# Luther Burbank

## Plant Breeder
## Horticulturist
## American Hero


**Papers presented at ASHS workshop**
**Edited by**
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**2015**

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# Introduction to the Workshop


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The workshop was held on Monday, 22 July 2013 in Desert Springs, CA, at the 110th Annual Meeting of the American Society for Horticultural Science to celebrate the extraordinary career of the most famous American Horticulturist. Its purpose was to honor Luther Burbank, legendary plant breeder and horticulturist; to examine his contributions and present the fate and impact of his creations; and to emphasize the role of artistry and horticulture in plant breeding. Burbank was an outstanding horticulturist, an innovative, truly amazing plant breeder, and a self-promoter who established the concept that plant breeding could be a business. He was a controversial figure and although he cannot be considered a scientist or geneticist in the academic sense, he made outstanding contributions to plant breeding, where he was truly an artist. In his lifetime he was considered in the panoply of great American inventers who include Samuel Morse, Thomas Alva Edison, Alexander Graham Bell, Henry Ford, and Cyrus McCormick. He was known as the plant wizard and he still remains the best known American horticulturist.

There were a total of seven speakers in the workshop. Jules Janick gave the opening presentation entitled "Luther Burbank: Plant Breeding Artist, Horticulturist, and Legend," which presented a biographical overview and career overview from his birth in Lancaster MA, in 1849, his glory days in Santa Rosa, CA, where he established his famous nursery, through his death in 1926. As a very young man he created his most famous plant discovery— the famous potato that bears his name, which incredibly was derived from 23 seeds and 15 seedlings of open-pollination of an introduction known as 'Early Rose'. This discovery and impact were treated in a presentation by Charles Brown entitled "Russet Burbank: "No Ordinary Potato." The contribution of Burbank to ornamentals was presented by Neil O. Anderson entitled "A Vast Array of Beauty: The Accomplishments of Luther Burbank, Father of American Ornamental Breeding," which includes the development of the 'Shasta' daisy, one of his most creative contributions. Two papers on plums followed: the first presented by David A. Karp entitled "Luther Burbank's Plums," which highlights the development of Japanese plums, and the second presented by Ann Callahan entitled "21st Century Approach to Improving Burbank's Stoneless Plum." This was followed by a presentation of John Preece entitled "Luther Burbank's Contribution to Walnuts." Finally Kim E. Hummer concluded with a presentation entitled "Luther Burbank's Berries." The workshop was well attended with vigorous discussion. The entire workshop has been videotaped and is available from the American Society for Horticultural Science.

# Luther Burbank: Plant Breeding Artist, Horticulturist, and Legend

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*Additional index words.* California, history, Santa Rosa

***Abstract*. Luther Burbank (1849–1926), the best-known horticulturist in the United States, was honored in 1940 by having a U.S. postage stamp in his honor—as a scientist! Burbank became a legend in his time as the plant inventor and horticultural wizard releasing a prodigious 800 new cultivars, a number of which are still being grown, the most famous being the 'Burbank' potato, the 'Santa Rosa' plum, and the 'Shasta' daisy. During his lifetime he was considered as a coequal with Henry Ford, inventor of the assembly line factory, and Thomas A. Edison, inventor of the light bulb and phonograph. Hugo de Vries, Liberty Hyde Bailey, and Nikolai Ivanovich Vavilov visited him and lauded his operation. Burbank promoted the concept that plant breeding could be the basis of a business and his headquarters in Santa Rosa, CA, became world famous. He established a publication company to disseminate his work and was instrumental in the eventual passage of the Plant Patent Act of 1930. However, Burbank was not a scientist. Although a strong supporter of Darwin and the theory of natural selection, he did not understand the contributions of Mendel to genetics and breeding. He performed no experiments in the classical sense and his notes were fragmentary. In 1904, he received a large grant from the Carnegie Institution ($10,000 annually) to promote the scientific study of plant breeding, which was discontinued after 5 years when the reviewer, George Harrison Shull, determined that Burbank's procedure was more art than science. However, Burbank is justly famous as a successful plant breeder. He intuitively followed the modern rationale of plant breeding by obtaining abundant diversity, using repeated and successive hybridization, and carrying out rigorous selection. Above all he had an eye and feel for plants. His success is an affirmation that plant breeding is an art as well as a science. As an innovative plant breeding artist, Luther Burbank remains an inspiration to plant breeders and horticulturists.**

Luther Burbank still remains the best known horticulturist in the United States and has become a legend as a plant wizard and inventor of plants. In 1940 he appeared on the U.S. postage stamp (Fig. 1) in the Famous Americans series along with John James Audubon (ornithologist and painter), Crawford W. Long (physician and anesthesiologist), Walter Reed (physician and epidemiologist), and Jane Addams (sociologist and reformer). Through his innumerable plant creations (over 800 releases), he became known as a plant breeder extraordinaire, and in his lifetime, he was thought of as the "high priest of horticulture" and the "plant wizard." His charming personality endeared him to the public. Burbank appears in paintings by Frida Kahlo and Diego Riviera and he was lionized in the popular press in innumerable articles. After his death, rights to his plant material were sold to Stark Brothers' Nursery, which sold the vegetables and seed rights to Burpee Seed Company in 1931, where Burbank's creations continued to be promoted to the public. In 1991 he was elected to the ASHS Hall of Fame and the Luther Burbank Home and Gardens was honored as an ASHS Horticultural Landmark in 2003. His life and career have been the subject of books and articles in the popular and scientific press including works by Peter Dreyer (1993), Walter Howard (1945, 1945–46), Jane S. Smith (2009), and Henry Smith Williams (1915), Williams et al. (1915). His position as a scientist has been critically reviewed by James Crow (2001) and Donald F. Jones (1937).

Luther Burbank (Fig. 2) remains a horticultural enigma and this brief review of his life is an attempt to put his contributions to horticulture and plant breeding into perspective. A retrospective review of his accomplishments is the goal of this workshop. It includes papers entitled "Russet Burbank: No Ordinary Potato" by Charles R. Brown; "A Vast Array of Beauty: The Accomplishments of Luther Burbank, the Father of American Ornamental Plant Breeding," by Neil O. Anderson and Richard T. Olsen; "Luther Burbank's Plums" by David A. Karp; "21st Century Approach to Improving Burbank's 'Stoneless' Plum" by Ann Callahan, Chris Dardick, and Ralph Scorza; "Luther Burbank's Contributions to Walnuts" by John Preece and Gale H. McGranahan; and "Luther Burbank's Berries" by Kim E. Hummer, Chad E. Finn, and Michael Dossett. These papers make clear that Luther Burbank is justly famous as an extraordinarily successful plant breeder. He intuitively followed the modern rationale of plant breeding by obtaining abundant diversity, using repeated and successive hybridization, and carrying out rigorous selection. He cannot be considered a scientist in the modern sense, but he was clearly a plant breeding artist for above all he had an eye and feel for plants. His success is an affirmation that plant breeding is as much an art as a science. As an innovative plant breeding artist, Luther Burbank remains an inspiration to plant breeders and horticulturists.

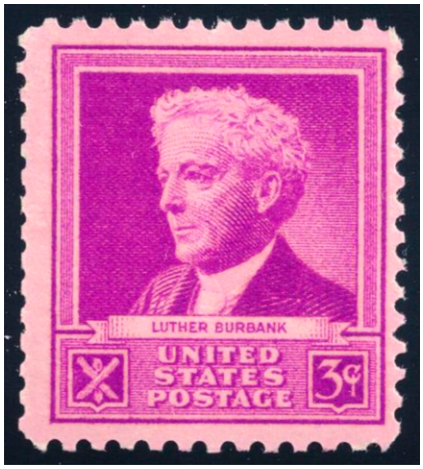


Fig. 1. Luther Burbank portrait in a 1940 U.S. postage stamp, one of five scientists of the Famous Americans series. Burbank is the only U.S. horticulturist so honored.

*Early years.* Luther was born in Lancaster, MA, on 7 Mar. 1849, a son of Samuel Burbank, owner of a small brick factory, and his third wife, Olive Burpee Ross. Young Luther was educated at the Lancaster Academy. In the early 1870s, he obtained Darwin's *Variation of Animals and Plants under Domestication* (published in the United States in 1869) from the local library and Burbank would later claim that it opened up a new world for him to create new plant varieties. At the same time he became interested in horticulture based on a book, *Gardening for Profit, in the Market and Family Garden* by Peter Henderson. In 1871 he purchased 17 acres of farmland in nearby Lunenburg where he planned to raise

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vegetables for sale, but he did not lose sight of his larger ambitions to accelerate evolutionary changes by human intervention.

In 1872, he noticed a seedpod on a planting of 'Early Rose' potato, a white-fleshed variant of 'Garnet Chili' imported from somewhere in South America that had some resistance to late blight caused by *Phytophthora infestans*. He harvested 23 seeds and the rest is history. The seedlings produced variable populations but two had large tubers, and one (# 15) proved to be high-yielding (3 pounds from one plant) with smooth skin, good taste, and long storage. In 1874 he sold rights to the potato to J.H. Gregory (the seedsman who named the 'Hubbard' squash from an introduction grown in Marblehead, MA) for $150 (Burbank had asked for $500). More important was that Gregory agreed to name the potato 'Burbank'. A subsequent mutation became the 'Russet Burbank', the most famous potato in U.S. history, the source of McDonald's fries and the baked potato that adorns our steaks.

*Move to California.* In 1875, the 26-year-old Burbank left the rocky soil of Massachusetts to join his brothers in California. He sold his Lunenburg farm and traveled to Santa Rosa 60 miles north of San Francisco with the expressed aim of repeating his success in plant improvement achieved with the potato. It was a fateful decision that would change his life. It was not easy. Supplemented by his skill at carpentry, Burbank went into a small nursery business. Using some land of his mother, who also immigrated to Santa Rosa, Luther started a small nursery based on his improved hybridized material. In 1880, he printed his first catalog, but his annual returns barely were greater than he would have achieved as a carpenter. However, in 1881 he entered a new direction. Catering to the demand for the burgeoning fruit industry of California, he took a daring challenge to fulfill an order of 20,000 trees of the newly introduced 'Agen' plum for drying. Burbank proved to be a skilled horticulturist. He produced nursery trees in a single year by germinating almond seedlings in the field, inserted buds of 'Agen' into the growing shoots, and fulfilled the order in 9 months, an amazing feat. Burbank nurseries prospered and by 1894 Burbank's advertisements proclaimed a stock of 500,000 fruit and nut trees (Fig. 3). At the same time he continued his hybridizations on an increasingly larger scale. His modus operandi was to make extensive crosses, with few notes that only Burbank could decipher. His nursery operation expanded to nearby Sebastapol. Seeds and plant materials such as plums from Japan were imported. He introduced the fruiting nursery and grafted seedlings to mature plants to reduce juvenility. He had assistants but carried out all selection personally. In 1888 he sold his nursery to concentrate on his passion, producing new plants and plant forms (Fig. 4). At the age of 40 years, Burbank proved himself a successful nurseryman and entrepreneur and he spent a year traveling, collecting seed.

Spurred by a change on postal rates, Burbank entered the mail order nursery business based on his own catalog of horticultural wonders. Bolstered by exuberant promotion and a wide assortment of plants, a new business plan was developed. Burbank's market was not the general public, but rather other nurserymen. He offered his creations at very high prices (from $250 to $3000

Fig. 2. Photographs of Luther Burbank.


FRUIT TREES.

SANTA ROSA NURSERIES!

— THE ABOVE NURSERIES ARE AMONG THE —

Largest and Most Complete in Northern California!

AND MY FRUIT TREES HAVE ALWAYS OBTAINED THE HIGHEST PRAISE FOR THEIR RELIABILITY, THRIFTY GROWTH, AND ABSOLUTE FREEDOM FROM SCALE AND OTHER INSECT PESTS.

— In growing Trees I use only —

THE BEST SEEDLING STOCKS

AND HAVE NEVER USED THE SUCKERS,

Which come up around old trees, and which are so often used to graft on. I do not ask any one buy trees of me who can do better elsewhere, but invite all who intend planting next season to call and see my stock before closing contracts with traveling agents. There can be no reason for purchasing trees from outside Nurseries, for I have now growing thriftily in my two nurseries in Santa Rosa, trees in quantity as follows:

| | |
|---|---|
| 150,000 Pear Trees, | 3,000 Cherry Trees, |
| 125,000 Peach and Nectarine Trees, | 10,000 Monterey Cypress Trees, (for hedges.) |
| 90,000 Plum, Prune and Almond Trees, | 7,000 Walnut and other Nut-Bearing Trees, |
| 10,000 Apricot Trees, | |
| 12,500 Apple Trees, | |

Besides an abundant supply of Shade and Evergreen Trees and Small Fruits, and the largest and most complete collection of Greenhouse Plants in this part of the State.

apl-wk-dtw LUTHER BURBANK.

WE NOW HAVE

500,000

VIGOROUS

FRUIT AND NUT TREES!!

GROWING IN OUR TWO NURSERIES AT SANTA ROSA.

Which we will Sell for Less Money than "Drummers" or "Tree Peddlers" can for the same Quality of Trees, and all can See what they are Buying

Don't Be Fooled!

By timely, Painted Pictures, as by Reports (but we have no trees for sale) See Come and See. Catalogues will soon be ready.

SANTA ROSA, SONOMA CO., CAL. LUTHER BURBANK,

Advertisement, Santa Rosa Nurseries, 1884.
Courtesy Luther Burbank Home & Gardens, Santa Rosa, California

Fig. 3. Advertisement of the Santa Rosa Nurseries, 1884.

and more) on an exclusive basis, the buyer acquiring all stock and rights. He in a sense initiated the business of marketing selections and germplasm derived from plant breeding. His annual catalogs over the next 20 years are a testament to his abilities as a breeder and his skill as a promoter. There were many outstanding releases (Table 1). Backed by the results of his breeding and selection success as well as self-promotion, Burbank created his public image as the plant wizard. However, Burbank was not an imposter for he delivered remarkable new innovations.

Burbank promoted his personal brand. Soon the name Luther Burbank added to a selection increased its commercial value. A series of newspaper and magazine articles and testimonies promoted his skill and his business as a creator of scientific and horticultural marvels. He played the press as a violin. He had his critics, but the truth was that he delivered. He had very successful commercial dealings with John Lewis Childs, a successful nurseryman, Stark Brothers' Nurseries, and Burpee Seeds (Washington Atlee Burpee was a distant cousin). Most impressive were the great diversity of species that Burbank improved.

*Plant wizard and legend.* By the turn of the century, interest in Burbank was so high that he became a magnet for a stream of distinguished personalities who toured his operation in Santa Rosa (Fig. 5). His pleasant personality endeared him to many visitors including Helen Keller, Jack London, and the King of Belgium as well as the scientists including Hugo de Vries, Liberty Hyde Bailey, and Nikolai Ivanovich Vavilov. All were charmed with what they saw and were duly impressed by the enormous variety of plants under development and the wealth of diversity in his nursery garden. He created a stir in the academic community. In 1904, David Starr Jordan, the president of Sanford University, invited Burbank to join the faculty as a lecturer on evolution. Burbank described inheritance as an intricate web of vibrations and magnetic forces, but the lantern slides of his creations impressed everyone. Finally his supporters succeeded in getting him an enormous grant from the Carnegie Institution of $10,000 a year but with the stipulation that a trained biologist was to prepare a report on his work. The observer chosen was George Harrison Shull, an eminent biologist who was to become famous in plant breeding through his studies on inbreeding and outbreeding of maize that led directly to hybrid corn. Although Shull admired Burbank's accomplishments, he was not impressed with Burbank as a scientist and accurately attributed his success to his abilities as a selector. Burbank was not about to record his methods or achievements in scientific journals but chose rather to embark on a publishing venture that led to a 12-volume work of his creations (Fig. 6). It soon became clear that his methods were best explained by his results. Oddly enough his major scientific contribution, that it was possible to create new hybrids that were essentially a new true breeding species (allopolyploids), was rejected by Hugo de Vries. His new achievement, the 'Sunberry' (relabeled the 'Wonderberry'), derived from a cross of two nightshade species was derided (today it is coming back). His plumcots were not accepted as true hybrids but today they are. His funding from the Carnegie Institution was discontinued in 1909. Burbank was in large part responsible for the enactment of the Townsend-Purnell Plant Patent Act of 1930. In committee, Congressman Purnell read a letter of Burbank despairing over his ability to be rewarded from his discoveries:

> *"A man can patent a mousetrap or copyright a nasty song, but if he gives to the world a new fruit that will add millions to the value of earth's annual harvests, he will be fortunate if he is rewarded by so much as having his name connected with the result."*

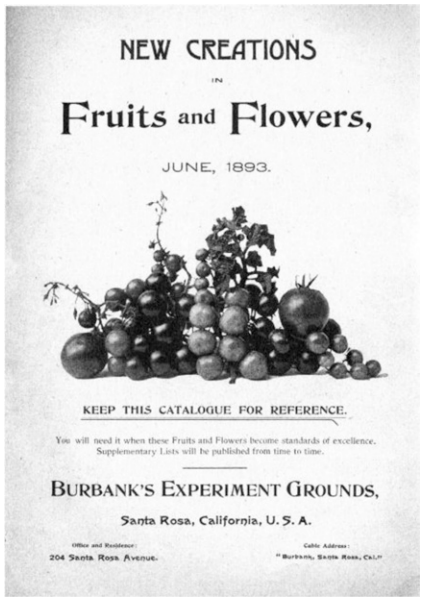


Fig. 4. Advertisement of New Creations of Fruits and Flowers from Burbank's Experimental Grounds, Santa Rosa, 1893.

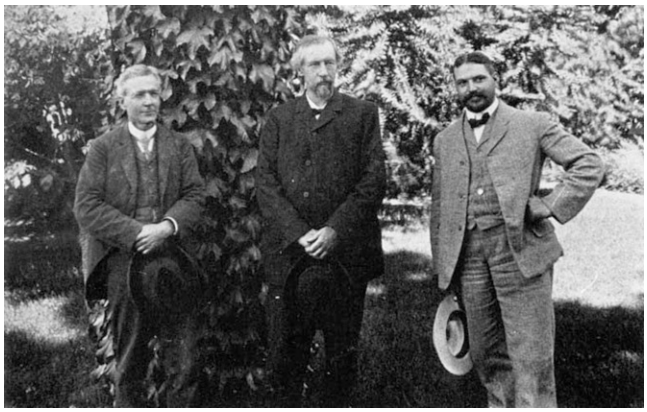

Fig. 5. Luther Burbank, Hugo de Vries, and George Harrison Shull, 1907.

Table 1. Some of the better known creations of Luther Burbank from his 800 releases and their issue dates.[z]

| | | | | | |
|---|---|---|---|---|---|
| Burbank potato | 1873 | Miracle (stoneless) plum | 1901 | Black Giant cherry | 1911 |
| Himalaya blackberry | 1885 | Shasta daily | 1901 | Rainbow corn | 1911 |
| Satsuma plum | 1886 | Burbank cherry | 1903 | Santa Rosa artichoke | 1911 |
| Paradox walnut | 1893 | Santa Rosa dahlia | | Hybrid sunflowers | 1914 |
| Royal walnut | 1893 | Burbank Crimson California poppy | 1904 | New Burbank Early tomato | 1915 |
| Van Deman quince | 1893 | Santa Rosa Shirley poppies | 1904 | Sunrise daylily | 1917 |
| Lemon Giant calla lily | 1893 | Rutland plumcot | 1905 | Elephant garlic | 1919 |
| Iceberg white blackberry | 1894 | Burbank's Giant Hybrid amaryllis | 1906 | Robusta strawberry | 1920 |
| Wickson plum | 1894 | Santa Rosa plum | 1906 | Sebastopol thornless blackberry | 1920 |
| Tarrytown canna lily | 1895 | Spineless cacti | 1907 | Molten Fire amaranthus | 1922 |
| Burbank rose | 1899 | Burbank Admiral pea | 1908 | Tower of Gold knophoria (poker plant) | 1923 |
| New gladiolus hybrids | 1899 | America Admiral pea | 1908 | Burbank Giant Dahlia zinnia | 1935 |
| White agapanthus | 1899 | Sunberry (Wonderberry) | 1909 | Gold nectarine | 1927[y] |
| Crimson Winter rhubarb | 1900 | America Evening primrose | 1910 | July Elberta peach | 1932[y] |

[z]Adapted from Smith (2009).
[y]Posthumous.

