *Chenopodium album* (common lambsquarter) extract as your reducing agent the next time you want to synthesize some gold or silver nanoparticles (Dwivedi and Gopal 2010). And perhaps greater focus is needed on the minor grain crops and their associated weedy relatives to feed our growing world population. For example, millets are minor grain crops that receive very little attention for breeding efforts compared to traditional crops. Millets such as *Eleusine coracana* Gaertn. (finger millet), *Panicum miliaceum* L. (proso millet), *Pennisetum glaucum* (pearl millet), and *Setaria italica* (L.) R.Br. (foxtail millet) have been utilized as grain supplements for millennia and are currently used by subsistence farmers in Africa for both human consumption and forage crops (Murphy 2007). Each of these millets has known weedy relatives—*Eleusine indica* (L.) Gaertn, *Pennisetum polystachion* (L.) Schult, and *Setaria glauca* (L.) Beauv as examples—in agricultural crop production or other managed systems. Diversity in weedy relatives of millets could potentially advance breeding efforts and genetic understanding of the desirable millets leading to increased development of these underutilized crops. As stated by Vavilov, ‘‘The plant breeder, interested in the selection of varieties of rye, must turn his attention to the weedy rye that infests the fields…’’ (Vavilov 1992, p. 89).

New weed control technologies are being suggested that could reintroduce a need to understand Vavilovian mimicry in weed science. Weed control technologies are being developed that utilize sensor technologies to differentiate weeds, which are then targeted with a directed herbicide application or are physically removed (Young and Meyer 2012; Zijlstra et al. 2011). Researchers are developing automated robots able to move through fields removing weed species and leaving the desirable crop. Automation assumes that technology can be programed to differentiate between desirable plant and weed. The eventual adaptation of weeds to appear phenotypically similar to crops and thus become resistant to automated differentiation of weed species via sensor technology could bring the scientific community back around full circle to the initial observations of Nikolai Vavilov and his theory of Vavilovian mimicry.

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