Luther Burbank: Honorary Member of the American Breeders' Association

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Luther Burbank (1849–1926) was once widely acclaimed to be America's most famous horticulturist and plant breeder. Today, however, his name may not be recognized by many in the general public. I found that he is also unknown to even some academic horticulturists whose formal coursework apparently did not include a history of their discipline. To those scientists who know something of him, he is often viewed as a tyro and/or a charlatan. Even highly respected modern plant-breeding books fail to mention his name (e.g., Allard 1960). His life's work straddled the post-Darwinian period and nearly three decades into the 20th century. During this era, Francis Galton initiated eugenics studies, August Weismann asserted that there is no connection between the germ plasm and the somatoplasm (thus rendering the theory of the inheritance of acquired characteristics untenable), Hugo de Vries proposed that mutations were the basis of rapid species formation, and Gregor Mendel formulated some basic laws of heredity. Burbank embraced eugenics but rejected Weismannism, the mutation theory of de Vries, and the gene concept of Mendel. Instead, he clung to the theory of the "inheritance of acquired characteristics," an ancient notion popularized in 1809 in a book by the French naturalist J. B. Lamarck (1744–1829). Burbank claimed that his success as a plant breeder rested firmly on Darwinian principles. In his book *On the Origin of Species* (1859), Charles Darwin resorted to the theory of the inheritance of acquired characteristics because it was the only explanation for heredity at the time. Lamarck did not explain how the effects of changed environments could result in heritable adaptive changes in organisms, so Darwin resurrected an old theory he called "pangenesis" in his 1868 book *The Variation of Animals and Plants under Domestication*. Cells in various parts of the body released hereditary particles (Darwin called them "gemmules") that found their way to the reproductive cells (eggs and sperms). During the development of progeny from the fertilized egg, each gemmule would guide the formation of the part of the body from which it was derived. Thus, it might be possible that environmental modifications of the traits of parents could become heritable (capable of being transmitted to offspring). Burbank retained his belief in the inheritance of acquired characteristics even after the discovery of Mendel's paper in 1900 and throughout the rest of his life.

At the opening meeting of the American Breeders' Association (ABA) at St. Louis in 1903, Burbank was unanimously elected to honorary membership. In the early proceedings of the association, a number of articles by him appeared under the titles "Heredity," "Right Attitude Toward Life," "Another Mode of Species Forming," and "Evolution and Variation with the Fundamental Significance of Sex." So why was Burbank held in such high regard in the early days of genetics? What happened to his reputation in his later years? And whatever became of the theory of the inheritance of acquired characteristics?

Burbank's Rise to Prominence

Burbank was born and raised in Massachusetts where, at the age of 22, he began truck gardening and selling his vegetables at a local market. In 1873, Burbank found a very rare pod of seeds on an Early Rose variety of potato plant. He planted all 23 seeds, grew 23 seedlings, and selected two of the best. He propagated one cluster asexually and named it the Russet Burbank. Over 100 years later, it was still the most widely grown potato in the United States, albeit under different names. Looking for a more equitable climate than in Massachusetts, he moved to Santa Rosa, California, in 1875 and established a nursery there in 1877. It is said that after he arrived in Santa Rosa he found "enough new and curious plants . . . to set a botanist mad" (Dreyer 1993). He brought 10 of his potatoes to Santa Rosa and continued propagating them for sale. He bought seed and plants from sources elsewhere (sometimes from nurserymen in foreign countries) and propagated the plants for sale, locally at first, but as his reputation grew, eventually nationwide and internationally. He claimed that in his plant-breeding programs, he often made crosses between different varieties of a species (sometimes even between closely related species) in order to disrupt in the hybrids inherited tendencies from the parents. First-generation hybrids tended to be intermediate for many