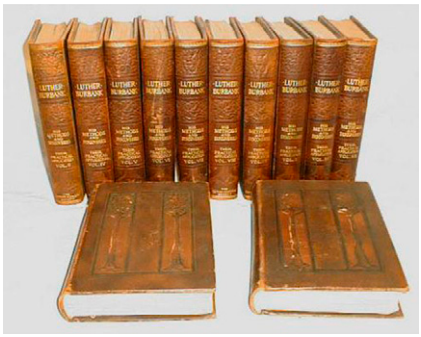

Fig. 6. The 12-volume set of Luther Burbank: His Methods and Discoveries, 1914–15.

A famous photograph (Fig. 7) taken in Santa Rosa on 22 Oct. 1915 with Thomas Edison, Luther Burbank, and Henry Ford in an informal pose on the steps of his garden is a testament to his new status. Ford and Edison had taken a pilgrimage after the opening of the Panama-Pacific Exposition in San Francisco to visit the "wizard of Santa Rosa." The three men obviously enjoyed each other's company with their hats in hand epitomized the American dream: three country boys, self-made men, who achieved concrete results based on their abilities. For Luther it was a vindication of his life's work that announced his membership in the trinity of American inventive heroes. In popular imagination, Burbank was to enter the panoply of great inventors along with Alexander Graham Bell, the Wright Brothers, Thomas A. Edison, and Henry Ford. A collection of Burbank memorabilia would be collected by Ford for his Dearborn Museum of Americana.

*Epilogue.* Who was Luther Burbank? Perhaps the best metaphor is Frida Kahlo's mystical, surrealist portrait of Burbank dressed in a dark suit and holding a philodendron emanating from a hollow stump with roots feeding on a corpse (Fig. 8). In the background are two trees laden with fruit in a desiccated landscape of California. Indeed, Burbank was a plant mystic who created new plants with little more than his imagination, his pollinating abilities, and his skill for selection. His guiding light was not Mendel but Darwin (whose evolutionary concepts were not reconciled with Mendelian genetics until the work of R.A. Fisher in 1918) who led him to the belief that plants could be altered to better serve the needs of humans. The proof of the pudding is in the eating, and the proof of Burbank's genius as a horticulturist and plant breeder was his creations that still enrich our lives.

Fig. 7. Three famous Americans: Thomas A. Edison, Luther Burbank, and Henry Ford at Santa Rosa, 1915.


Fig. 8. Portrait of Luther Burbank as the plant breeding mystic by Frida Kahlo, 1931.

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# Russet Burbank: No Ordinary Potato

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*Additional index words.* Burbank, Luther Burbank, hybridization, late blight, 'Early Rose'

***Abstract*. The 'Russet Burbank' potato cultivar currently occupies first place in acreage planted in North America and is worth in the United States $1.4 billion annually. It is a sport of 'Burbank's Seedling', which was selected by Luther Burbank in 1873. The ancestry of Burbank stems from a plant introduction brought to the United States by the Rev. Chauncey Goodrich of New York State in 1853. The priorities of potato breeding had been transformed by repetitive crop failures caused by the emergence of the plant pathogen *Phytophthora infestans*. Modern testing suggests that derivatives of Goodrich's potatoes were slightly more resistant to *Phytophthora*. Burbank discovered a single fruit on one of these derivatives, 'Early Rose', in his mother's garden. Taking the 23 true seeds, he nursed them to full-sized plants and selected ultimately No. 15. It produced an unusually high yield of large, very oblong tubers, stored well, and was a good eating potato. Burbank's life was destined for a long career in California and he attempted to sell the clone to J.H.J. Gregory of Gregory's Honest Seeds, a successful businessman. Ultimately Gregory agreed to buy it for $150, far less than Burbank wanted, but enough to propel him to California. Gregory named the potato 'Burbank's Seedling', which no doubt engendered fame for the entrepreneur. Luther Burbank had been allowed by Gregory to keep 10 tubers, which became the seed source for the 'Burbank's Seedling' to spread north and south along the West Coast of North America with a crop value, stated by Burbank, of $14 million in 1914. It is not clear that Luther Burbank prospered from 'Burbank's Seedling' in the West. A skin sport with a russet skin was found in Colorado in 1902 and was advertised by a seed company under the name 'Netted Gem'. 'Burbank's Seedling' per se disappeared from commerce and 'Netted Gem' slowly increased, finding a special niche in production of French fry potatoes. It is clear that Luther Burbank gained tremendous insight into the dynamics of hybridization in revealing genetic variation from clonally propagated species. During the rest of his career he would use this technique to produce new and amazing forms of numerous food and ornamental species. 'Burbank's Seedling' was his entrez into the world of plant breeding.**

There are many different plant species where Luther Burbank was responsible for innovative creations. Potato is one of these. Luther Burbank's potato breeding must be seen from an historical perspective. Potatoes were found in South America by Spanish Explorers in the Central Andes. Introduced more as a botanical curiosity ≈1570, the potato appears to have been grown in gardens and recognized as a nutritive food as judged by a letter written by Saint Teresa of Avila, founder of the Barefoot Carmelites, who wrote of their restorative traits when she ate them while in ill health.

In 1843, starting in North America, a mysterious disease began afflicting potato in the northeast of the United States. Two years later, starting on the continent, in Belgium, the same type of fast-moving epidemic started early and then appeared throughout a large area in Ireland (Bourke, 1993). This led to an almost total potato crop failure in 1845 and by the fall of 1846, after another crop failure, an all-encompassing food scarcity. Food stores disappeared in pockets, especially in western Ireland, subsequently vanishing throughout many parts of Ireland. In the previous 55 years, Ireland's population had risen from 2 to 8 million at least partly the result of the success and succor of potato as a crop. Infrastructure was ill-prepared to address famine, and as many thousands of people died, others, with their last remaining energy, took to the road seeking food. Human diseases appeared, foremost among these cholera. Science understood neither the fast-moving, moisture-loving, air-dispersed late blight nor the drinking waterborne cholera, which vanquished the hunger-debilitated population with spectacular rapidity.

Wherever rumors of food stores emerged, hordes of desperate people would arrive and break into supposed food warehouses. Violence and death ensued, while food became unavailable, at any price in ever widening regions. Meanwhile in England, a debate raged on the appropriate response to the famine. It was one of the first philosophical clashes on the value of welfare to help the poor. There was a prevailing socioreligious standpoint that the massive death occurring in Ireland was an act of God. Above all, harmony had been lost in Ireland and its return was best left to natural processes. When Parliament finally attempted to purchase shiploads of grain for Ireland, the process was much delayed and resulted in a worldwide increase in grain commodity prices (Kelly, 2012).

In the end it is estimated that 1 million Irish perished and 1.5 million emigrated mostly to the United States. Emigration took place during and after the famine. Ireland has yet to recover previous population levels. Perhaps the greatest tragedy of the 19th century, the Irish potato famine was caused by the oomycete *Phytophthora infestans*. The potato varieties of the time in Ireland were completely susceptible (Salaman, 1949). It still is the most serious disease of potato worldwide.

It was in this context, and considering that potato breeding was in private hands in 1850, that the Reverend Chauncey Goodrich undertook his calling to fight hunger on receiving potatoes from the Panamanian Consulate, which came with the name "Chili," perhaps denoting the country of origin as Chile. Out of this exotic germplasm Goodrich selected, from openpollinated fruits, first, 'Rough Purple Chili', then 'Garnet Chili', and subsequently another breeder, Albert Bresee, released a seedling derived from 'Garnet Chili', which he named 'Early Rose' (Goodrich, 1863a, 1863b; Plaisted and Hoopes, 1989; Smith, 2009). At this time the greatest goal of plant breeders was to breed varieties more resistant to disease, probably referring to late blight.

The origin of 'Burbank's Seedling', a story filled with unbelievably good fortune, evokes the incredulity of any plant breeder. Luther Burbank as a young man in Massachusetts took on potato as one of his first plant business projects and discovered a fruit in his mother's 'Early Rose' garden patch. This in itself was almost unheard of in the non-fruiting Early Rose cultivar. Carefully marking the fruit, he waited for it to mature. The fruit initially was lost, but was found after 3 full days of searching. Yielding a scant 23 seeds, each of them was carefully germinated and transplanted to his garden. After nurturing each plant to full maturity, he harvested them and made his assessment. Of the 23 seedlings, two were unusual and outstanding. After a second year of propagation, No. 15 was the sole selection, offering an astounding yield of large tubers, good storability, and very good eating quality (Dreyer, 1993). By today's standards the derivatives of Goodrich's potatoes were not particularly resistant as tested in modern resistance trials, but the fact that 'Russet Burbank', a later sport of 'Burbank's Seedling', was not particularly susceptible to late blight might have been an achievement at its highest level (Inglis et al., 1996) (Table 1). Although it is often said that no resistance to

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Table 1. Area under the disease progress curve (AUDPC) on exposure to a field source of late blight (*Phytophthora infestans*) pathotypes identified after 1990 in Mount Vernon, WA.[z]

| Cultivar | AUDPC 1993 | Significance | AUDPC 1994 | Significance |
|---|---|---|---|---|
| Elba | 529 | a[y] | 135 | a |
| Kennebec | 748 | b | 247 | ab |
| Ranger Russet | 1,101 | bc | 389 | bc |
| Russet Burbank | 1,035 | b | 650 | d |
| White Rose | 1,060 | bc | 834 | de |
| Shepody | 1,169 | cd | 807 | cd |
| Superior | 1,516 | f | 1,079 | ef |
| Russet Norkotah | 1,214 | de | 1,424 | g |
| Hi Lite Russet | 1,388 | ef | 1,456 | g |

[z]Clones are ranked from most to least resistant. Russet Burbank is less resistant than Elba but more resistant than Superior, Russet Norkotah, and Hi Lite Russet. Table extracted from Inglis et al. (1996).
[y]AUDPC values not sharing a letter are significantly different at $P < 0.05$ according to analysis of ranked AUDPC values and a least significant difference test.

late blight was present in varieties of the day in 1845 nor in varieties released for more than three-fourths of a century afterward (Spooner et al., 2005), modern studies place 'Russet Burbank' in an intermediate susceptible status of resistance, relative to many other potato varieties. Not a matter for superlatives, neither resistant nor very susceptible, it and its relatives may have been notable for a greater, albeit slight, abatement of disease than that offered by any other cultivar of the time. Therefore, the overwhelming use of 'Early Rose', 'Burbank's Seedling's' immediate maternal ancestor, as a parent in breeding programs in Europe and North America may have had a basis in a conspicuous ability to transmit some resistance to late blight to the progenies (Reader, 2008).

This could explain the longevity and international dissemination of 'Early Rose', which was used extensively in breeding in Europe. In fact, it is difficult to find a pedigree that does not include 'Early Rose' as an ancestor in the early 20th century (Plaisted and Hoopes, 1989).

At the time, breeding of new potato varieties was of intense commercial interest to a few private breeders. It was customary to harvest open-pollinated berries from field-grown plants; hence, the pedigrees often only indicated the plant from which the berries were taken. Formal trials really did not exist and much of the description of a cultivar was hearsay, rarely with actual yields included. Keeping quality and culinary traits on boiling were foremost in the minds of the potato cultivar merchants. A bushel of seed of a new cultivar could sell for $50, $900 in today's currency (Best, 1870). Burbank decided to relocate to the West and needed traveling funds. He offered his clone to J.H.J. Gregory, a successful seedsman, for $500 in 1873. Gregory countered with $150, which Burbank accepted disappointedly. Gregory generously named the clone 'Burbank's Seedling'. It appeared in the Gregory Seed Catalog in 1880 (Fig. 1). However, by 1920, it was no longer part of the Gregory Seeds offerings. Now in California, Burbank became remorseful of his sale to Gregory and sent a letter asking for greater remuneration. Gregory was quite direct in his response:

"*My Dear Sir,*

*I have given you great fame by attaching your name to the potato and spreading it through the length and breath (sic) of the land. I purchased the Early Ohio at just about the same price I gave you for your seedling, did not give the originator's name to it, and have made greater sale of this than the Burbank.*

*As to the profit of selling potatoes in my business, with the cost of advertising and handling and loss by freezing and the filling out of orders comes with the opening of spring, just when we are heel over head with filling seed orders, causing us such a week behind hand I have half resolved more than once to(forsake) the whole potato business as unprofitable and a great nuisance .You mistake in inferring that all this notoriety upon Burbank means money for me. It rather means fame for you. The more generally it is advertised, the more completely it is taken out of my hands.*

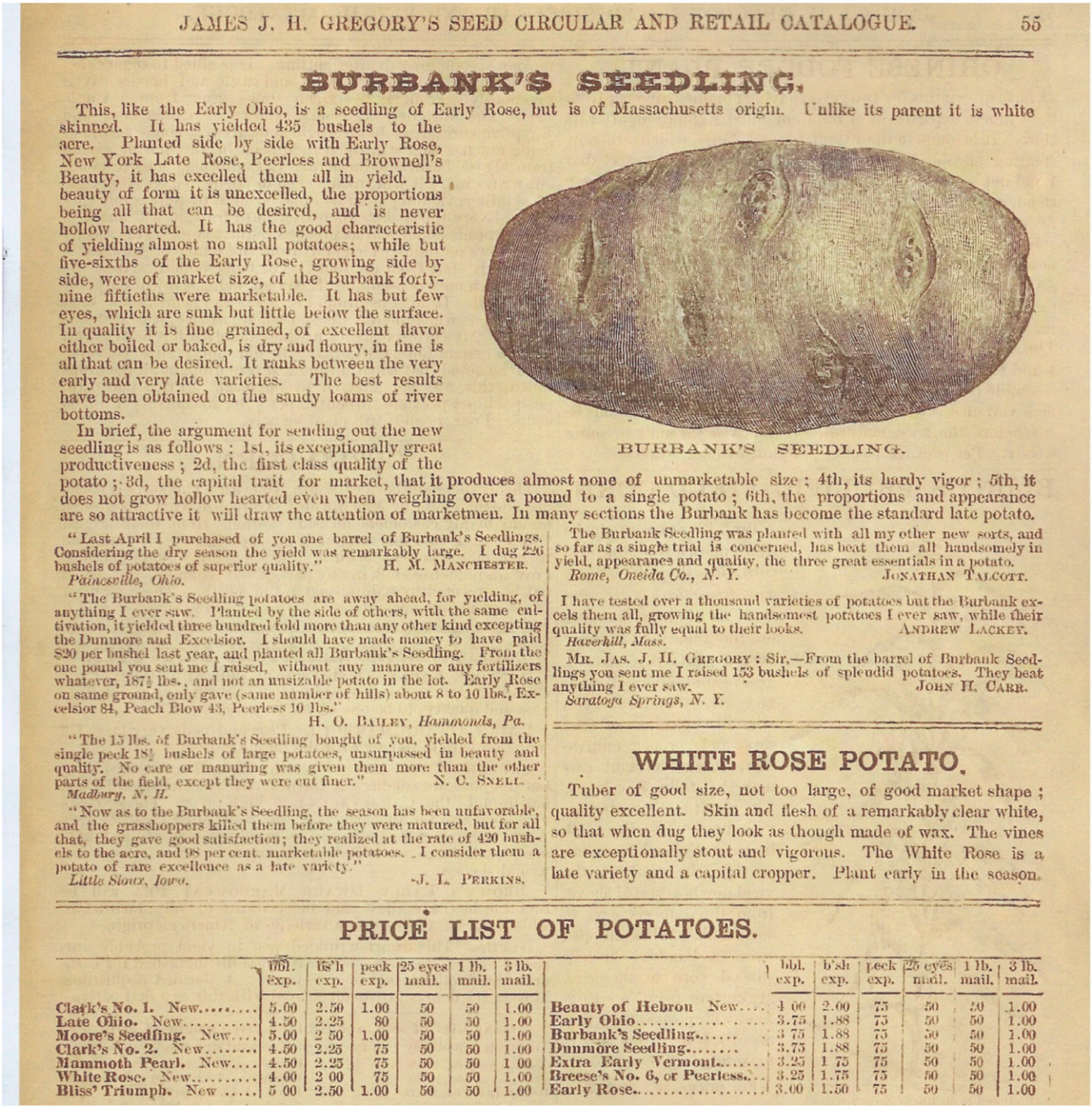
*I have stated the facts in the case and now enclose 25 dollars; for whatever I may write I know you will feel that some recompense is owed you.*" (Smith, 2009; Worrell, 2013)

Gregory had allowed Burbank to keep 10 tubers, which he used to start the cultivar in California. It spread on the west coast of North America where in 1914 it was stated to be worth $17 million (Burbank, 1914). There is no evidence that 'Burbank's Seedling' was remunerative to Burbank despite the potential. It was a casualty to its ready vegetative propagation without legal means to recover royalties. Luther Burbank himself attributed the discovery of a russet skin mutant to Lou Sweet, a Colorado farmer, in 1914 (Burbank, 1914). However, it appears to be clear now that the russet sport was discovered earlier and called 'Netted Gem' (Bethke and Donnelly, 2014). Newspaper articles and seed catalogs place this in the year 1895. It was officially introduced in 1902 in the L.L. Mays seed catalog. Today the name 'Netted Gem' is used in Canada and 'Russet Burbank' in the United States and elsewhere. Eventually 'Burbank's Seedling' disappeared and 'Russet Burbank' increased in acreage, especially in the Intermountain West.

'Russet Burbank' found market acceptance heretofore unknown in potato cultivars. In the Pacific Northwest, 'Russet Burbank' comprised 85% of the crop in Washington State, destined largely for processing.

Ray Croc, who undertook the expansion of McDonald's restaurants on a franchise model, started with one restaurant in San Bernardino, CA. He made an interesting discovery early in the process that proved essential to McDonald's French fries' reputation for excellence. First he determined that 'Russet Burbank' potatoes needed to sit and slightly dehydrate after delivery. Second, he found that fries were most appealing if they went through a two-step cooking process. The fries were half-cooked in hot oil and allowed to sit. The second step could be a short oil fry that imparted appropriate texture, taste, and unique mouth feel. All of this was done with 'Russet Burbank' as the model raw product. Continuous use of 'Russet Burbank' ensured exclusive preference for it as the raw product that most frequently performed the best. Processing innovations were always accomplished on 'Russet Burbank'. At first Ray Croc manufactured his once-cooked product, shipped in his raw potatoes, and stored on site (Croc, 1985). He found a willing industrial partner, J.R. Simplot Company, which pre-cooked the fries and sent them frozen in easily storable boxes to the restaurants. So successful was this that the brand McDonald's became synonymous with the most delicious French fries in the business. Ray Croc eventually bought out the McDonald Brothers and presided over the expansion of the McDonald's brand with construction of tens of thousands of new restaurants on a franchise model (CNBC, 2007; Croc, 1985). Today almost all quick service restaurants receive parfried frozen fries from potato processors, which the restaurants finish off with a second fry. Today 33% of McDonald's sales are French fries, estimated at 7 billion pounds per year. A highly trained tasting team tries out new varieties every year, and the lack of new recommendations characterizes a static situation, which protects 'Russet Burbank's' retention of such a large portion of the market (Love, 1995). A cultivar acceptable as a McFry® must perform in a narrow range in the following list of characters:

1. Crispness;
2. Color;
3. Texture external crusty surface, internal soft but not mushy;
4. Optimum absorption of oil. McDonald's has switched to a healthier Canola® vegetable oil for frying, the result of close collaboration with Cargill researchers (Cargill, La Crosse, WI);
5. Percent limp units (or fries that have lost their stiffness and become soft) at a specified time after frying;
6. Retention of freshly fried taste and texture after a specified number of minutes postfry;
7. A mix of strip lengths that occupy a certain volume and stay below a specified weight. Strips that are similar in



JAMES J. H. GREGORY'S SEED CIRCULAR AND RETAIL CATALOGUE. 55

## BURBANK'S SEEDLING.

This, like the Early Ohio, is a seedling of Early Rose, but is of Massachusetts origin. Unlike its parent it is white skinned. It has yielded 435 bushels to the acre. Planted side by side with Early Rose, New York Late Rose, Peerless and Brownell's Beauty, it has excelled them all in yield. In beauty of form it is unexcelled, the proportions being all that can be desired, and is never hollow hearted. It has the good characteristic of yielding almost no small potatoes; while but five-sixths of the Early Rose, growing side by side, were of market size, of the Burbank forty-nine fiftieths were marketable. It has but few eyes, which are sunk but little below the surface. In quality it is fine grained, of excellent flavor either boiled or baked, is dry and floury, in fine is all that can be desired. It ranks between the very early and very late varieties. The best results have been obtained on the sandy loams of river bottoms.

BURBANK'S SEEDLING.

In brief, the argument for sending out the new seedling is as follows: 1st, its exceptionally great productiveness; 2d, the first class quality of the potato; 3d, the capital trait for market, that it produces almost none of unmarketable size; 4th, its hardy vigor; 5th, it does not grow hollow hearted even when weighing over a pound to a single potato; 6th, the proportions and appearance are so attractive it will draw the attention of marketmen. In many sections the Burbank has become the standard late potato.

"Last April I purchased of you one barrel of Burbank's Seedlings. Considering the dry season the yield was remarkably large. I dug 226 bushels of potatoes of superior quality." H. M. MANCHESTER.
*Painesville, Ohio.*

"The Burbank's Seedling potatoes are away ahead, for yielding, of anything I ever saw. Planted by the side of others, with the same cultivation, it yielded three hundred fold more than any other kind excepting the Dunmore and Excelsior. I should have made money to have paid $20 per bushel last year, and planted all Burbank's Seedling. From the one pound you sent me I raised, without any manure or any fertilizers whatever, 187½ lbs., and not an unsizable potato in the lot. Early Rose on same ground, only gave (same number of hills) about 8 to 10 lbs., Excelsior 84, Peach Blow 43, Peerless 10 lbs."
H. O. BAILEY, *Hammonds, Pa.*

"The 15 lbs. of Burbank's Seedling bought of you, yielded from the single peck 18½ bushels of large potatoes, unsurpassed in beauty and quality. No care or manuring was given them more than the other parts of the field, except they were cut finer." N. C. SNELL.
*Madbury, N. H.*

"Now as to the Burbank's Seedling, the season has been unfavorable, and the grasshoppers killed them before they were matured, but for all that, they gave good satisfaction; they realized at the rate of 420 bushels to the acre, and 98 per cent. marketable potatoes. I consider them a potato of rare excellence as a late variety."
*Little Sioux, Iowa.* J. L. PERKINS.

The Burbank Seedling was planted with all my other new sorts, and so far as a single trial is concerned, has beat them all handsomely in yield, appearance and quality, the three great essentials in a potato.
*Rome, Oneida Co., N. Y.* JONATHAN TALCOTT.

I have tested over a thousand varieties of potatoes but the Burbank excels them all, growing the handsomest potatoes I ever saw, while their quality was fully equal to their looks. ANDREW LACKEY.
*Haverhill, Mass.*

MR. JAS. J. H. GREGORY: Sir,—From the barrel of Burbank Seedlings you sent me I raised 153 bushels of splendid potatoes. They beat anything I ever saw. JOHN H. CARR.
*Saratoga Springs, N. Y.*

## WHITE ROSE POTATO.

Tuber of good size, not too large, of good market shape; quality excellent. Skin and flesh of a remarkably clear white, so that when dug they look as though made of wax. The vines are exceptionally stout and vigorous. The White Rose is a late variety and a capital cropper. Plant early in the season.

## PRICE LIST OF POTATOES.

| | bbl. exp. | b'sh exp. | peck exp. | 25 eyes mail. | 1 lb. mail. | 3 lb. mail. | | bbl. exp. | b'sh exp. | peck exp. | 25 eyes mail. | 1 lb. mail. | 3 lb. mail. |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Clark's No. 1.** New..... | 5.00 | 2.50 | 1.00 | 50 | 50 | 1.00 | **Beauty of Hebron** New.... | 4 00 | 2.00 | 75 | 50 | 50 | 1.00 |
| **Late Ohio.** New..... | 4.50 | 2.25 | 80 | 50 | 50 | 1.00 | **Early Ohio**..... | 3.75 | 1.88 | 75 | 50 | 50 | 1.00 |
| **Moore's Seedling.** New.... | 5.00 | 2 50 | 1.00 | 50 | 50 | 1.00 | **Burbank's Seedling**..... | 3 75 | 1.88 | 75 | 50 | 50 | 1.00 |
| **Clark's No. 2.** New..... | 4.50 | 2.25 | 75 | 50 | 50 | 1.00 | **Dunmore Seedling**..... | 3.75 | 1.88 | 75 | 50 | 50 | 1.00 |
| **Mammoth Pearl.** New.... | 4.50 | 2.25 | 75 | 50 | 50 | 1 00 | **Extra Early Vermont**..... | 3.25 | 1 75 | 75 | 50 | 50 | 1.00 |
| **White Rose.** New..... | 4.00 | 2 00 | 75 | 50 | 50 | 1.00 | **Breese's No. 6, or Peerless**... | 3.25 | 1.75 | 75 | 50 | 50 | 1.00 |
| **Bliss' Triumph.** New ..... | 5 00 | 2.50 | 1.00 | 50 | 50 | 1.00 | **Early Rose**..... | 3.00 | 1.50 | 75 | 50 | 50 | 1.00 |

Fig. 1. Gregory's announcement of the Burbank Seedling in his seed catalog in 1880. Kindly provided by Shari Kelley Worrell, J.H.J. Gregory's great great granddaughter and author of "Remembering James J.H. Gregory: The Seed King, Philanthropist, Man," 2013.

length tend to fill the serving container with too high a weight; and

8. Retention of good fry quality after 8 months of storage.

At this writing only four varieties are acceptable for the McFry brand: 'Russet Burbank', 'Shepody', 'Ranger Russet', and 'Umatilla Russet' (CNBC, 2007).

## CONCLUSIONS

Luther Burbank's early success with 'Burbank's Seedling' certainly fed his confidence that he was following the right route to fame. The domination of 'Russet Burbank' of the North American market makes Luther Burbank the most successful breeder of potatoes in history. In present-day terms, 'Russet Burbank' is worth $1.5 billion annually. This is true despite decades of decline in acreage. In Washington State for instance, 'Russet Burbank' has declined from 82% to 45% of the acreage from 1990 to 2011 (Pavek and Knowles, 2013; USDA/NASS, 2012) (Fig. 2). In addition, the pattern of variation in the progenies coming from the fruit of an 'Early Rose' plant reinforced his philosophy about revealing genetic variation. The variation accumulated over many generations of sexual reproduction was hidden only to be unfettered by hybridization. "We have observed that the latent qualities of diverse strains of ancestors are permitted to come to the surface and make themselves manifest once the tendency to relative fixity has been broken by hybridization" (Burbank, 1914). Certainly this contention has proven useful in vegetatively propagated crops, which when perpetuated vegetatively only change slightly over time as a result of somatic "sports." Sexual reproduction reveals the highly heterozygous composition underlying an otherwise unvarying line of clonal reproduction. After looking at another half million seedlings, Burbank could state another

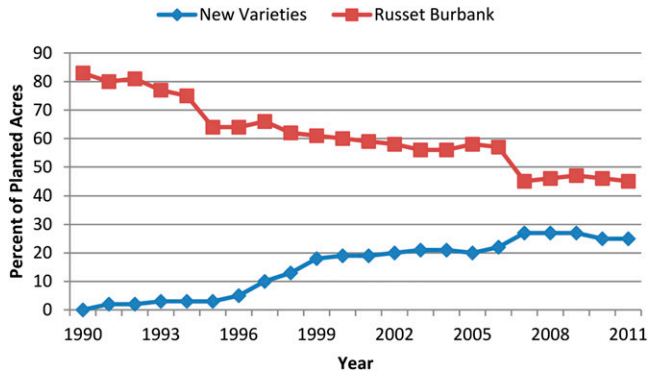



Fig. 2. Decline in percentage of total potato acreage planted to 'Russet Burbank' compared with new varieties from 1990 to 2011.

breeding truism from experience; sexual reproduction rarely produces a progeny as good as a highly successful clonally propagated parent (Burbank, 1914). 'Russet Burbank' always has been very hard to beat. Donnelly et al. (2014) have concluded using the most sensitive test available (Li et al., 2008) that 'Early Rose' and 'Burbank's Seedling' were derived from outcrosses to other unidentifiable pollen parents.

Luther Burbank's lifelong belief that 'Burbank's Seedling' was a self of 'Early Rose' was not correct. He made crosses of 'Burbank's Seedling' with a red-skinned potato brought in from Chile, reportedly, but nothing commercially viable emerged (Burke, 2007). What is clear is that his experience with potato and the discovery of 'Burbank's Seedling' informed one of his first principles in his philosophy of plant breeding. Nearly all of his work was done with clonally propagated species. It is well known now that sexual crosses yield highly variable progenies as a result of the inherent heterozygosity in clonally propagated species. If one were to pick out the single dogma that Burbank resorted to again and again, it was to make crosses to come up with new combinations. His ability to conceive of the new types that were needed in the marketplace and in a single-minded way to select for these was the rarest of gifts.

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# A Vast Array of Beauty: The Accomplishments of the Father of American Ornamental Breeding, Luther Burbank

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***Abstract*. Luther Burbank (1849–1926) was a prolific ornamental plant breeder, who worked with 91 genera of ornamentals, from *Abutilon* to *Zinnia*, and released nearly 1000 cultivars to the industry. His innovative work included both herbaceous and woody plant materials as well as ornamental vegetables such as corn, tomatoes, and spineless cacti. His most popular ornamental release, the shasta daisy hybrids—first released in 1901, is still on the global market. This article focuses on Luther Burbank's breeding techniques with ornamental plants and how both the germplasms that he developed and his methodologies used permeate modern flower breeding. Genera with the highest number of cultivars bred and released by Burbank include *Amaryllis*, *Hippeastrum*, and *Crinum* followed by *Lilium*, *Hemerocallis*, *Watsonia*, *Papaver*, *Gladiolus*, *Dahlia*, and *Rosa.* With *Lilium*, he pioneered breeding the North American native lily species, particularly those from the Pacific coastal region, producing the eponymous *Lilium* ×*burbankii*. Burbank's breeding enterprise was designed to be self-sustaining based on profits from selling the entire product line of a new cultivar or crop only to wholesale firms, who then held exclusives for propagation and selling, although financial hardships necessitated selling retail occasionally. Entire lots of selected seedlings were sold to the highest bidder with Burbank setting the price in his annual catalogs such as the Burbank Hybrid Lilies lot for U.S. $250,000 or some of the "very handsome, hardy ones" for U.S. $250 to U.S. $10,000 each. Other flower cultivars also commanded high prices such as seedling Giant *Amaryllis* that sold for U.S. $1.55/bulb in 1909. Cacti were another area of emphasis (he released more than 63 cultivars) from the spineless fruiting and forage types (*Opuntia ficus-indica*, *O. tuna*, *O. vulgaris*) to flowering ornamentals such as *O. basilaris*, *Cereus chilensis*, and *Echinopsis mulleri.* Interest in cacti during 1909–15 rivaled the Dutch Tulip mania with exorbitant fees for a single "slab" of a cultivar, speculative investments, controversy with noted cacti specialists (particularly David Griffiths), and lawsuits by The Burbank Company. Although most cultivars have been lost, Burbank's reputation as the Father of American Ornamental Breeding remains admirable from critics and devotees alike.**

Luther Burbank passionately bred all commodities of horticultural plants, particularly ornamentals (herbaceous and woody flowers, trees, shrubs), on his own properties, first at his 4-acre home and nursery in Santa Rosa, CA, but later, and primarily, on his own Research Station known as Luther Burbank's Gold Ridge View Experiment Farm located at 7781 Bodega Avenue, Sebastopol, CA (Fig. 1A; Dreyer, 1993; Smith, 2009; Williams, 1915). Perhaps best known for his work on small fruits and vegetables, ornamentals (herbaceous and woody flowers, trees, shrubs) did not escape the work of the "Plant Wizard of Santa Rosa." The Gold Ridge View Experiment Farm was an efficient, 16- to 18-acre site (Bush, 1982; Hall, 1939) with continuous rotations of new generational hybrids growing in successive plots in the fields, coldframes/hot beds, or glasshouses. It was common to find rows of mature selections of flowers and other ornamentals growing alongside plums or apples. Yearly bonfires in the fall were commonly used to destroy all unwanted (rogued) breeding stock and grow-outs.

As a result of his prominence in the growing circle of horticultural plant breeders, Burbank had numerous volunteer plant collectors across the globe that shipped him enormous quantities of germplasm as well as direct access to the USDA Bureau of Plant Industry germplasm introductions by David Fairchild. This afforded Burbank the opportunity to focus on developing his methodologies of breeding, selection, and commercialization of floral products, which singularly have surpassed the efforts of any individual flower breeder to the present day. For example, the purchase of many elite breeding lines, germplasm, and market-ready cultivars after Burbank's death in 1926 allowed Stark Brothers Nurseries to offer a wide array of ornamental products to the market (Fig. 1C).

The objectives of this article focus on the art and science of Luther Burbank's techniques with ornamental plants and how both the germplasm that he developed and his methodologies used thereon still permeate modern flower breeding. Rather than focusing on every floral product that he bred (Table 1; covered quite extensively by Howard, 1945), a few exemplary ones are used to illustrate the methodological approaches used by Burbank to achieve his world status as the Father of American Ornamental Breeding.

## BREEDING AND MARKETING METHODOLOGY

Luther had very little formal education, which ended at the age of 19 years as a result of his Father's untimely death in 1868 (Howard, 1945). Two years later he became a Market Gardener, where he attempted his first crosses with vegetables to create earlier types (Howard, 1945). This was not successful because he used noninbred parents, which meant that the $F_1$ hybrids did not possess hybrid vigor or heterosis. Later, on reading Darwin's "Variation of Animals and Plants Under Domestication" (Darwin, 1868), he learned about backcrossing and breeding for multiple generations to obtain segregants with variation. After immigrating to California in 1875, he worked for less than 1 year in a nursery (Petaluma, CA) collecting bulbs and open-pollinated (OP) seeds of California wildflowers, which he sold to seedsmen in the eastern United States (Howard, 1945). He started his first nursery in Santa Rosa, CA, in 1877, but soon focused strictly on highly

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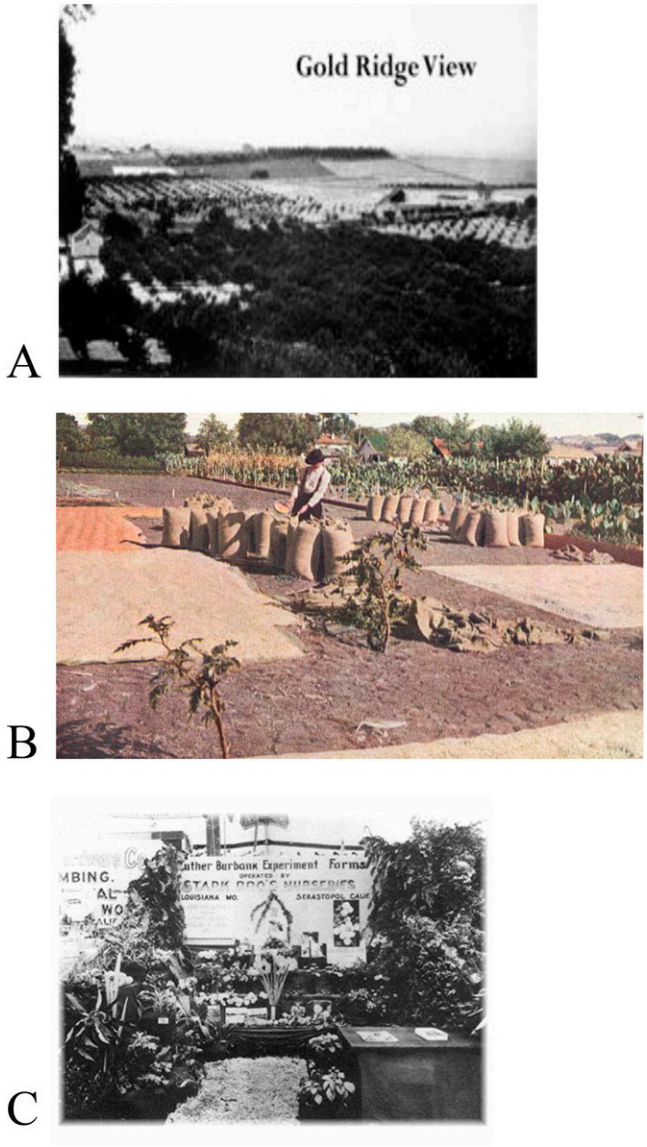


Fig. 1. Operational views of the Burbank Experiment Station: (**A**) The Luther Burbank's Gold Ridge View Experiment Farm, Sebastopol, CA, at the hiatus of Burbank's breeding endeavors; (**B**) winnowing and bagging seed from the season's collection—large quantities were often open-pollinated; (**C**) a display of the Luther Burbank Experiment Forms of ornamental plants by Stark Brothers' Nurseries, which purchased most of the remaining stock after Burbank's death (Smith, 2009).

valued fruit and flower "novelties" sourced from grow-outs of germplasm collected in the wild, "chance seedlings," exotic imports, or limited breeding (Howard, 1945). This unique process helped Burbank develop his "eye" for variation and mutations, the foundation for his success as well as for today's ornamental industry. As Claude Hope, the famous $F_1$ hybrid *Impatiens* and *Petunia* breeder (Martinez, 1992) noted years later, "A successful breeder has to be a good observer" (Pollan, 2001). The ability to identify and select variants in large populations is an art still used by modern public and private sector flower breeders.

*Exclusivity.* After Burbank purchased The Gold Ridge Experiment Farm, undoubtedly this along with the Santa Rosa farm became the largest such private sector breeding station in the world, both in its timeframe of Burbank's life and for many decades thereafter. He employed a very small seasonal staff—by modern standards—(Smith, 2009), one of whom can be seen busily bagging the seasonal seed of a crop (Fig. 1B). At least three field managers have been identified as working with Burbank: Wilbur Hall who edited Luther's biography (Hall, 1939), John Y. Beaty who authored a book on plant breeding and claims to have worked under him (Beaty, 1954), and Bill Henderson, who did *Crinum* breeding, opening his own Experimental Garden in Fresno, CA. He did not trust any of the seasonal workers who had to empty their pockets each day when leaving the premises (Smith, 2009). Even his secretaries were not allowed too much information about the breeding and domestication processes. Burbank trusted no one, ever afraid of losing his trade secrets.

The business was meant to be a self-sustaining, profitable, and non-conventional nursery selling the entire product line of a new cultivar or crop only to wholesale firms instead of selling as retail (Howard, 1945). Several large firms participated in this endeavor, both nationally (Stark Brothers Nurseries, John Lewis Childs, W.A. Atlee Burpee Co.) and internationally (J.M. Rutland, Victoria, Australia) (Howard, 1945; Smith, 2009). The highest bidder earned exclusive rights as a propagator, distributor, or retailer to sell the products on the market.