characteristics (especially quantitative ones with complex heredity), but Burbank recognized that some traits were like those of one of the parents due to "prepotency of the life forces" (Dreyer 1993). This was in 1893 before Mendelian dominance had been rediscovered. Rigorous selection of desired individuals (saving perhaps only one in a thousand plants) from the first generation produced parents for the second-generation hybrids, which usually had much greater variability than the first generation. Sometimes backcrosses or additional hybridizations, together with continued rigorous selection in subsequent generations toward his ideal phenotypes, were often required to move the lineage in the direction he desired and to fix the traits so they would essentially breed true thereafter. He had an uncanny ability to select, sometimes over many generations, for several traits simultaneously toward an ideal type that he envisioned at the start. Sometimes hundreds of grafts were made on the same tree, enabling Burbank to raise the entire progeny of a cross to maturity only 2 years from the planting of the seed. He regularly sent out catalogs listing his newest products to potential buyers across the country. His ability to produce new varieties or improve old ones became legendary. Some people labeled him a "wizard." De Vries initially declared him "a gardener touched with genius" (Dreyer 1993).

In 1902, Burbank submitted a short paper on "The Fundamental Principles of Plant Breeding" to be read at the First International Conference on Plant Breeding and Hybridization in New York that same year. Burbank hated speaking in public, but he did not mind expressing himself in writing (if he had the time). Thus, his fame was well established by this time, and the next year he was given honorary membership in the ABA (predecessor of the American Genetic Association). A Committee on Eugenics was established in 1906 by the ABA, chaired by David Starr Jordan, a well-known biologist and chancellor of Stanford University. Among other luminaries on the committee was Alexander Graham Bell, inventor of the telephone, sheep breeder, and eugenics researcher into hereditary deafness (Stansfield 2005). Despite his belief in the inheritance of acquired characteristics, Burbank was made a member of the eugenics committee (Dreyer 1993). Even though he had no biological children of his own at the time (he became a stepfather to a child only a few years old when he married his secretary Elizabeth Jane Walters in 1916), Burbank felt competent enough to write a eugenics essay entitled "The Training of the Human Plant." It first appeared in *Century* magazine (1906) and was later reissued in book form in 1907. In this essay, he vacuously defined heredity as "simply the sum of all the effects of all the environments of all the past generations on the responsive, ever-moving life forces." Later in his essay he states:

> My own studies have led me to be assured that heredity is only the sum of all past environment, in other words environment is the architect of heredity; and I am assured of another fact: acquired characters *are* transmitted and—even further—that *all* characters which *are* transmitted have been acquired, not necessarily at once in a dynamic or visible form, but as an increasing latent force ready to appear as a tangible character when by long-continued natural or artificial repetition any specific tendency has become inherent, inbred, or "fixed," as we call it.

Burbank saw in human populations of the United States a vast reservoir of biological diversity in its genetic composition. He envisioned that from the "blending" (hybridization/intermarriage) of these various types plus the rearing of children in the most favorable environments, repeated generation after generation, a far better class of humans would emerge. Among the favorable "environments" for children he lists are love, honesty, self-respect, absence of fear, sunshine, good air, and nourishing food. Because he believed that children were being abused by the American educational system, he declared that "No boy or girl should see the inside of a school house until at least ten years old." Obviously, the latter recommendation did not sit well with professional educators, but nonetheless about 20 schools were named after him in California alone. Although the eugenics movement was sometimes viewed as an offshoot of Social Darwinism, it actually was more of an attempt to use science against the excesses of some Social Darwinists who favored inhumane social policies at home (mandatory sterilization of the mentally incompetent, biased immigration laws) and imperialism abroad (as later exemplified in the extermination of Jews by the Nazis during World War II) (Dreyer 1993). Despite the good intentions of the founders of the American eugenics movement, they eventually became labeled as "racists" by widespread public opinion.

Before 1889, Burbank crossed the Siberian raspberry (*Rubus crataegifolius*) with the cultivated variety of the California dewberry (*Rubus vitifolius*). He selected one of about 500 hybrid seedlings that showed many of the properties of both parents. The most surprising thing about it was that its progeny bred true from seed and did not revert back to either parental type in subsequent generations. Burbank claimed he had created a new species in a paper entitled "Another Mode of Species Forming" read at the annual meeting of the ABA in Columbia, Missouri, January 5–8, 1909; it was reprinted in *Popular Science Monthly*, September 1909. Some plant breeders thought that true-breeding hybrids simply could not exist. Burbank, however, believed that the same process by which he artificially produced true-breeding intermediate hybrid species also occurs in natural populations. Dreyer (1993) opines that "[T]his may be the first recorded report of this phenomenon" and "Burbank is not given the priority that he deserves for producing and putting these on record."

Although as early as 1886 Dutch botanist Hugo de Vries claimed to have found true-breeding "elementary species" arising in a single generation by "mutation" in the wild evening primrose (*Oenothera lamarckiana*), Dunn (1965) opined that most of them "were not 'species' but a heterogeneous collection of forms, none of which could take rank as a new taxonomic category." De Vries announced these examples of instant speciation in his book *Mutationstheorie* (1901). However, neither de Vries nor Burbank understood either the chromosomal mechanisms that produced these novelties or the importance of reproductive isolation that would later define the biological species concept. It was not until the 1920s

that amphidiploidy or allotetraploidy was identified as one of these mechanisms. The biological species concept would not become popular until the era of the modern synthesis in the 1930s and 1940s. Due to the work of Renner, Cleland, Sturtevant, S. Emerson, and others in the period 1915–1938, it was discovered that most races of *O. lamarckiana* probably evolved by (1) segmental interchanges or reciprocal translocations between nonhomologous chromosomes (Dunn 1965), (2) incorporation of gametic or zygotic balanced lethals, and (3) establishment of self-pollination (Swanson 1957). Because of these features, the structural heterozygosity peculiar to each race tends to breed true when self-pollinated. However, outcrossing may occur occasionally to break up the structural complex. Thus, most of the *Oenothera* races are not well isolated reproductively from one another and therefore are not considered to be "good" biological species.

If, on the other hand, two diploid ($2n$) species produce a viable diploid hybrid and the chromosomes of the hybrid zygote are doubled, a fertile $4n$ double diploid (amphidiploid, allotetraploid) may be created. If the chromosomes from each parent pair exclusively with their own members, the amphidiploid would be fully fertile, breed true to type from seed, and also be strongly reproductively isolated from its parental or other species; that is, it behaves as a "good" biological species. This mode of speciation was reported in 1939 to occur in the genus *Rubus* (Swanson 1957) and was presumably the mechanism responsible for Burbank's true-breeding hybrids. Most of de Vries' *Oenothera* hybrids did not always breed true, suggesting that they might have had a different origin from those of Burbank. Apparently, Burbank did not recognize this fact when he declared that

> I have selected mutants from my plants, and have developed from them new fixed races. But in the vast majority of cases I knew precisely how and why these mutations originated. They were hybrids; and they were mutants *because* they were hybrids. And so from the outset I have believed that Professor de Vries' celebrated evening primroses had the same origin. (Dreyer 1993)

De Vries and others claimed that Burbank had not created anything new in his hybrids but merely recombined traits present in the parent varieties or species. However, Burbank noted that hybrids between the great African "stubble berry" (*Solanum guine*[*e*]*nse*) and the Pacific coast "rabbit weed" (*Solanuum villosum*) are new species, and while the "*fruit of neither parent species is edible*, the fruit of the *newly created one is most delicious*" (Dreyer 1993).

Burbank's Fall from Grace

While Burbank enjoyed the company of many famous scientists and wanted to be recognized as an experimental scientist, he was not one himself. He was a commercial nurseryman/seedsman/horticulturist/plant breeder who had to make a living by propagating existing varieties (sometimes importing them from foreign countries) or by creating new or improved plant varieties and offering them for sale. Burbank commonly sold his "new creations" along with standard varieties to other nurserymen, some of whom would misleadingly advertise them as being all Burbank products. Too often, these secondary sources failed to maintain quality control of their products, and they soon began to deviate from Burbank's original types. The Luther Burbank Company was incorporated in 1912 to assume responsibility for propagating and marketing all of Burbank's products. Burbank neither invested in any of the company's stock nor took any interest in it. Instead, he was to receive $300,000—$30,000 in cash and the balance at $15,000 per year. Unfortunately, the company misrepresented its products, failed to maintain quality control, and soon went out of business. When the company declared it was bankrupt in 1916, stockholders received little or no compensation from the sale of the remaining assets. Burbank then resumed full control of his plant products and received the wrath of a lot of angry investors.