Speculation and selling to the highest bidder were common occurrences with Luther Burbank's floral products. Speculation was fueled by Burbank's own exaggerated claims for his new plant improvements as well as those of the wholesalers who sold his introductions to the general public. Through Burbank's annual catalog, new products were hawked with prices set by Burbank. For example, for his entire line of hybrid lilies (*L.* ×*burbankii*), the price was U.S. $250,000 or for individual "very handsome, hardy ones" U.S. $250 to U.S. $10,000 each (Burbank, 1914–15; Howard, 1945). Other flower cultivars also commanded high prices such as the seedling Giant amaryllis that sold for U.S. $1.55/bulb in 1909 (Burbank, 1909). Interest in cacti—particularly spineless ones—during 1909–15, rivaled the Dutch Tulip mania with exorbitant fees for a single "slab" of a cultivar, speculative investments, controversy with noted cacti specialists (particularly David Griffiths; Smith, 2009), and lawsuits by The Burbank Company. Thus, Burbank created the legacy of "exclusivity" in the flower world—still a common factor for all breeder, producer, and distributor companies driving limited supply and increased demand of novelty items (Anderson, 2006; Drew et al., 2010).

Because flowers and other ornamental crops are economically classed as nonessential food crops and are risky during economic downturns (Drew et al., 2010), many of Burbank's products did not sell in any given year (Howard, 1945). This leftover stock (seeds or vegetative plant material) had to be held over for another year's sales, prompting Burbank to continue to sell at the retail level. This practice ended when the Luther Burbank Company was founded in 1912 as a distributor firm, which had exclusivity to all products Luther Burbank bred (Howard, 1945). The Luther Burbank Company, however, was short-lived and in 1916 it went bankrupt—attributable in large part to the cactus debacle—and Burbank regained the business. Subsequently, Burbank focused on being a breeder–producer company within the horticultural distribution chain (Drew et al., 2010), selling only seeds until his death in 1926.

*Insourcing.* Because most of Burbank's competitors could not offer one or more new products each year to their customers, his market share increased as a result of the widening germplasm base used to select unusual mutants (Howard, 1945). Insourcing of germplasm on a global scale continued thereafter, allowing

Table 1. A vast array of beauty: ornamental flower crops from *Abutilon* to *Zinnia* (common, scientific, and cultivar names) bred by Luther Burbank, year introduced, and origin/salient features (Burbank, 1914–15; Howard, 1945).[z]

| Common name | Scientific name | Cultivar(s) | Yr introduced | Origin/salient features |
|---|---|---|---|---|
| Abutilon | *Abutilon vitifolium* | Pride of Chile (Burbank strain) | 1914 | A selected seedling from an imported seed lot |
| Agapanthus | *Agapanthus albo gigantea* | Lily of the Nile | 1899 | Show-white flowers, 1.25 m; developed from a small, blue type |
| | | New Agapanthus (Cape Colony Lily) | 1916 | Same description as 'Lily of the Nile', so probably the same |
| Alstroemeria, Lily of the Incas | *Alstroemeria chilensis* | Alstroemeria Chilensis (versicolor) | 1910 | Name mixup because it was not both species, although they are similar; Burbank also hybridized *Alstroemeria* with California *Lilium pardalinum* but the hybrids were not vigorous |
| Amaranthus | *Amaranthus* spp. | Combustion | 1925 | Originated in 1922; species unknown; sold to an unknown dealer; leaves resembled coleus; fiery red |
| | | Molten Fire | 1922 | Origin unknown; similar description as 'Combustion' |
| | | Sunshine | 1924 | Origin unknown; plants start coloration as seedlings; "scarlet semi-transparent rose" |
| Amaryllis | *Hippeastrum* (= *Amaryllis*) *vittatum*, *H. reginae*, *H. johnsonii* | Amaryllis hybrids | 1905 | Listed as *Amaryllis vittata* hybrida |
| | | Boy Rolf | ≈1905 | Origin unknown; possible *vittata* hybrid |
| | | Burbank's Dwarf Everblooming Fragrans | 1909 | Origin unknown; dwarf; sold to John Lewis Childs |
| | | Burbank's Giant Hybrid | 1906 | Large-flowered type; 10 generations of breeding; numerous species involved; most sold unnamed |
| | | Coronado | 1913 | Provisional name; giant hybrid with early flowering; multiplied well |
| | | Mrs. Burbank | 1901 | Briefly announced in a newspaper; 8-inch flowers |
| | | Pomona | 1913 | Giant hybrid with wide, overlapping flower petals |
| | | Portola | 1913 | Giant hybrid; flat flower, 9 inches; pure white |
| | | Profusion | 1903 | Early interspecific hybrid; John Lewis Childs potentially sold this as 'Vittata Profusion Amaryllis' |
| | | Seedling amaryllis | 1909 | 136 numbered hybrids; 4–5 species interspecifics; collectively known as Giant amaryllis; original lot had 3117 bulbs ($1.55 each, on average) |
| | *Hippeastrum vittata* × *Sprekelia formosissima* | Martinique | 1909 | Unique intergeneric hybrid; 18 = 2-inch long leaves; 58 large and 57 small bulbs offered together for $350 |
| Arabis | *Arabis blepharophylla* | Purple | 1905 | May have been collected from the wild |
| Argemone | *Argemone mexicana* × *A. grandiflora* | Unnamed seedlings | 1916 | No information |
| Asparagus yam | *Dioscorea* spp. | Asparagus yam | 1914 | Perennial vine from Chile; first ever "sweet potato vine" grown as an ornamental? |
| Aster | *Aster* spp. | Burbank's Fluffy Giant | 1925 | Interspecific California species; collection of seedlings with fluffy petal types, pastel shades |
| | | Crimson Cloud, Desert Sunset, Queen of the Market, Wreath of Snow | 1916–25 | Most likely standard type cultivars, typical of the time period |
| Australian star flower | *Cephalipterum drummondii* | Everlasting star flower, Burbank Strain | 1906 | Hybridized from a western Australia seed lot; star flowers, white to rose–crimson; annual; seed; introduced by Luther Burbank Co. (1914); distributed By Vaughan's Seed Store (Chicago, IL) |
| Bamboo | *Gallilea* spp. | Bryland Tule | 1914 | No information |
| Barberry | *Berberis dulcis*, *B. buxifolia* | Beauty Leaf | 1921 | Chilean seed source; ornamental foliage |
| | | Chilean | 1911 | Chilean; described by botanists in 1880 |
| Bluebell | *Campanula rotundifolia alba* | Blue bells of Scotland (White variety) | 1911 | Perhaps the first white-flowered strain released |
| Boltonia | *Boltonia latisquama* | New Dwarf | 1920 | Dwarf seedling selection |
| Bottlebrush | *Callistemon speciosus* | Bottlebrush | 1921 | Tender Australian shrub; most likely the same as those already in the trade at the time |
| Brazilian Perfume | *Origanum majorana?* | Brazilian Perfume | 1918 | Brazilian species; 0.3 m; "surpassing fragrance" |
| Briza | *Briza australis* | Briza | 1906 | Ornamental grass from Australia; larger than other types; "black spotted shoulders make it unusual" |

(*Continued on next page*)

Table 1. (*Continued*) A vast array of beauty: ornamental flower crops from *Abutilon* to *Zinnia* (common, scientific, and cultivar names) bred by Luther Burbank, year introduced, and origin/salient features (Burbank, 1914–15; Howard, 1945).[z]

| Common name | Scientific name | Cultivar(s) | Yr introduced | Origin/salient features |
|---|---|---|---|---|
| Brodiaea | *Brodiaea grandiflora major* | Brodiaea | 1910 | Most likely *B. californica*, growing near Burbank's home; better than *B. grandiflora* |
| Bulrush | *Scirpus* spp. | Flowering Bulrush | 1918 | Species unknown; pink flowers in early spring; "curious…plant from Chile" |
| Butterfly weed | *Asclepias* sp. | Butterfly weed | 1911 | Chilean species from the high plateaus |
| Cactus, "spineless" forage types | *Opuntia* spp. | Actual | 1907? | Hybrid from the cross: 'Anacantha' × 'Smith' |
| | | Anacantha | 1907 | Original stock source (David Fairchild); nearly devoid of spines |
| | | Arbiter | 1911 | One of the best for fodder |
| | | Avalon | 1925 | Giant spineless; 22 inches × 8 inches (length × width) slabs; few white fruit; best ever produced |
| | | Banana | ? | OP seedling |
| | | Blanco | 1907 | Indian-fig class; Walter Bryant (source); known as 'White Cactus' |
| | | Burbank Standard | 1911 | From "selective breeding" |
| | | Buster | 1911 | Closely resembles 'Competent', 'Signal' |
| | | California | 1907 | Similar to 'Sonoma' 24 inch × 12-inch slabs |
| | | Chico | 1907 | Tapuna class; one of the best in this class |
| | | Columbia | 1912 | Compact; easy propagator; smoothest, dark green slab. |
| | | Competent | 1911 | $F_2$?; smooth slab seedling; nearly free of spines; 24 to 36 inches × 6 to 8-inch slabs |
| | | El Dorado | ? | OP seedling |
| | | Feeder | 1916 | Compact, glossy slabs; 10 inches × 8 inches |
| | | Fresno | 1907 | Indian-fig class; distributed by American Cactus Farming Co. |
| | | Hemet | 1909 | Tapuna class ("tunas"); smooth with "pearly white" pads' hardy |
| | | Marin | 1907 | "Absolutely without spines or bristles"; smaller plants; may have been introduced as 'Marine' by Don Francisco de Paula Marin in 1791 |
| | | Melrose | 1909 | Tapuna class; smooth; strong grower |
| | | Model | 1912 | Seedling from 'Smith'; no thorns |
| | | Monterey | 1907 | Tapuna class; most rapid-growing; distributed by American Cactus Farming Co. |
| | | Morada | 1907 | Tapuna class; from Tepic, Mexico; similar to 'Blanco' |
| | | Meyers | 1907 | Perhaps a natural cross of Tapuna and Indian fig types; discovered by Frank Meyers near Irapuato, Mexico; free from even the least traces of spines |
| | | Opaline | 1911 | Tapuna; large fruit |
| | | Pyramid | 1909 | Indian fig class; upright growth; one of the best for poultry and livestock |
| | | Robusta | 1911 | Hybrid of Burbank; pale green slabs (2–5 lbs. each) |
| | | Rosamel | 1915 | Little known; hardy |
| | | Santa Rosa | 1907 | Indian-fig; Burbank's best and highest priced cactus; distributed by American Cactus Farming Co. |
| | | Signal | 1911 | Hybrid; 4 feet in length; 10 to 20 lbs./slab |
| | | Smith | 1907 | Collected in north Africa; named after E.E. Smith |
| | | Solano | 1909 | Indian fig; compact, weeping habit |
| | | Sonoma | 1907 | Pale yellow; 20 inches × 10 inches; exclusive rights for the southern hemisphere sold to Mr. Rutland (Melbourne, Australia) |
| | | Special | 1911 | Tapuna; silvery slabs; truly spineless |
| | | Texas | 1925 | Developed from a Texas type; 10 inches × 6 inches |
| | | Titania | 1911 | Light grass green color; 36 to 48 inches × 1.5 to 3 inches |
| | | Trailing | 1907 | Small, spreading plant; glossy green; occasional long spine |
| | | Vertex | 1911 | Hybrid; tree-like, bluish green |
| | | White Fruit | ? | Parent of OP 'Banana' and 'El Dorado' |
| | | Wooly | 1911 | Wooly leaves but nearly spineless |
| | | Zalisco | 1912 | Smith seedling; similar to 'Model' |

(*Continued on next page*)

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| Common name | Scientific name | Cultivar(s) | Yr introduced | Origin/salient features |
|---|---|---|---|---|
| Cactus, ornamental types | *Echinopsis mullerii*, *E. pentlandii* | Favorite | 1911 | Peruvian hedgehog cactus; imported; sold under both species names |
| | *Opuntia basilaris* | Opuntia species | 1911 | Most likely collected from the southern California or Arizona deserts |
| | *Echinocactus chilensis*; *Cercus chilensis* | Quisco | 1911 | Sold under both species names; native to Chile; resembled *E. visnaga*; barrel type with many, "not vicious spines" |
| Calandrinia | *Calandrinia umbellata?* | Calandrinia | 1911 | Annual succulent; most likely not the perennial species, *C. umbellate*; trailing; rose–crimson or "solferino," large flowers |
| Calla lily (Richardia or Zantedeschia) | *Zantedeschia albo-maculata*, *Z. hastata*, *Z. elliottiana*, *Z. pentlandii*, *Z. melonoleuca*, *Z. nelsonii*, *Z. rehmannii* | Dwarf everblooming | 1901? | A 'Little Gem' selection |
| | | Dwarf-scented | 1894? | Similar to or the same as 'Fragrance'; distributed by the Conrad and Jones Co., West Grove, PA |
| | | Fragrance | 1894 | $F_2$ seedling from 'Little Gem' with "fully developed and really delightful perfume" |
| | | Giant | 1893 | A sport of some white calla lilies; most likely *Z. albo-maculata* |
| | | Giant Selected | 1893 | Name later changed to 'Lemon Giant' |
| | | Golden Variegated | 1893 | Selected from *Z. hastata* 'Pride of the Congo' |
| | | Hybrids | 1901 | Five species hybrids; large leaves with white or yellow flowers |
| | | Lemon Giant | 1893 | First introduced as 'Giant'; interspecific hybrid: *Z. hastata* × *Z. albo-maculata* |
| | | Snowflake | 1893 | Seedling of 'Little Gem' which was half its height |
| | | Variegated Little Gem | 1893 | Sport from 'Little Gem'; marbled gold leaves |
| | | Willie Hearst | 1904? | Most likely from the cross: *Z. albo-maculata* × *Z. hastata*; yellow |
| | | Yellow Calla | 1911 | Close affinity *Z. hastata* 'Pride of the Congo' |
| Calliopsis | *Coreopsis bicolor* | Burbank Tiger | 1915 | Various shades of nearly black, orange, yellows, and purple |
| Camassia | *Camassia leichtlinii* | Burbank Hybrids | 1911 | All hybrids may be composed of several additional species; large bulbs, huge flowers, new colors of purple, dark and sky blue |
| | | Camassia Hybrids | 1918 | Largest, brightest colors of *Camassia*; also called 'Indian Potato' |
| | | Camassia Leichtlinii | 1906 | Collected in California |
| | | Compacta | 1914 | No information |
| | | Multiplier | 1927 | Interspecific hybrid between California species; this easily multiples by "natural division" |
| Canna | *Canna* ×*generalis* ('Crozy' type) × *Canna flaccida* | Burbank | 1899 | Yellow orchid type; semidouble; 1.2 m (Burbank) or 1.75 to 2 m (Vaughan's); introduced by Vaughan's Seed Store (Chicago, IL) |
| | | California | 1920 | No information |
| | | Conowingo | 1920 | Unknown origin; large scarlet flowers; bronze–green leaves |
| | | Cristata | 1922 | 1.25 m; dark green foliage; orchid-type flowers |
| | | Fire | 1920 | Unknown origin; similar to 'Firebird' with larger flowers |
| | | Firebird | 1907 | Unknown origin; scarlet flowers; large size; 1.5 m |
| | | Rainbow | 1907 | Unknown origin; ornamental foliage plant; "elaborate coloring" of leaves |
| | | Tarrytown | 1895 | Orchid type; large, green leaves; 1.25 m; vermilion–salmon with a light yellow edge; won the 1901 Gold Medal at the Pan-American Exposition, Buffalo, NY |
| | | Wyoming | 1913? | No information; yellow flowers with red streaks |
| | | Yellow King Humbert | 1918 | Yellow flowers with red transposable elements; otherwise the same as 'King Humbert' |
| Carnation | *Dianthus chinensis* | Burbank Everblooming | 1925 | Most likely a selection of Chabaud's Everblooming |
| | *D. caryophyllus* | Marguerite, Royal or Burbank strain | 1910 | Similar to the Marguerite offered by other seed houses, only dwarfer |
| Celosia | *Celosia* spp. | Ostrich Plume | 1911 | Apparently a selection out of another variety |

(*Continued on next page*)

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| Common name | Scientific name | Cultivar(s) | Yr introduced | Origin/salient features |
|---|---|---|---|---|
| Cherry | *Patagonia ciruelo* | Evergreen Patagoni | 1911 | An ornamental tree; also called the S. American Wild Black Cherry; most likely in the genus *Prunus* only it is not deciduous; from seeds of the Sociedad Explotadora de Terra del Fuego (Rio Aysen, Chile) |
| Chilean Blue Flowering Bulbous Plant | *<Unknown>* | Burbank Selection | 1914 | Released as a selection before having correct nomenclature; from a collector in Chile; summer flowering with 2-foot stems, cobalt blue to white |
| Clematis | *Clematis jackmanii*, *C. crispa*, *C. coccinea* | Clematis Hybrids | 1893 | Five seedlings, most likely selfs or open pollinated; three were later named: 'Snowdrift', 'Ostrich Plume', 'Waverly'; most were disease-susceptible |
| | *C. jackmanii-lanuginosa* | Double Clematis | 1894 | No information |
| | *C. jackmanii* | Jackman Hybrid Seedlings | 1892 | Most likely the first announcement of the 'Clematis Hybrids' (1893) |
| | | Ostrich Plume | 1894 | Double white; from the 'Clematis Hybrids' |
| | | Paraguay | 1922 | Sent from a collector in Paraguay; resembles *C. verticillata* |
| | | Snowdrift | 1894 | Double white; from the 'Clematis Hybrids' |
| | | Waverly | 1894 | From the 'Clematis Hybrids' |
| Columbine | *Aquilegia caerulea* | Burbank's New Clematis-flowered | 1903 | Crossed with a spurless cultivar; introduced by Vaughan's Seed Store (Chicago, IL) |
| | | New Hybrids | 1894 | Hybrid mix |
| Coreopsis | *Coreopsis lanceolate grandiflora* | Burbank strain | 1911 | Most likely a perennial, selected seedling with yellow–gold flowers |
| Corn, Ornamental | *Zea mays variegata* | Aurora | 1914 | An improved cultivar of 'Rainbow' |
| | | Rainbow | 1911 | $F_2$ seedlings selected for several years for six stripes/leaf; from "quadri-colored" corn (Germany) |
| Crinum | *Crinum americanum*, *C. amabile*, *C. asiatica* | Burbank Hybrids | 1902, 1906, 1914, 1927 | Interspecific hybrids of complex ancestry (like his amaryllis or Hippeastrum) |
| Dahlia | *Dahlia juarezii* | Burbank | 1903 | Cactus type; Vaughan's Seed Store (Chicago, IL) |
| | | Burbank Dahlias | 1914 | Scarlet to crimson giant singles |
| | | Burbank's Selection | 1903 | Hybrid mix, most likely cactus types; Vaughan's Seed Store (Chicago, IL) |
| | | California | 1903 | Large yellow, upright habit; Vaughan's Seed Store (Chicago, IL) |
| | | Caviota (Gaviota?) | 1903 | Snow white; Vaughan's Seed Store (Chicago, IL) |
| | | Coronato | 1910 | Single, fragrant; flowers in first year from seed! |
| | | David Burpee | 1922? | No information |
| | | Estrelia | 1903 | Snow white cactus type; Vaughan's Seed Store (Chicago, IL) |
| | | Golden West | 1922 | No information |
| | | Lavendera | 1918 | 'Geisha' seedling; remained on the market for many decades |
| | | Marigold | 1903 | Double; selected from 'Gloria'; Vaughan's Seed Store (Chicago, IL) |
| | | Mariposa | 1903 | Upright habit, pale yellow; Vaughan's Seed Store (Chicago, IL) |
| | | Oakland | 1918 | Large, pure white; became "the official flower of the city of Oakland, California" as a publicity stunt because this is not true |
| | | Santa Rosa | 1903 | Cactus type; fragrant, red with salmon tints; Vaughan's Seed Store (Chicago, IL) |
| | | Sebastopol | ≈1905 | Orange–red; remained on the market for many decades |
| | *D. purpusii* | Sonoma | 1903 | Light yellow; Vaughan's Seed Store (Chicago, IL) |
| | | Dazzling | 1918 | Scarlet; from crossing a cactus type with a wild scarlet collected by Dr. Purpus in Mexico; also known as 'Mountain Dahlia' |
| | | Scarlet | 1918 | Cactus type, single |
| | *D. purpusii* × *D. variabilis* | Sunset | 1915 | Looked like tiger lilies from a distance |

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| Common name | Scientific name | Cultivar(s) | Yr introduced | Origin/salient features |
|---|---|---|---|---|
| Daisy, Shasta | [(*Leucanthemum vulgare* × *L. maximum*) × *L. lacustre*] × *L. nipponicum* | Abundance | 1913 | One of the many selected seedlings in the 'Shasta' collection |
| | | Alaska | 1904 | Closely related seedling, selected 3 years after the original 'Shasta' |
| | | California | 1904 | Closely related seedling, selected 3 years after the original 'Shasta' |
| | | Double Fluted Shasta | 1915 | Frilled petals, "glistening white" |
| | | Shasta Daisy Hybrids | 1901 | The original 4-species hybrid with white flowers resembling the snow-capped Mt. Shasta; hardy herbaceous perennial; widely adaptable across the U.S. and worldwide for greater than one century; Burbank's best accomplishment in flower breeding; Hugo De Vries countered that it was just a selection from the wild species growing near Mt. Shasta (De Vries, 1905) |
| | | Shasta Giant | 1925 | Flowers the same size as 'Alaska' on 3- to 4-foot stems |
| | | Westralia | 1904 | Similar to 'Alaska'; good branching habit |
| Day lily | *Hemerocallis thunbergii* | Burbank | 1917 | Hybrid; yellow; 34 inches; distributed by Carl Purdy, Ukiah, CA |
| | | Calypso | 1918 | No information; distributed by Carl Purdy, Ukiah, CA |
| | | Cygnet | 1924 | No information; mentioned in House Beautiful 55:69 (1924) |
| | | Miss Clara Burton | 1914 | No information |
| | | Surprise | 1917 | Hybrid? |
| | | Surprise No. 2 | 1914 | No information |
| Delphinium | *Delphinium hybridum* | Burbank Hybrids | 1910 | Selected seedlings |
| | | Burbank's Giant Perennial Hybrids | 1911 | Selected seedlings |
| | | Burbank Select Hybrid | 1915 | Selected seedlings |
| | *D. bakeri* | Unnamed Larkspur | 1918 | New, yellow species, collected near Bodega Bay, CA |
| Dicentra | *Dicentra chrysantha* | Golden eardrop | 1895 | Selected from the wild in north California; originally listed as *Diclytra chrysantha* |
| Dimorphotheca | *Dimorphotheca sinuata* | Burbank Hybrids | 1915 | African orange daisy |
| Erysimum | *Erysimum grandiflorum* | (Unnamed) | 1904 | Most likely a selection from the wild |
| Galium | *Galium boreale* | Galium | 1899 | From a collection in the wild, Saskatchewan, Canada; perennial, white-flowered |
| Gladiolus | *Gladiolus ×grandiflorus* | Abutilon | 1917 | Dwarf type; related to 'America' |
| | | Acanthus | 1917 | No information |
| | | Arica "D" | 1914 | No information |
| | | Benetta | 1926 | No information |
| | | Best Blue in Existence | 1914 | No information |
| | | Betty Jane | 1926 | May be a complex hybrid |
| | | California | 1889 | 'America' × Gandavensis-type hybrid; flowers a tightly held like a Hyacinth, often double (10 to 16 petals each); a "remarkable freak"; sold to A. Blanc and Co. (Philadelphia, PA) who lost the stock when it froze |
| | | Cisco | 1899 | Another 'America' × Gandavensis type hybrid; rose pink with salmon |
| | | Conquest | 1911 | Seedling of 'America'? |
| | | Dazzling | 1911 | Seedling of 'America'? |
| | | Del Oro | 1925 | A "complex hybrid" |
| | | Del Rosa | 1925 | A "complex hybrid" |
| | | Dog Star | 1926 | No information; released after Burbank's death |
| | | Doro | 1926 | No information; released after Burbank's death |
| | | Elegance | 1911 | No information |
| | | Elena | 1926 | A seedling of 'Elora' |
| | | Elora | 1917 | No information |
| | | Esthetic | 1911 | Flowers of a "peculiar rosy crimson" |
| | | Fire | 1917 | No information |
| | | Gigantic | 1911 | No information |
| | | Good Morning | 1925 | No information |
| | | Graceful | 1911 | No information |
| | | Harmonious | 1911 | No information |
| | | Igo | 1889 | An 'America' × Gandavensis-type hybrid |

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|---|---|---|---|---|
| | | Kiva | 1925 | A multicultivar hybrid |
| | | Luther Burbank | 1926 | Released after Burbank's death; a multicultivar hybrid |
| | | Mariposa | 1889 | Most likely an 'America' × Gandavensis-type hybrid |
| | | Mary Ellen | 1925 | No information |
| | | Modesto | 1889 | An 'America' × Gandavensis-type hybrid |
| | | Mono | 1889 | An 'America' × Gandavensis-type hybrid |
| | | Navajo | 1926 | A result of "numerous crosses" |
| | | Opaline | 1911 | Most likely an 'America' × Gandavensis-type hybrid |
| | | Pentstemon | 1917 | A multicultivar hybrid; name misspelled |
| | | Perla | 1926 | A multicultivar hybrid |
| | | Pinnacle | 1911 | Wide, broad petal, salmon–scarlet; purple stamens; most likely an 'America' × Gandavensis-type hybrid |
| | | Pohono | 1889 | Most likely an 'America' × Gandavensis-type hybrid |
| | | Radio | 1911 | First named 'Rajah'; most likely an 'America' × Gandavensis-type hybrid |
| | | Santa Rosa | 1889 | Most likely a Gandavensis type |
| | | Scarlet | 1917 | No information |
| | | Seedling Gladioli | 1893 | Ten numbered seedlings |
| | | Seedlings of California Strain | 1890 | Obviously seedlings of 'California' |
| | | Seeds of Burbank New Hybrid Gladioli | 1914 | Most likely 'America' × Gandavensis-type hybrids |
| | | Shasta | 1889 | Most likely an 'America' × Gandavensis-type hybrid |
| | | Signal | 1911 | Most likely an 'America' × Gandavensis-type hybrid |
| | | Summit | 1926 | A multicultivar hybrid |
| | | Symmetry | 1911 | Most likely an 'America' × Gandavensis-type hybrid |
| | | Tiger Face | 1926 | A multicultivar hybrid |
| | | Waukena "F" | 1914 | No information |
| Godetia | *Godetia magellanica* | Burbank's New Lavender Trailing | 1910 | From a Chilean collector; trails when vegetative then upright upon flowering (similar habit to English ivy, *Hedera helix*) |
| | | Godetia Hybrids | 1910 | Open-pollinated; announced as *Godetia amoena* |
| Goldenrod | *Solidago* spp. | Golden Fluff | 1916 | No information |
| | | Pale Gold | 1916 | No information |
| Grasses, ornamental types | *Lippia repens* | Dxie | 1911 | A lawn cover |
| | | Mohave | 1911 | A lawn cover |
| | *Cortaderia selloana* | Bonita | 1914 | Distinct, new |
| | *C. quila* | New Dwarf Pampas grass | 1901 | Mislabeled as *Gynerium jubatum*; discovered in South America; 2 months earlier than other types; introduced by John Lewis Childs in 1903 |
| | *Pennisetum setaceum* | New Paraguay Fountain Grass | 1921 | Collected by Guanaco Indians in South America as directed by Francisco Mueller; perennial |
| | *P. ruppelii* (= *P. ruppellianum*) | Pennisetum Ruppellianum | 1895 | Most likely imported from Ethiopia |
| Hawthorn | *Crataegus pinnatifida* | Hawthorn | 1929 | Shrub selection from seeds received from Prof. Joseph Bailie, University of Nanking, China |
| Herbertia | *Herbertia pulchella* | Little Blue Tigridia | 1910 | Listed 1 year later as *H. platensis*; blue; resembled giant *Tigridia* |
| Heuchera | *Heuchera cristata* | Heuchera | 1906 | Burbank collected seeds of *H. micrantha* on Mount Saint Helena (California); one selection had crinkly leaves; in the fourth generation of selfing or OP, most were crinkled; named a new species |
| Horehound | *Marrubium vulgare* | Golden Marrubium | 1921 | Pure gold-colored leaves; selected from a wild seedling; 60% of seedlings were gold |
| Iris | *Iris laevigata* | Unnamed | ND | Mixture from an entire seed lot |
| | *Sisyrinchium striatum* | Chilean Giant Sisyrinchium | 1911 | Species name assigned by Burbank; from Chile; yellow flowers; 1.2 m |
| Lavender | *Lavandula angustifolia* | Pinnacle | 1923 | No information; sold directly to a distributor |

(*Continued on next page*)

Table 1. (*Continued*) A vast array of beauty: ornamental flower crops from *Abutilon* to *Zinnia* (common, scientific, and cultivar names) bred by Luther Burbank, year introduced, and origin/salient features (Burbank, 1914–15; Howard, 1945).[z]

| Common name | Scientific name | Cultivar(s) | Yr introduced | Origin/salient features |
|---|---|---|---|---|
| Lily | *Lilium pardalinum*, *L. washingtonianum*, *L. humboldtii*, *L. parryi*, *L. maritimum*, *L. auratum*, *L. batemanniae*, *L. florum*, *L. martagon*, *L. parvum*, *L. speciosum*, *L. superbum*, *L. tigrinum*, *L. wallichianum*, *L. purpureum* | Burbank | 1909? | *L. pardalinum* × *L. washingtonianum*; distributed by J.J.H. Gregory & Sons (Marblehead, MA) |
| | | Hybrid lilies | 1893–4 | Two offered in 1893; multiples in 1894; numerous species in these interspecifics |
| | | Hybrid P-2,854 | 1893 | *L. pardalinum* only |
| | | Hybrid P-72,721 | 1893 | Most likely selected from *L. pardalinum*; original dwarf parent plant collected on Pluton Creek (north California) |
| | *L. bloomerianum* | Wild Species of Lily | 1888 | *L. maritimum* and/or *L. humboldtii* |
| Lippia | *Lippia canescens* (= *L. repens*) | Dixie | 1909 | A replacement for lawn grasses; purportedly collected in Chile but others in the United States were from Rome, Italy |
| | | Mohave | 1911 | Larger and faster growing than 'Dixie'; good for soil erosion on slopes; did not resist traffic or drought |
| Marigold | *Calendula officinalis*, *Tagetes patula*, *T. erecta* | Calendula Hybrid | 1915 | Listed as *Calendula hybrida*; single and doubles; white, orange, yellow |
| | | Chilean Fragrant | 1911 | From a Chilean seed lot; exact species unknown |
| | | Corona | 1925 | Unknown hybrid |
| | | Giant Calendula | ND | No information |
| Mimulus | *Mimulus cardinalis* | New Hybrids | 1904 | Range of flower colors (yellow, red, orange, pink, white) |
| | *Mimuls grandis* | M. Grandis | ND | A "rare California perennial" collected in the wild |
| Montbretia | *Crocosmia* spp. (= *Montbretia*) | New California Strain | 1888 | "Like small gladioli"; selected or collected in the wild |
| Morning-glory | *Ipomoea purpurea* | Burbank's Giant Crimson | 113 | "Imperial carmine" flowers |
| Myrtle | *Myrtus ugni* | Improved Chilean | 1916 | From Chile; edible huckleberry fruit, bronze–red; evergreen shrub 0.75 to 1 m |
| | *Myrtus communis* | New Myrtle | 1893 | Silver variegation; mutation |
| Nicotiana | *Nicotiana alata*, *N. glauca*, *N. purpurea*, *N. suaveolens*, *N. affinis*, *N. colossea* | Unnamed | 1893 | Many interspecific hybrids; most were vegetative; marbled or mottled leaves |
| ×*Nicotunia* | *Nicotiana wigandioides* var. *rubra* × *Petunia hybrida* var. *grandiflora* | Nicotunia | 1893 | Sterile, vegetative integeneric; semitrailing; green, pink, red, or purple picotee flowers; ruffled |
| Peach, Ornamental | *Prunus persica* | Double Flowering | 1915 | Profuse dark pink flowers, upright growth |
| Penstemon | *Penstemon* spp. | Burbank Scarlet Bugle | 1915 | Mislabelled as "*Pentstemon*"; 0.5 to 0.75 m |
| | | Crimson | 1914 | No information |
| Platycodon | *Platycodon grandiflora* | Japanese Bell | 1910 | Blue and white |
| | | New Double White | 1919 | Perennial; dwarf to 0.75 m |
| Plum, Chinese climbing | *Actinidia chinensis* | Mao-li-dzi | 1910 | Received from a Chinese collector; resembled plums but not a Prunus; furry skin; small seeds |
| | *Actinida agrita* (*A. arguta?*) | Tara | 1910 | Korean seedling; climbing vine |
| | *Actinidia chinensis* | Yang-tao | 1910 | Less hardy than 'Mao-li-dzi' but similar fruit |
| Plum, Ornamental Blackleaf | *Prunus cerasifera* | Thunder Cloud | 1919 | Most likely a selection from the 'Myrobalan' rootstock; with purpled leaves |
| Poppy, CA | *Eschscholtzia californica* | Burbank Crimson *Eschscholtzia* | 1904 | Red selection; distributed by Burpee Seed Co. (Philadelphia, PA) |
| | | Burbank Reselected Giant White | 1911 | Best white |
| | | Extra Mixed | 1900 | White, yellow, red in the strain |
| | | Firefly | 1915 | Light yellow with crimson |
| | | Golden Cup | 1907 | Red; distributed by the Santa Rosa, CA, Chamber of Commerce |
| | | Mixed | 1911 | Shades of all colors Burbank developed |
| | | Orange Cream | 1919 | Released as *Papaver californicum* |
| | | Pink Eschscholtzia | 1900? | No information; distributed by Burpee Seed Co. (Philadelphia, PA) |

(*Continued on next page*)

Table 1. (*Continued*) A vast array of beauty: ornamental flower crops from *Abutilon* to *Zinnia* (common, scientific, and cultivar names) bred by Luther Burbank, year introduced, and origin/salient features (Burbank, 1914–15; Howard, 1945).[z]

| Common name | Scientific name | Cultivar(s) | Yr introduced | Origin/salient features |
|---|---|---|---|---|
| Poppy, Tulip | *Papaver glaucum* | Burbank Selected | 1910 | Red with "large flowering proclivities" |
| Poppy, Shirley | *Papaver rhoeas* | Burbank Mixture of Blue Shades | 1913 | Perhaps the same as 'Celestial White' |
| | | Burbank Strain | 1911 | From 10 years of selection |
| | | Celeste | 1911 | Gray, lavender to blue shades |
| | | Celestial Strain | 1910 | Pink, salmon, white shades; "crimped" petals |
| | | Giant Shirley | 1920 | *Papaver rhoeas* × *P. glaucum* hybrid |
| | | Santa Rosa Strain | 1904 | Large flowers; clear colors as well as striped ones, blue and salmon; introduced by J.C. Vaughan (Chicago, IL) and John Lewis Childs |
| | | Shirley Art Poppies | 1921 | White to pink to salmon; crepe-like petals |
| | *P. rhoeas* var. *umbrosum* | Silver Lining | 1893 | Sport with silver white on the inside of the petals; red outside; distributed by Burpee Seed Co. (Philadelphia, PA) |
| Poppy, Prickly | *Argemone munita* | Mariposa | 1922 | Red-flowered selection from the wild |
| | | New Large Flowering Hybrids | 1918 | Yellow to cream |
| Poppy, Wind | *Meconopsis heterophylla* | Meconopsis | 1906 | Released as *Meconopsis californica* |
| | | Mixed California Hybrids | 1926 | No information |
| Poppy, Crimson | *Papaver orientale* × *P. somniferum* | New Everblooming Crimson–Scarlet Perennial Hybrid | 1916 | Flowered continuously for 10 to 12 months; single; red to orange |
| Poppy, Opium | *Papaver somniferum* | Queen | 1892 | No information |
| | | Rosy Giant | 1921 | 1 m tall |
| Primrose, Evening | *Oenothera acaulis* | America | 1910 | Flat-flowered, nearly 4.5 to 5 inches in width; "snowy white"; came true from seed |
| Quince, Ornamental | *Chaenomeles japonica* | Dazzle | 1893 | No information |
| Rose | *Rosa* ×*hybrida* | Burbank | 1899 | Rosy crimson hybrid from crossing 'Hermosa' × 'Bon Silene'; introduced by W. Atlee Burpee Co. (Philadelphia, PA) in 1900; won the Louisiana Purchase Exposition Gold Medal, St. Louis, MO, in 1904; reintroduced by Stark Brothers (Louisiana, MO) in 1936 |
| | | Coquito | 1901 | Sibling of 'Burbank' with larger flowers; deep rose |
| | | Corona | 1911 | Crimson red rambler type (semi-climber) |
| | | Garland | 1918 | Shell-pink flowers; 'Crimson Rambler' × 'Cherokee' |
| | | Hacienda | 1914 | No information |
| | | La Paloma No. 60 | 1914 | No information |
| | | Peachblow | 1893 | M-17,806 rose seedling; hybrid tea; pale silver–peach/pink inside of petals; outside a "dark, bronzy carmine–pink |
| | | Pipette | 1909 | Parents included 'Bon Silene', 'Hermosa', etc. |
| | | Rose of Oregon | 1909 | Sent to the Portland, OR, Rose Carnival, 22 Feb. 1909 |
| | | Santa Rosa (Hybrid bourbon Tea) | 1898 | $F_2$ seedling of 'Hermosa'; shell pink flowers; double-reflexed; Burbank sold this retail |
| | | Seedling Rose H. 813 | 1893 | 'Hermosa' seedling; rich pink |
| | | Seedling Rose J. 26,940 | 1893 | Similar to 'General Jacqueminot' |
| | | Seedling Rose M. 11,120 | 1893 | Everblooming; mixed seed lot |
| | | Seedling Rose M. 19,928 | 1893 | Resembled 'Papa Gontier' with additional petalage |
| | | Waynoka No. 59 | 1914 | No information |
| | *Rosa rugosa* | Rugosa Hybrids | 1893 | Pink climber; awarded a California Floral Society medal |
| Scilla | *Scilla peruviana* | Burbank Scilla | 1914 | Peruvian species; deep blue |
| | *Scilla autumnalis* | German Scilla | 1914 | Blue/white mix; dist. by Luther Burbank Co. (San Francisco, CA) |
| Scyphanthus | *Scyphanthus elegans* | Unnamed | 1908 | Chilean import; gold |
| Silphium | *Silphium laciniatum* | Square Plant | 1916 | From the Midwest states; square stems; yellow |

(*Continued on next page*)