Burbank's sale catalogs (and those of his secondary sources) failed to adequately inform potential buyers that his plants might not perform as well as he described them if they were grown in climatic and/or soil conditions different from those of his gardens in Santa Rosa. Some of his plants were grown as far away as Europe or South Africa. Horticulturists should have been aware of the effects of different environments on the growth and health of plants, but Burbank often got the blame when the plants failed to perform as advertised in his catalogs.

Although Burbank claimed to have unearthed the laws of plant improvement, he never succeeded in clearly formulating them. Both amateur gardeners and professional horticulturists gained nothing new about how to successfully breed plants from reading Burbank's writings. Beyond providing good soil (texture, nutrients), plenty of sunshine, adequate space and moisture, weed removal, pest and disease control, pruning when needed, etc., all of which were known and practiced even by most amateurs, Burbank cited little else in the way of providing environmental conditions that would bring out the best attributes of different plants. As an avowed believer in the inheritance of acquired characteristics, one might expect that he would have been subjecting different plant species to more specifically altered environmental factors. He did not report doing so.

Mendel's work was rediscovered in 1900 (de Vries was one of three to independently do so), but not everyone was ready to jump on the Mendelian bandwagon. The theory of the inheritance of acquired characteristics was still very much alive. The mutation theory of de Vries nicely explained the origin of species, and most quantitative characters failed to follow Mendelian patterns of inheritance. It was a time of turmoil with many options yet to be tested. The establishment of the ABA in 1903 occurred against this historical backdrop. In true scientific spirit, the association members were eager to test these options even if some of them did not sound very promising. So they invited Burbank into their association and published his papers.

In 1905, the Carnegie Institution of Washington, D.C., gave Burbank a grant of $10,000 for the purpose of furthering his experimental investigations in the evolution of plants.

Another $10,000 was contemplated annually for as long a time as was mutually agreeable. A young botanist at the Carnegie Institution's Cold Spring Harbor Station for Experimental Evolution, named George H. Shull (later to become famous in large part for his work with hybrid corn genetics), was commissioned to go to Santa Rosa and find out everything he could in this regard. Aside from noting the wealth of new and improved varieties Burbank had produced, he found that there were scant records of ancestries and little of scientific value to report. Shull found that in many artificial hybridizations, no attempts were made to prevent a flower from self-fertilization or crossing with any other plant whose pollen might find its way thereto. In some cases, Burbank would apply pollen from several species to the same flower. Shull, in frustration, reported to his institute that such methods "lead to results that can not give any confirmation of Mendelism or any other theory of inheritance that rests upon statistical inquiry." The grant was terminated in 1909, and Shull was directed to complete his report in 1910. But the report was never completed, and thus whatever scientific value it might have contained was never published.

Around 1907, Burbank crossed Indian corn (*Zea mays*) with a related wild grass called teosinte (*Euchlaena mexicana*) and produced a hybrid with intermediate characters. From this, Burbank theorized that teosinte was very likely the wild ancestral form of modern corn (maize). The origin of maize remained a contentious issue for many years thereafter, but by the mid 1990s the "molecular evidence overwhelmingly favored the notion that teosinte was the ancestor of modern maize" (Fedoroff 2003). Burbank never received credit from Shull or anyone else for originating this idea.

Some folks objected with cries of "blasphemy" when Burbank or those who reported his work in the popular press referred to his plant introductions as new "creations." One jealous horticulturist quipped that he had "no more right to claim the title of 'creator' of new plants than he has to apply it to the bee that flits from flower to flower and carries the pollen" (Dreyer 1993). Undoubtedly, Burbank lost favor through the religious intolerance of more people when he called himself an infidel.