Table 1. (*Continued*) A vast array of beauty: ornamental flower crops from *Abutilon* to *Zinnia* (common, scientific, and cultivar names) bred by Luther Burbank, year introduced, and origin/salient features (Burbank, 1914–15; Howard, 1945).[z]

| Common name | Scientific name | Cultivar(s) | Yr introduced | Origin/salient features |
|---|---|---|---|---|
| Sunflower | *Helianthus annuus H. californicus* | California | 1919 | Double, yellow |
| | | Manteca | 1917 | White-seeded, from "crossing the… black-seeded double California sunflower with the Giant Russian" |
| | | Primrose Colored | 1891 | No information |
| | | Prolific White | 1920 | White seeds; large heads; single |
| | | Single Helianthus (Burbank Strain) | 1914 | Large flowers; tall |
| | | Snow | 1915 | 20-inch seed head width; large flowers; white-seeded |
| Sweet Pea | *Lathyrus odoratus* | Burbank's Long Season | 1913 | From crossing an early × late Spencer type |
| | *L. latifolia* | Perennial | 1918 | No information |
| | *L. splendens* | Pride of California | ND | Selected from the wild |
| Tellima | *Tellima affinis* | Woodland Star | 1909 | Selected from the wild in California; distributed by John Lewis Childs |
| Teosinte | *Teosinte* sp. × *Zea mays variegata* | Burbank New Rainbow | 1926 | Colors lasted longer than Rainbow corn; 6 to 18 ears/plant |
| Tigridia (Tiger flower) | *Tigiridia pavonia*, *T. conchifloa*, *T. buccifera* | Burbank New Hybrids | 1914 | Various shades; all *Tigridia* were distributed by John Lewis Childs |
| | | Chilean Dwarf | 1920 | Light blue |
| | *T. grandiflora* | New Hybrid Tigridias | 1899 | Large flowers; new colors |
| | *T. grandiflora alba* | Tigridia (Large White Flowered) | 1888 | Pearly white with red–brown spots |
| | *T. mexicana* | Tigridia (Mexican) | 1910 | From the wild in Mexico |
| Tomato, Ornamental | *Solanum esculentum*, *S. pimpinellifolium* (= *Lycopersicon*) | Combination | 1893 | Interspecific hybrid; 0.3 m; "leaves are curiously plaited, twisted and blistered, but handsome"; fruit non-edible |
| | | Ornamental Cross-bred | 1893 | Interspecific hybrid with a Dwarf Champion type; no information |
| Tomatillo, Chilean | *Physalis ixocarpa* | Burbank Selection | 1910 | Red fruits with larger fruits than *Solanum pseudo-capsicum*, although resembling this species |
| Tritoma | *Kniphofia grandiflora*, *K. macowanii* | Cazique | 1914 | No information |
| | | Exquisite | 1914 | 1.25 m; dark green leaves |
| | | Flameflower or Torch lily | 1926 | Sold as *Tritoma hybrida* |
| | | Hybrid Seedlings (Red-Hot Pokers) | 1911 | Mix of various shades |
| | | Tower-of-Gold | 1923 | Perhaps a hybrid; no information other than gold flowers |
| Verbena | *Verbena hybrida* | Elegance | 1901 | White center in lavender–purples; fragrant |
| | | Fragrance | 1901 | Dist. by Conrad and Jones Co. (West Grove, PA) as 'New Fragrance'; the Luther Burbank Co. later sold it (1913) as 'Burbank's Fragrance, 1913 Selection' |
| | | Giant Mayflower | 1910 | Very fragrant, similar to the trailing arbutus |
| | | Hybrids | 1910 | Mammoth mix; fragrant |
| | | Mayflower | 1901 | The first 'Mayflower' was released, unannounced, in ≈1895 and sold to John Lewis Childs |
| | | Mayflower Pink | 1900 | Shades of pink; strains of 'Mayflower', each given separate names |
| Watsonia | *Watsonia ardernei*, *W. coccinea* | Combustion | 1917 | Dwarf, short leaves; red–salmon |
| | | Crimson | 1915 | Dwarf, red |
| | | Garland | 1915 | Rose–lavender; branched stems |
| | | Hybrid Seedlings | 1908 | Large flowers; mix; offered from $100 to $500/cultivar |
| | | Hybrid Seedlings (Burbank New) | 1911 | Several shades |
| | | Hybrids (Burbank) | 1918 | Single and double whites and various other shades |
| | | Meteor | 1915 | Very tall; 3.5-inch flowers |
| | | Paragon | 1915 | Red-purple; saucer shape; 2.5 m |
| | | Radiance | 1915 | Very early; nearly everblooming; salmon |
| | | Royal White | 1917 | Very white |
| | | Salmonia | 1917 | Hot salmon |
| | | Snow Storm | 1917 | Very white |
| | | Vesta | 1915 | Snow white |
| Wax-myrtle | *Myrica cerifera* | Unnamed | 1894 | Improved hybrid of the eastern species |
| Zauschneria | *Zauschneria californica* | Improved Coast Crimson | 1904 | Large-flowered wild form |
| Zinnia | *Zinnia elegans* | Burbank Dwarf | 1918 | Red and yellow; double |
| | | Burbank's Giant | 1913 | Bright coloration of varying shades |
| | | Burbank's Giant Dahlia Zinnia | 1925 | Large double flowers just like dahlias |

[z]Note: For many introductions, "No information" indicates that the cultivar name and year of introduction is all that is known from the Bill of Sale.
OP = open-pollinated.

him to breed and select a vast array of beauty in ornamentals during his lifetime: 91 genera of flowers from *Abutilon* to *Zinnia* with nearly 1000 cultivars released to the industry (Table 1), which no competitor could equal and few—if any—individual breeder has done since. Even Claude Hope, a founder of PanAmerican Seed Company, bred numerous products, but not as many as Luther Burbank (Martinez, 1992). Genera with the highest number of cultivars bred and released by Burbank include *Amaryllis*, *Hippeastrum*, and *Crinum* followed by *Lilium*, *Hemerocallis*, *Watsonia*, *Papaver*, *Gladiolus*, *Dahlia*, and *Rosa* (Table 1).

Two of Burbank's outstanding ornamental and/or edible herbaceous cultivars—the shasta daisy and spineless cacti (discussed below)—were derived from germplasm provided by numerous collectors worldwide (Howard, 1945). The constant need for incorporating wild germplasm into cultivated ornamental crops is still an imperative for any modern flower breeder to avoid inherent risks associated with narrow cultivar bases, e.g., North American Easter lily sales are based on a single cultivar, Nellie White, which is experiencing clonal decline after greater than 60 years of asexual propagation (Zlesak et al., 2007; Zlesak and Anderson, 2007). Similarly, specific environmental requirements to flower *Pelargonium domesticum* (Martha Washington geraniums) and *Fuchsia* ×*hybrida* have limited their seasonality to spring conditions although intraspecific, wild germplasm exists with genes and alleles that promote flowering in high temperatures (Anderson, 2006).

*Mass breeding.* Because Luther did most of the breeding, selection, and grow-outs of his complex hybrids, it was not unusual for a guest to see him busily working in the fields. For instance, crossing was often done outdoors without pollen protection or emasculation of composite flower crops such as *Calendula officinalis* (Fig. 2). Thus, many of his pollinations were often contaminated with self-pollinations or other pollen sources brought in by pollinators or wind. As such, grow-outs required selection of off-types at the seedling or transplant stages, if possible. This practice is still in use with ornamental seed crops that are OP, e.g., *Capsicum annuum*, *Dahlia variabilis*, *Delphinium hybridum*, etc. (PanAmerican Seed Company, 1999) and most, if not all, heirloom flowers and vegetables.

Burbank became famous as a mass breeder, growing up advanced selections and generations en masse in the fields and harvesting immense seed quantities (Fig. 1B). Hugo De Vries, famous for his discovery of genetics independently from Gregor Mendel, referred to Burbank as "the greatest mass breeder of plants in either Europe or America" (De Vries, 1905). Slate (1939) wrote on Burbank's mass breeding of *Lilium* that his was "probably the most extensive lily hybridizing project ever undertaken" such that, by 1894, Luther had 3 acres of seedlings derived from crossing *L. pardalinum* with a large number of male parents, which were native, Pacific coast species. Purdy (1895) noted that from mass selection, breeding of "extreme" or off-types for several generations, created a population with "every intermediate form…from giants nine feet tall to dwarfs from six inches to a foot in height." Many "freaks and monstrosities" were created such that some seedlings had the recurved petals of *L. pardalinum* transformed into either flat petals or trumpets and the entire population of greater than 100,000 hybrids were fragrant (unlike *L. pardalinum*, the original female seed parent) and could be smelled miles away (Purdy, 1895).

*Lack of record-keeping and hybrid mixups.* Keeping accurate records is an essential feature of modern plant breeding and genetics, but Luther Burbank was more interested in profitable results than in process and his few record books were consequently non-scientific. One critic even said that he "was constitutionally incapable of keeping careful notes" (Smith, 2009). He did not keep careful records and was not interested in process, but rather products with market value and, in so doing, maintain secrecy. Such secrecy continues to permeate private sector plant breeding, although most modern breeders do maintain good notebooks. Only a few notebooks and a 5000-page scrapbook remain from his years of extensive breeding (Howard, 1945) in which he wrote notes on seedlings with reference to their potential marketable qualities (Fig. 3). For example, reading through his notes on the "Hybrid Best Selected" *Lilium* "of 1882 flowering," Selection Nos. 1 to 16, dated 10 Nov. 1882 (Fig. 3), he wrote that seedling No. 2 was variegated, whereas No. 3 was the tallest flowering plant, etc.

Hugo De Vries, and other scientists such as George H. Shull, noted that Burbank's keen "eye" and excellent memory meant that he could nearly always identify the male parent of a seedling without any records for referral (Howard, 1945). Interestingly to Burbank, making a cross was an experiment—although most were uncontrolled and non-scientific. In fact, the subtitle to the volumes of his "autobiography" says that his discoveries were "prepared from his original field notes covering more than 100,000 experiments…" (Burbank, 1914–15). Although mass breeding does not require extensive record-keeping as, say pedigree breeding, nonetheless, accurate records enable future breeders working on a crop to remake crosses or continue pedigrees and breeding objectives (Allard, 1960). This lack of records and incorrect labeling as well as Burbank's practice of selling off new introductions to wholesalers caused hybrid mixups to occur or multiple names were attached to the same plant. Some of these errors continue to the present day with confusion over his hybrid rose introductions, 'Burbank' and 'Santa Rosa'. Both of these cultivars were derived from a cross between *Rosa* 'Bon Silene' and an 'Hermosa' seedling (Burbank, 1914–15) but they were both released by different companies or Burbank himself (Howard, 1945). Had records of phenotypic differences between the two seedlings existed, these could have cleared up the continuing confusion of these two cultivars. Despite extreme care exerted by producer and distributor companies, hybrid mixups are still recurring phenomena (Anderson et al., 2010). Likewise, in modern-day private sector breeding programs, for instance, a flower breeder may not necessarily breed the same crop(s) during their lifetime, so continuity is lost when records are poorly kept. Sadly, when Burbank died, the vast majority of his breeding knowledge kept in his memory vanished forever.

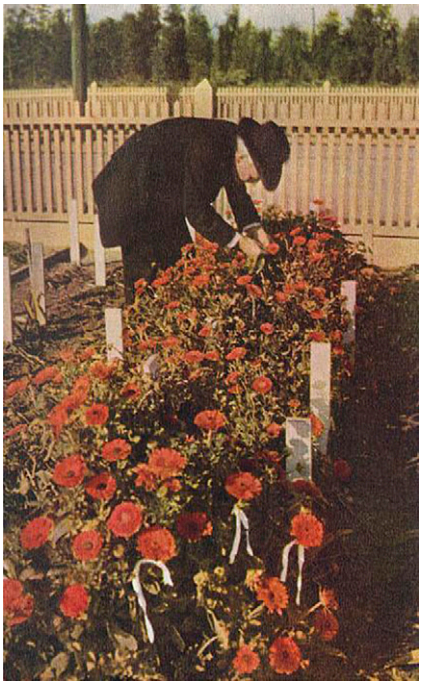

Fig. 2. Luther Burbank making crosses of *Calendula officinalis*. Note tall white row markers demarcating different parents or hybrid populations and the white cloth "tags" denoting crosses (Burbank, 1914–15).

*De Vries and mutations.* Hugo De Vries (Fig. 4) made two trips to California in 1904 and 1906 during Burbank's life to lecture at the University of California (De Vries, 1905). However, De Vries visited Burbank each time for a few days to visit with him and discuss the origin of new traits or mutations and develop a theory on their origination. De Vries was disappointed by Burbank's disbelief in mutants and who remained adamant that new traits in his hybrids were the products of recombination through wide crosses derived from "pre-existing old characters" (Howard, 1945). The novel, variegated leaves found in a seedling *Acer negundo* (Fig. 5), for instance, was viewed as an ancient trait now being expressed despite its rarity as "the only hardy tree known that produces such beautiful variegated foliage" (Burbank, 1914–15).

During these midcareer years, Burbank was called on to talk at the 1902 International Conference on Plant Breeding and Hybridization and the growing circle of plant breeders and early geneticists wanted to hear more

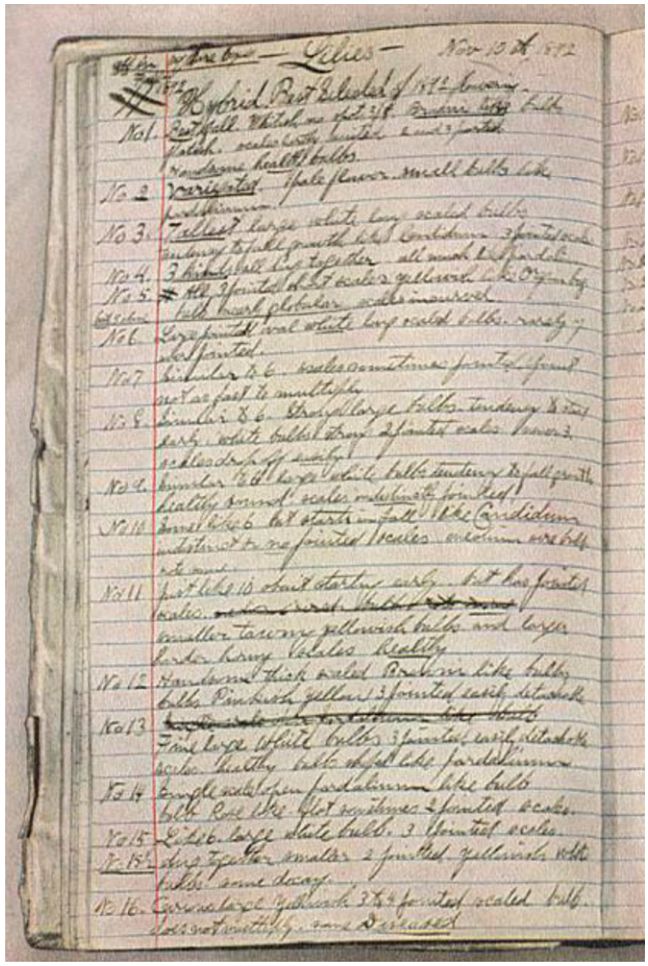

Fig. 3. Sample breeding records for "Hybrid Best Selected" *Lilium* "of 1882 flowering," Selection Nos. 1 to 16, dated 10 Nov. 1882 (Burbank, 1914–15). Note No. 2 was variegated, whereas No. 3 was the tallest flowering plant.

Fig. 4. Hugo De Vries visited Burbank in 1904 and 1906 and hoped that he would explain the origin of mutants (De Vries, 1905).

about his scientific methods (Smith, 2009). Indeed, 2 years later the Carnegie Institution entertained the first funding nomination for Luther Burbank (which was rejected). In 1904, however, under a new director, Burbank received a U.S. $10,000/year grant (the first ever to an individual) to continue his breeding efforts with less market risk involvement.

Fig. 5. One of the first variegated cultivars of woody shade trees, *Acer negundo*, "the only hardy tree known that produces such beautiful variegated foliage…" (Burbank, 1914–15).

Such a grant catapulted Burbank to national fame with numerous articles subsequently appearing about this "wonder worker of science" (Smith, 2009). Satiric poetry and cartoons appeared frequently in the popular press such as *The Los Angeles Times* and *Harper's Monthly* (Smith, 2009). This funding lasted for only 5 years, ceasing as a result of numerous reasons, not the least of which was the lack of information that Burbank was supposed to supply to George Harrison Shull for the Carnegie Institution (Smith, 2009). Shull, a trained biologist who later founded the scientific journal *Genetics*, was required to file a report for publication; Burbank was loathe to divulge his breeding techniques for publication and obfuscated Shull's efforts completely (Crow, 2001). Later, the scientific community withdrew its support of Burbank as a result of his reluctance to share experimental techniques—in contrast with the scientists' information exchange—and that most of his techniques were not unusual although his eye for selection was acute.

## BURBANK TECHNIQUES WITH MODERN RELEVANCE

*Flower power and convenience.* In 21st century flower breeding, successful floricultural crops—particularly annual bedding plants—have to possess flower power and convenience (Anderson, 2006; Anderson et al., 2006a, 2006b). Flower power denotes the presence of large, showy flowers with minimal foliar displays and/or colorful foliage plants of trendy colors, patterns, and forms. Convenience refers to the ease of production, distribution, growing, postharvest adaptation, and long shelf or vase life at retail followed by superior performance with minimal maintenance inputs by the consumer (Anderson, 2006). Both tenets of modern flower breeding were exemplified by Burbank because he was at the cusp of the discovery of modern genetics and hybrid vigor.

Burbank worked for several decades breeding bulbous or geophytic relatives in the Amaryllidaceae, notably amaryllis (mainly, *Hippeastrum* but also *Amaryllis*) *Crinum*, and *Sprekelia* (Burbank, 1909, 1914–15). He discovered that wide intraspecific, interspecific, and intergeneric crosses produced progeny that, when backcrossed, selfed, or cross-pollinated (mass or OP) for two to three generations, resulted in segregants with immense flower sizes and/or increased numbers thereof. Selections of such types created increased flower power in many crops. After several years of interbreeding and selection of bulbous *Hippeastrum vittatum*, *H. reginae*, and *H. johnsonii*, a "colony of mixed hybrids" of significant difference from ancestral forms was produced, which he termed the "Giant Amaryllis" (Burbank, 1914–15; Howard, 1945). Wide, intergeneric crosses involving *Amaryllis belladonna* (female) × *Crinum americanum* (male) produced larger petal sizes in amaryllis (Fig. 6A). Other products emerging from the race of "Giant Amaryllis"

included new floral patterns such as the classic 'Apple Blossom' hybrid (Fig. 6B), which are still popular today as well as double flowers produced from turning anthers and filaments into petals (Fig. 6C). Burbank released as many as eight to 10 named amaryllis cultivars (Table 1) and a large number of hybrid selections (136 at one time, consisting of 3117 bulbs at an average price of U.S. $1.55 each), which were sold unnamed (Burbank, 1909, 1914–15; Howard, 1945). Many of the named cultivars were sold to John Lewis Childs, some of which were listed in his 1909 catalog. All of the original cultivars have now disappeared but their Giant Amaryllis descendants still populate the market as winter and spring bulbous houseplants.

The 'Apple Blossom' *vittatum* types in the Giant Amaryllis collection were subsequently used to cross with the Jacobean lily, *Sprekelia formosissima* (Table 1). Only one transgressive segregant from the wide, intergeneric cross actually flowered and produced seed, but it possessed immense flowers, 12 inches (30.5 cm) in diameter, with twisted petals unlike either parent; it was released as 'Martinique' (Fig. 7). Other intergeneric crosses were not as successful and became controversial. For instance, Burbank claimed that he crossed *Amaryllis belladonna* × *Crinum americanum*, which produced only sterile progeny with oddly shaped leaves (Howard, 1945). His critics did not believe the validity of this cross, proposing that it was equally likely the male parent could have been *C. amabile* (= *C. augustum*), *C. asiaticum*, *C. moorei*, or *C. longifolium* for these were also in Burbank's breeding nursery (Howard, 1945). Dr. Geoge H. Shull who worked for the Carnegie Institution (Washington, DC)—from which Burbank had received a research grant—spent 5 years confirming the scientific validity of this and other crosses. Dr. Shull at least weakly acknowledged that a cross between *Amaryllis belladonna* and a *Crinum* species had been made (Howard, 1945). As a final note, the intergeneric cross does exist, now recognized as ×*Amaricrinum* (Ingram, 1975) and, although Burbank's hybrid has been lost, other crosses are commercially available.

Luther Burbank focused on a variety of other flower crops to increase flower size. In the marigolds (*Calendula officinalis*, *Tagetes patula*, *T. erecta*), he created series of flower types with varying numbers of petals. In the case of *Calendula*, he released a cultivar, Giant Calendula, with extremely large flowers (Table 1) as well as a series ranging from duplex types (two rows of disc florets) to fully doubles (Fig. 8). He termed the process of breeding such series as "educating the *Calendula*" (Burbank, 1914–15). Interspecific *Crinum*, derived from crossing "tropical species with our native [N. American] Florida species" also reached immense sizes with bulbs weighing as much as 7 pounds (3.2 kg) with large, fragrant flowers from the tropical species but with the added "hardiness of the natives" (Fig. 9) (Burbank, 1914–15). *Crinum* 'White Queen', a Burbank hybrid released after his death by his assistant, Bill Henderson, is an example, with large, wide white and fragrant flowers on "massive bulbs, and leaves up to ten feet long" (Kelly, 1983). Although no breeding records exist explaining the crosses within daylilies (*Hemerocallis*), of the several cultivars that were released to the market (Table 1), 'Surprise' has immense light yellow flowers for the year (1917) in which it was released (Fig. 10). Burbank mentioned this as a "cross-bred seedling," but no other pedigree information is known as a result of a lack of records (Burbank, 1917, 1918b). Another example of increased flower size is *Oenothera* 'The


Fig. 6. Wide crosses produce huge flowers: (**A**) the cross *Amaryllis belladonna* (top) × *Crinum americanum* (lower two sets of flowers) produced even larger-sized amaryllis flowers (**B**) depicted by the famous 'Apple Blossom' hybrid; even double flowers were produced from turning anthers and filaments into petals (**C**) (Burbank, 1914–15).

Fig. 7. Burbank's Giant Amaryllis 'Martinique', an intergeneric hybrid (*Hippeastrum [= Amaryllis] vittatum* × *Sprekelia formosissima*) producing flowers 12 inches in diameter (Burbank, 1914–15).

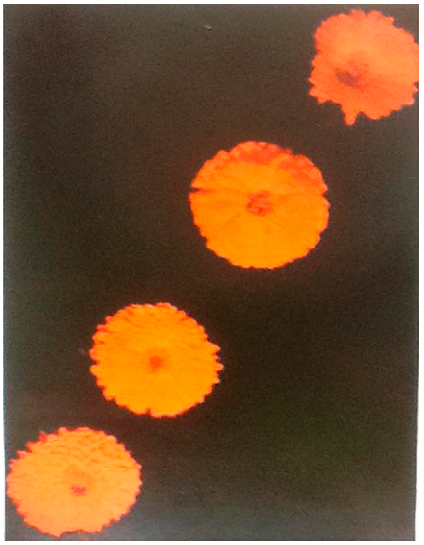

Fig. 8. Educating the *Calendula* (*C. officinalis*): double (lower left) to duplex (upper right) flower types (Burbank, 1914–15).

America' (Fig. 11) which Burbank described as having petals so large they "…would completely cover the entire flower of any other evening primrose on the market. These gigantic flowers look like pocket handkerchiefs thickly strewn over the foliage" creating a glowing effect at dusk (Burbank, 1914–15). Breeding for increased flower sizes and/or enhanced petal production (changing singles into doubles) continues unabated as a primary focus of modern flower breeders, although it is not always possible to achieve in every crop. For instance, *Tagetes patula* (dwarf french marigolds) have never had significant increases in flower size beyond the initial breeding efforts. Such species' limits were aptly described by Burbank's statement: "if new habits are hard to start, new traits are even harder" (Burbank, 1914–15).

*Variegated tropical ornamentals.* Variegation in tropical foliage plants commenced during this time period and consumer interest in them has continued to the present day. Burbank contributed to canna development at the tail end of the first wave of interest in these tropical perennials. Coincidentally, Burbank unknowingly crossed a canna 'Crozy'-hybrid selection with *Canna flaccida*, a North American native to produce an Orchid-type canna just after Italian breeders had [except they used a different 'Crozy' strain (Howard, 1945)]. Subsequent crossing and selection of these interspecific hybrids resulted in numerous canna cultivars (Table 1), the best of which were 'Burbank' (Fig. 12A) and 'Tarrytown' (Burbank, 1911). 'Burbank', sporting lovely clear yellow and white flowers with a few transposable elements in the throat grew to 3.5 feet (1.25 m) in the first year and as high as 5 to 6 feet (≈1.75 m) in the second year, was sold through Vaughn Seed Company and the Luther Burbank Company, although Burbank retained some control because he also sold it retail in 1911 (Burbank, 1911, 1914–15, 1915b, 1920b). The cultivars Rainbow and Yellow King Humbert (Fig. 12B and C) were both variegated cannas with 'Rainbow' being compared as an equal to "New Giant or Rainbow-Leaved Coleus" (Burbank, 1914–15). 'Yellow King Humbert' sports sectorial leaf variegations (Fig. 12B) with speckled (transposable elements) and chimeric flower petals (Fig. 12C) and is still available in the nursery industry.

*Flower surround and increased density.* Indeterminant inflorescences that are spicose, racemose, panicled, or thyrse types have flowers spaced along the stems. Some wild species may have the flowers pointing upward or outward from the nodes at anthesis but many do not and are faced (flowers on just one side of the stem), e.g., *Gladiolus* and *Delphinium.* In floral design, faced-flower types are commonly used in one-sided designs such as funeral bouquets (Hunter, 2012). Although faced inflorescences are useful, significantly greater flower power arises if the floral positioning can be rotated around the stem (flower surround), providing a 360° view, increasing their value for bedding plants, herbaceous perennials, cut flowers, and flowering potted plant use (Anderson, 2006). Burbank sought to change floral display in larkspur or delphiniums, sowing a population of the species *Delphinium hybridum*, which trace back primarily to *D. elatum* (Burbank, 1914–15). He selected one seedling closest to his breeding objective, sowing the seeds from it and released one cultivar but discarded the remainder, although he released three series that were all derived from *D. hybridum* (Table 1). All of these series had been bred and selected for flower surround and increased flower density (Fig. 13) such that there was very little space between the individual flowers. Breeding for both flower surround and increased density are common domesticated traits incorporated by modern flower breeders.

Luther Burbank also attempted to cross in the tall *D. californicum* species with *D. hybridum* but met with a high failure rate. Eventually he made different interspecific crosses, releasing an unnamed hybrid that had yellow flowers derived from another native California species, most likely the coastal *D. bakeri.* To the best of our knowledge, all of Burbank's *Delphinium* hybrids have vanished but most likely the gene(s) and allele(s) he selected for flower surround and increased density remain in modern *Delphinium* such as Pacific Giant hybrids, possibly bred with other *Delphinium* spp. by Frank Reinelt, a self-taught Czech flower breeder who, after emigrating to the United States, founded Vetterle & Reinelt Company in nearby Capitola, CA.

*"Harnessing heredity" with new flower colors.* Modern marketing criteria for new floral products, once the first cultivar is released, are the rapid development of a wide-ranging color palette with as many flower colors as can be generated within the species to form a series (Anderson, 2006). Many such series on the market consist of cultivars—each with a different flower color—that share a common female parent but differ in the male parents (Anderson, 2006), such that the resultant hybrid cultivars are half-sib families. The desire for new or enhanced flower colors to follow the fashion trends each year (Anderson, 2006; Hunter, 2012) was developing in Burbank's time. He devoted considerable effort to breeding new flower colors in as many genera and species as possible to enhance sales (Burbank, 1914–15).

Like with so many other breeding objectives and techniques used, Burbank used many native California species that he saw traveling between Santa Rosa and Sebastopol, CA, as well as plant collection trips

Fig. 9. Hybrid *Crinum* interspecific hybrid lilies of immense size from crossing "several tropical species with our native Florida species" growing in the Sebastopol trial gardens. Bulbs were as large as 7 pounds produced flowers with the "size, beauty and fragrance of the tropical species with the hardiness of the natives" (Burbank, 1914–15).

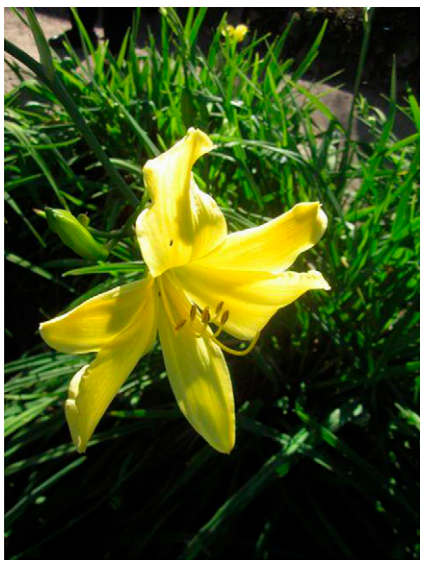

Fig. 10. *Hemerocallis* 'Surprise' is a clear yellow with immense flower size for the time in which it was bred (Burbank, 1914–15).

Fig. 11. Enhanced flower size produced in *Oenothera* 'The America' (Burbank, 1914–15).

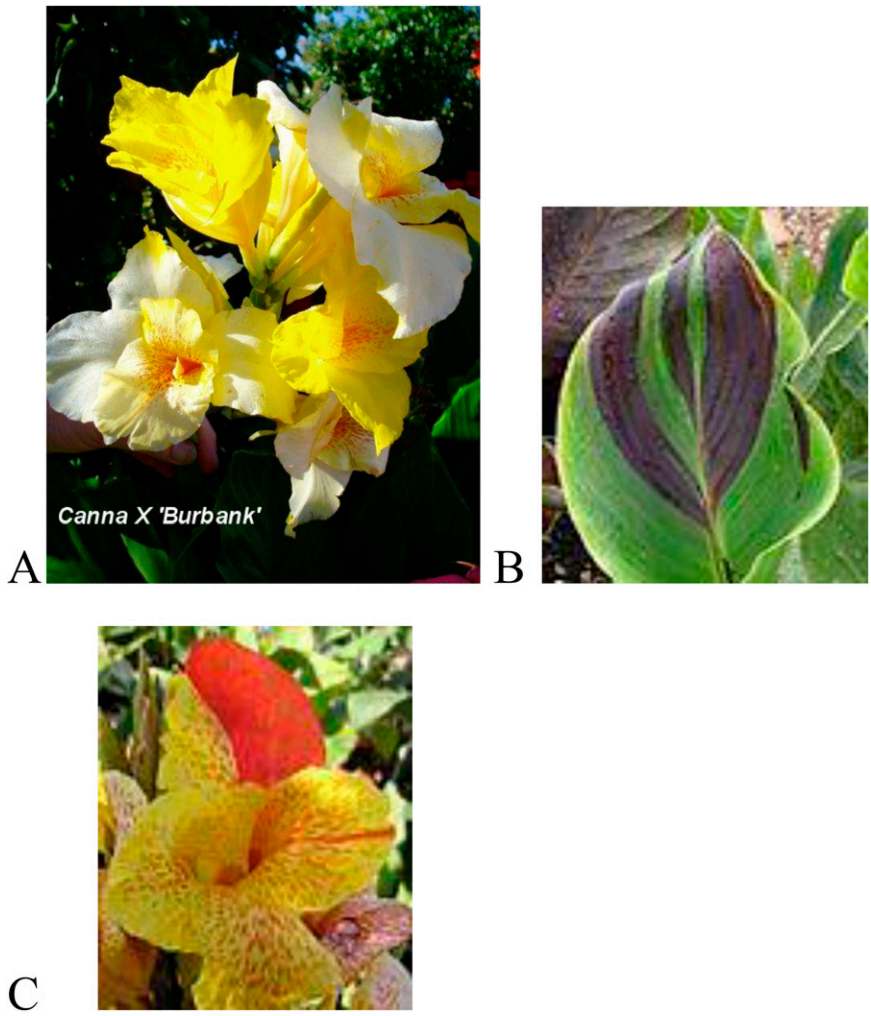


Fig. 12. *Canna* 'Burbank' (**A**) resulted from crossing 'Crozy' × *C. flaccida* (<http://3.bp.blogspot.com/JhMjOi3-rUE/R4L8QdZh89I/AAAAAAAAAGQ/PAnyHyPboLU/s1600-h/Burbank2.jpg>); 'Yellow King Humbert', in the Italian Group of the genus, with variegated leaves (**B**) and speckled, chimeric flowers (**C**). Burbank is reputed to be the first to recognize and name this *Canna* 'Roi Humbert' mutation (Burbank, 1914–15).

through the state. The California poppy, *Eschscholtzia californica*, grows throughout the coastal foothills but the annual species predominantly has yellow–orange flowers. Burbank "harnessed heredity" (Burbank, 1914–15) and bred or selected new flower colors, particularly red ones, named 'Crimson' (Fig. 14A) and sold in 1904 to the W. Atlee Burpee Company in Philadelphia, PA, at that time (Table 1; Burbank, 1914–15; Howard, 1945). He enhanced the intensity of the orange through selection and also released 'Fire Flame' (Fig. 14B) or, perhaps, 'Firefly' as a result of different sources naming it differently (compare Burbank, 1915b and Howard, 1945). Subsequently, white and pink forms also were selected from wild sources (Fig. 14C). White ones were derived from light yellow types and, most likely, were the result of a homozygous recessive allelic configuration. Other examples evoking flower color changes not present in wild species included *Osteospermum* hybrids insourced from South Africa by an unknown collector/supplier. He created orange (Fig. 15A) and pink (Fig. 15B) daisy selections; the latter was used as his example of "harnessing heredity" (Burbank, 1914–15). Both flower colors and variations thereof were recently recreated by breeder/-producer/distributor companies such as 'Orange Symphony' by Proven Winners™ (<http://www.provenwinners.com/plants/osteospermum/>) or 'Flower Power Compact Light Pink' by Ball Seed Co. (<http://www.ballseedco.com>).

"Color blending" was a term Burbank used to describe multiple colors blended into a single flower (Burbank, 1914–15). He used the term for his Japanese iris selections (*Iris laevigata*), one of which had purple edges and veination along with yellow and white (Fig. 16A). These selections, which were claimed to have all of the colors of the rainbow (i.e., red, orange, yellow, green, blue, indigo, and violet), were sold "as a mixture, without names or number" (Burbank, 1914–15). Surprisingly, as the rainbow colors in the Japanese mixture suggest, he created a red iris (Fig. 16B)—more of a Dutch iris type (*I.* ×*hollandica*) than Japanese—but there is no record if it was ever released as a separate cultivar. How he accomplished breeding a red iris is a mystery because current-day amateur iris breeders have determined that the carotenoid pigments necessary to produce red iris flowers do not exist in the genus (Meckenstock, 2005)!

*Fixing traits.* In contrast with blue flower color, a trait that could not be "fixed" in Shirley poppy, *Papaver rhoeas* (Burbank, 1925; Howard, 1945), some floral species Burbank found had traits that were easily or "readily fixed" and came true from seed (Burbank, 1914–15). Such was the case with the annual sunflower, *Helianthus annuus* (Fig. 17). However, because these were OP hybrids, the off-types had to be rogued out. Although the breeding records for this crop are scant, he worked with both *H. annuus* and *H. californicus* with interspecific breeding objectives to increase seed yield, seedcoat coloration, and flower size (Howard, 1945). He released single- ('Prolific White', released in 1920) and double-flowered forms ('California', released in 1919; Table 1). Additionally, seedcoat colors of pure white ('Manteca', released in 1917; 'Prolific White'; 'Snow' released in 1915; Table 1) were released. Most of the flower forms and seed types are still commonly bred and grown throughout North America, favored as bedding plants and garden cultivars.

*Lilium and wide, intersectional crosses.* Lilies were a crop that Burbank focused on with intensity. Indeed, one lily expert critical of Burbank said that his breeding within the genus was his finest contributions (Howard, 1945). The immense scale with which he undertook breeding this genus in 1875 was unrivaled by other ornamental crops (Slate, 1939). Nineteen years later, Burbank had 3 acres (1.2 ha) devoted to his hybrid lilies. With *Lilium*, he pioneered breeding the North American native lily species (section Pseudolirion), particularly those from the Pacific coastal region (*L. washingtonianum*, *L. humboldtii*, *L. parryi*, *L. pardalinum*, and *L. maritimum*), and he is honored in the interspecific hybrid name, *L.* ×*burbankii*, for hybrids between *L. parryi* × *L. pardalinum* (Slate, 1939).

The Pacific coast lily species—particularly *L. pardalinum*—were most often used as seed parents, although to make intersectional, interspecific hybrids, Burbank also used lily species as male parents from eastern North America (section Martagon—*L. parryi*, *L. parvum*, *L. superbum;* section Pseudolirium—*L. washingtonianum*) and Eurasia (section Archelirion—*L. auratum*, *L. brownii*, *L. speciosum;* section Leucolirion—*L. longiflorum*, *L. wallichianum;* section Liriotypus—*L. candidum*, *L. chalcedonicum;* section Martagon—*L. martagon*). Most phenotypic traits were rarely visible in these hybrids (Slate, 1939). Several thousand crosses were made through the years (Purdy, 1895) to create massive segregating populations for further intermating and selection. Purdy (1895) reported seeing 400,000 1-year-old lily seedlings in 1891 that segregated for true leaf phenotypes. The vast seedling beds (from sowing 1 to 3 pounds of lily seed/year) were highly selected by virus

Fig. 13. *Delphinium*: increased flower density and stem surround (Burbank, 1914–15).

and other criteria with selection differentials as high as 75%. Three years later greater than 100,000 were in flower by mid-June 1894, nearly all of which "were fragrant," which was perceptible 5 miles (8 km) away (Purdy, 1895); a wide range of flower phenotypes was observed (recurved, Turk's caps and semi-trumpets to previously unknown horizontal types). Hybrid vigor or heterosis was widely observed throughout the segregating populations, particularly hybrids from the cross *L. parryi* × *L. humboldtii* (Purdy, 1895) with floriferous stems (30 to greater than 100 flowers/stalk). Other floriferous hybrids were derived from *L. pardalinum* var. *minor* × *L. maritimum* and *L. pardalinum* var. *minor* crossed with an unknown male species, which created a "tree lily" that, in Year 6, had multiple flowering branches with as many as 207 flowers/bulb (Purdy, 1895). Three species hybrids or triple hybrid lilies exhibited outstanding heterosis. Purdy (1895) reported observing *L. parryii* × *L. washingtonianum* × *L. pardalinum* hybrids that ranged from 18 inches (45 cm) to 8 feet (2.43 m) in height (Fig. 18). Some 50 years later, W.L. Howard (1945) wrote that Burbank's lily breeding was "boldly conceived and audaciously executed" although he only released one named cultivar ('Burbank') and a few unnamed seedlings (Table 1). None of these survived 50 years later primarily as a result of virus buildup in lily clones (Howard, 1945). Lily Latent Virus or Lily Symptomless Virus (LSV) was not discovered until the 1930s (McWhorter, 1937). LSV buildup is a continuing issue in clonal cultivars, particularly Easter lily, *L. longiflorum* 'Nellie White' (Zlesak et al., 2007).