> The idea that a good God would send people to a burning hell is utterly damnable to me—the ravings of insanity, superstition gone to seed! I don't want to have anything to do with such a God. I am a lover of man and of Christ as a man and his work, and all things that help humanity; but nevertheless, just as he was an infidel then, I am an infidel to-day. (Dreyer 1993)

Russia's most famous plant geneticist, Nikolai I. Vavilov, visited Burbank in 1921 and wrote an obituary (Crow 2001) when Burbank died in 1926. In this document, Vavilov highly praised Burbank's practical achievements and minimized his mistakes and scientific naivete. Russia had its own horticultural wizard in a man named Ivan V. Michurin (1855–1935). Like Burbank, he was a commercial nurseryman with no scientific training and believed in the inheritance of acquired characteristics. T. D. Lysenko (1898–1976) emerged from obscurity in the early 1930s and soon became the champion in the application of the dialectical principle underlying Marxist communism in agricultural practice. He claimed to be following in the footsteps of his predecessor Michurin. Lysenko admitted his admiration for Burbank, saying "Much attention was paid by some of the best biologists—Burbank, Vilmorin and particularly Michurin—to the practical value of plant organisms with destabilized heredity" (Lysenko 1954). Western scientists rejected Lysenko as a quack long before he gained the political power to silence his detractors. In the end, Vavilov, who fought against Lysenko from the outset, was "silenced" by being sent to prison where he eventually died. These dictatorial acts enraged western scientists, and Burbank unfortunately became a kind of Lysenkoist by posthumous association.

Can Acquired Characters Be Inherited?

Although the theory of the inheritance of acquired characters is commonly believed to be a myth, several papers claiming to have discovered examples of the phenomenon have recently been published in peer-reviewed journals. Offspring receive more than just a set of chromosomes from their parents. The maternal gamete may contribute mitochondria, Golgi bodies, ribosomes, RNA molecules, cytoskeletal fibers, and many other interactive substances to offspring. The nuclear genome of a diploid organism consists of the nucleotide sequences in each set of parental chromosomes from which it was derived. However, it is now recognized that DNA can be epigenetically modified, for example, by the addition of other chemicals such as methyl groups (Mattick 2004). Methylated sequences are usually genetically inactive. These epigenetic alterations do not change the sequence of nucleotides an individual inherits from its parents (i.e., they are not considered to be mutations), but once they are acquired they can be passed on from one generation to the next in some organisms, including mammals. In a gametogenic phenomenon known as imprinting, a gene becomes inactive in progeny only if its controlling element is methylated in the egg and demethylated in the sperm from which the progeny developed; in other cases, methylation of the gene might occur in the sperm but not in the egg. Other phenomena such as horizontal gene transfer, adaptive mutation, and behavioral inheritance through social learning have recently been suggested as possible examples of inheritance of acquired characters (Cohen 2004; Danchin et al. 2004; Jablonka et al. 1998; Landman 1991).

Epilogue

"Burbank introduced over 200 varieties of fruits alone, consisting of 10 different apples, 16 blackberries, 13 raspberries, 10 strawberries, 35 fruiting cacti, 10 cherries, 2 figs, 4 grapes, 5 nectarines, 8 peaches, 4 pears, 11 plumcots, 11 quinces, 1 almond, 6 chestnuts, 3 walnuts, and 113 plums and prunes" (Howard 1945). Altogether, it is estimated that he was responsible for introducing between 800 and 1,000 plants to American horticulture and agriculture.

Passage of the first Plant Patent Law in 1930 was being argued in Congress with Paul Stark, then chairman of the National Committee for Plant Patents, and Archibald Augustine, president of the American Association of Nurserymen, as advocates. Congressman Fiorello La Guardia, later to become famous as mayor of New York, was a major opponent. When the sponsor of the bill, Congressman Fred S. Purnell, asked La Guardia what he thought of Luther Burbank, he responded "I think he is one of the greatest Americans that ever lived." Purnell then read into the record a letter that Stark had received from Burbank just prior to the old plant breeder's death in 1926. Burbank's letter argued persuasively for enactment of a plant patent law. La Guardia withdrew his objection, and the bill was passed in the House of Representatives and later also in the Senate. "Burbank's posthumous authority had secured for plant breeders the protection he himself had lacked" (Dreyer 1993).

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