*An "interesting failure": sterile, semitrailing intergeneric hybrids.* Stretching the limits of crossability beyond the interspecific level, Burbank tried many different intergeneric crosses within ornamentals in the Amaryllidaceae [*Crinum* and *Hippeastrum* (= *Amaryllis*)], Iridaceae (*Tigridia* and *Ferraria*), and Solanaceae (*Nicotiana* and *Petunia*) (Burbank, 1893, 1914–15). At least one outstanding ornamental, 'Nicotunia' or ×*Nicotunia*, resulted from the intergeneric cross (made in 1893) between a Bolivian tobacco species with ruby flowers (*Nicotiana wigandioides* var. *rubra*) and a grandiflora petunia (*Petunia hybrida* var. *grandiflora*) (Burbank, 1893, 1914–15). As soon as the seeds ripened, they were sown (≈200 seedlings germinated) and then transplanted when ≈1 foot (0.3 m) tall and kept over the winter in the glasshouse. The next spring they were transplanted into the field and began segregating for foliage coloration (green, pink, crimson; Burbank, 1893). By the next winter and spring, some seedlings fell over (lodged) and began trailing, whereas other dwarf types trailed without lodging. All hybrids were completely sterile (Howard, 1945) but could be propagated asexually (through cuttings)—a common propagation method in petunias at that time. Severe hybrid breakdown or incongruity (Hogenboom, 1974) occurred with a "pinched" above-ground phenotype and few roots (Burbank, 1914–15). Some hybrids had astounding phenotypes (Fig. 19) with petunia-like flowers and a trailing plant habit; the latter phenotype was not discovered again in the genus *Petunia* until the 1970s (Peter Ascher, personal communication, unpublished data) and the 1980s when the interspecific Wave™ types emerged (Anderson, 2006). Sadly, all of the ×*Nicotunia* hybrids froze to death the next winter because they remained unprotected in the field.

*Sterility and everblooming (day-neutral).* Sterility, a useful trait to prevent reseeding and spread of invasive ornamental species (Anderson, et al., 2006a, 2006b), also surfaced with interspecific hybridization of ornamental species. In the genus *Papaver* (poppy), he created interspecific hybrids by crossing annual and perennial species (*Papaver somniferum* × *P. orientale;* Fig. 20A) that, by the $F_2$ generation of 2000 plants, began segregating for complete sterility (Fig. 20B; Burbank, 1914–15). Perhaps, as a result of sterility, these hybrids were "everblooming" throughout the growing season (Burbank, 1914–15). Burbank also created everblooming calla lilies, e.g., 'Dwarf Everblooming'

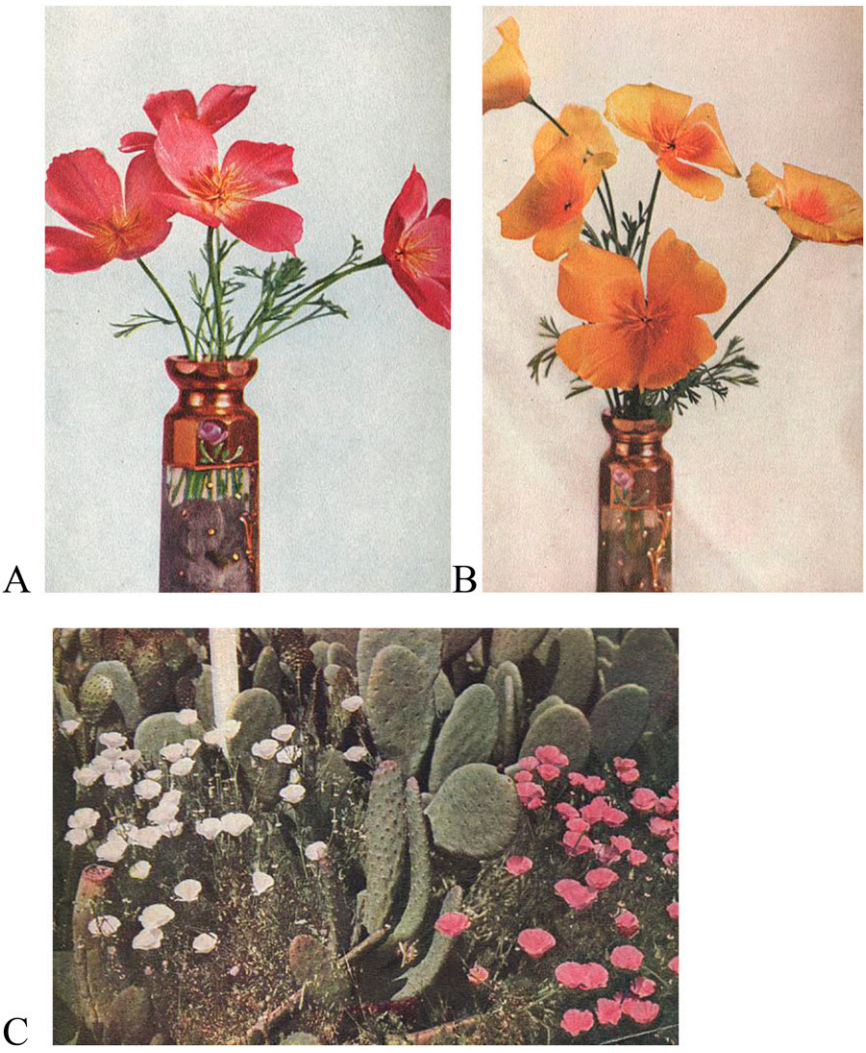


Fig. 14. New flower colors in *Eschscholtzia californica*. (**A**) 'Crimson', (**B**) 'Fire Flame', (**C**) white and pink selections growing alongside the spineless cacti seedlings (Burbank, 1914–15).

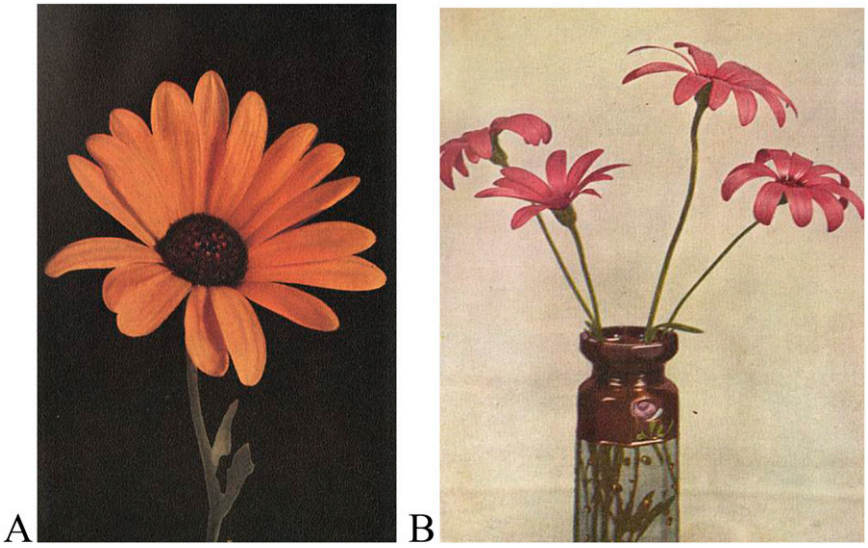

Fig. 15. Burbank's *Osteospermum* hybrids displaying new flower colors not present in the wild (**A**—orange; **B**—pink) as a result of "harnessing heredity" (Burbank, 1914–15), many of which have been recreated by modern-day breeders.

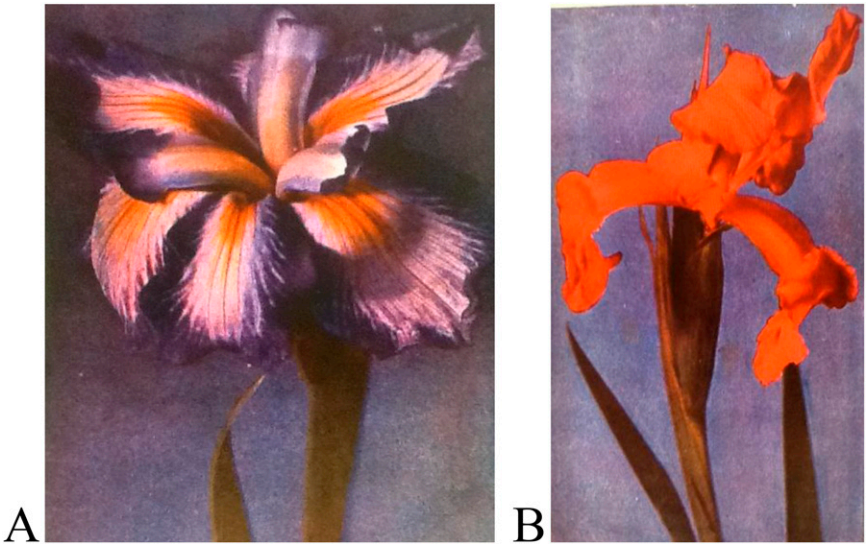

Fig. 16. Color blending (**A**) and new red color (**B**): "Improvements of the much-improved Iris" (Burbank, 1914–15).

(Table 1). The "everblooming" trait, now termed day-neutral, is a commonly desired trait, particularly in photoperiodic, herbaceous ornamentals (Anderson, 2006).

*Blue flowers.* True blue flowers have driven a centuries-long quest by flower breeders to create such colors in flower crops where it does not exist. Burbank was no exception, creating blue roses (compare with color photograph, Burbank, 1914–15, vol. 9, p. 42–45), poppies, and tiger flower (*Tigridia*). Interspecific crosses started in the 1880s with *Tigridia pavonia*, *T. conchiflora*, and *T. buccifera* (Burbank, 1914–15). Other *Tigridia* spp. would not cross with these hybrids so Burbank expanded to making intergenerics with the closely related genus *Ferraria.* He also tried, unsuccessfully, to make a triple intergeneric between these and *Herbertia platensis.* Nonetheless, the *Tigridia* interspecifics resulted in a unique blue-flowered 'Burbank' genotype discovered in 1894 and later released in 1914 (Fig. 21; Burbank, 1894) and 'Chilean Dwarf', released in 1920 (Burbank, 1920a). To the best of our knowledge, creation of such blue tiger flowers has not been achieved since.

*Convenience.* Numerous traits confer "convenience" to growers, retailers, and consumers and Burbank created many flower crops with sterility, heat/drought tolerance, dwarfism, free branching, and everblooming traits. His breeding and selection procedures also benefitted from implementation of convenience methodology, allowing him to concentrate breeding of numerous genera on the small Gold Ridge View Experiment Farm. Crossing of parents was often accomplished

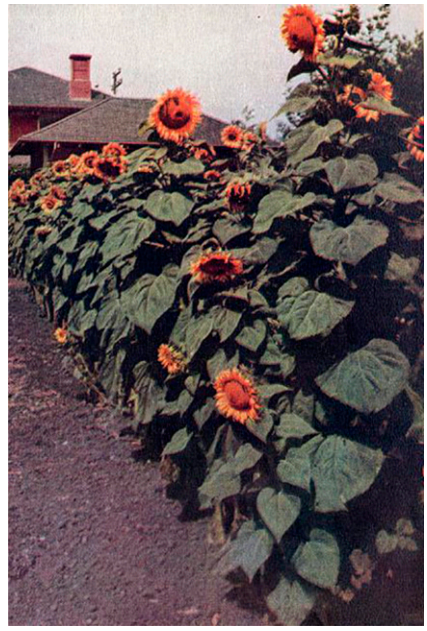

Fig. 17. *Helianthus annuus* hybrid breeding was completed with relative ease, since traits were "readily fixed" and came true from seed—provided one rogued out the off-types (Burbank, 1914–15).

in very tight plant spacing (Fig. 22A) as well as subsequent seedling and clonal hybrids in closer proximity than standard protocols (0.3 m on center). This space minimization for perennials requiring greater than 1 year to flower from seed efficiently created side-by-side flower color and type comparisons for ease in "reading" breeder trials such as *Tulipa* (Fig. 22B). As a result, the clearest and best colors could be readily selected in the same environment as well as determining the earliest and/or longest duration in flowering, heterotic or vigorous genotypes, disease or insect tolerance, etc. Such techniques are still implemented, particularly because space is a costly input in cultivar development for greenhouse, container, and field trials over years and locations (Anderson, 2006).

*Fragrance.* In addition to fragrance in lilies (discussed previously), the development of fragrant *Verbena* occurred twice in the history of Burbank's breeding efforts. Howard (1945) described this as his "chief attainment within the species," although, once again, the complete lack of breeding records meant that no subsequent verbena breeder could repeat his exact crossing scheme. 'Mayflower' was a fragrant verbena released in both 1895 and 1901 (Fig. 23; Table 1), along with 'Fragrance', 'Giant Mayflower', and 'Mayflower Pink' (Table 1). 'Mayflower' was at first clonally propagated, because it did not come true from seed, although the distributor, John Lewis Childs, reported slow cutting production that could not keep up with demand (Burbank, 1918a; Howard, 1945); this was later introduced as a seed product by 1899 (Fig. 23). Burbank later developed another race of fragrant verbena, 'Fragrance' (Table 1), which he released in 1901 and distributed as

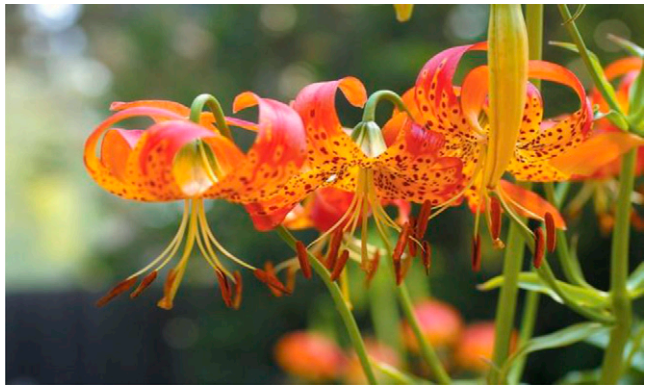

Fig. 18. Breeding with North American natives: triple hybrid *Lilium*, *L. parryii* × *L. washingtonianum* × *L. pardalinum* progenies ranged from 18 inches to 8 feet in height with fragrance that could be distinguished miles away (Burburbank, 1914–15).

Fig. 19. 'Nicotunia', an "interesting failure" with the first vegetative *Petunia* derived from the Intergeneric cross *Nicotiana wigandioides rubra* × *Petunia hybrida var. grandiflora* (Burbank, 1914–15).


Fig. 20. Flowers (**A**) on an everblooming, sterile, and interspecific poppy, derived from crossing annual and perennial species, *Papaver somniferum* × *P. orientale*. (**B**) Sterile (left) and rudimentary fruit (right) (Burbank, 1914–15).

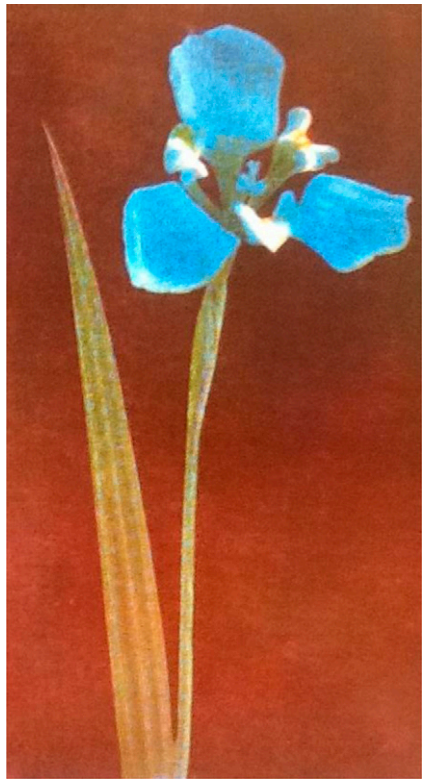

Fig. 21. Interspecific *Tigridia* hybrid 'Burbank' sporting a blue flower (Burbank, 1914–15). Such a hybrid has never been repeated. Burbank also released a blue *Herbertia pulchella*, that looked similar.

'New Fragrance' by Conrad and Jones Company (West Grove, PA); the Burbank Company sold it later in 1913.

Calla lily (*Zantedeschia*; = *Richardia*) is another example crop bred for fragrance. At first, Burbank concentrated on variegated foliage and dwarfism ('Variegated Little Gem' was released in 1893; Table 1). Later, however, he focused calla breeding objectives to fragrance in interspecific *Zantedeschia* and released three such cultivars, e.g., 'Burbank's Scented' (Fig. 24A), 'Lemon Giant' (Fig. 24B), and 'Dwarf Scented' (Table 1; Burbank, 1914–15). For the most part, scented callas have disappeared completely from the floriculture market.

*Ornamental vegetables.* Luther pioneered efforts to breed ornamental vegetables such as corn and teosinte, pink chives, tomatoes, and spineless cacti (Burbank, 1914–15). This is still a popular trend for flower breeders across the globe. Burbank's corn breeding started in 1870 focusing on sweet, edible types. In 1908, he began breeding ornamental corn by first selecting two "quadri-colored" stalks in an ornamental seed lot from Germany, which he proposed had originated from a cross between a green-leafed type and Japanese variegated corn (*Zea mays variegata*; Burbank, 1914–15). By several generations of selection later, Burbank had six colors of stripes in the leaves. 'Rainbow' was one such cultivar (Fig. 25). 'Rainbow' generated considerable publicity for Burbank as a result of the rarity of six stripe colors. He later released 'Aurora', a new and improved form of 'Rainbow' (Table 1). Rainbow-type corn is still on the market, although Burbank is not given any credit in their development. Burbank's breeding efforts in chard (*Beta vulgaris* ssp. *vulgaris*), although at the time not directed at ornamental features specifically, did result in the introduction of 'New Rainbow' with leaves of "mingling iridescent rainbow shades" (Howard, 1945), a precursor to the modern use of ornamental chard in cool-season bedding plant schemes.

*Species named after Burbank.* Flower breeders rarely have the opportunity to have plant species named after them because that is reserved for botanists and plant collectors finding new species in the wild. However, the wide interspecific hybrids created by Luther Burbank allowed this in four divergent families (Burbank, 1914–15). *Chrysanthemum* ×*burbankii* Makinoi (Asteraceae) is a white, single daisy hybrid (Fig. 26A) that was not used in the creation of the shasta daisy hybrids. *Lilium* ×*burbankii* (Liliaceae) is a Turk's cap lily created from crossing the North American *L. pardalinum* × *L. parryii* (Fig. 26B). Another interspecific hybrid in the Solanaceae is named for Burbank and remains on the market today, i.e., *Solanum* ×*burbankii* Bitter (Fig. 26C). This was derived from the cross *S. villosum* × *S. guineense* and was originally named 'Sunberry' by Burbank but sold by John Lewis Childs as 'Wonderberry'; this cultivar name continues to this day (Fig. 26D). The fourth

Burbank species is still under considerable taxonomic dispute: *Myrica* ×*burbankii* A. Chev. (Myricaceae) was based on Burbank's claim to have crossed *M. cerifera* × *M. californica*; no photographs of this species are available.

*The shasta daisy.* Burbank's most popular ornamental release, the shasta daisy hybrids (*Leucanthemum* ×*superbum*), remains to this day a significant flowering perennial on the global market with upward of 170 cultivars available (Hatch, 2013), including the original 'Alaska' (Burbank, 1904) (Fig. 27; Table 1). The shasta daisy hybrids were first released in 1901 as "*Chrysanthemum leucantheumum hybridum*," a complex hybrid strain of four species of chrysanthemum as Burbank knew them at the time: *Chrysanthemum leucanthemum*, *C. lacustre*, *C. maximum*, and *C. nipponicum* (= *Leucanthemum vulgare*, *L. lacustre*, *L. maximum*, and *Nipponathemum nipponicum*, respectively) (Fig. 28). The story, as countlessly retold by Burbank, begins with his childhood fascination with the common European oxeye daisy (*L. vulgare*) that was naturalized in his New England childhood home in Lancaster, MA, and which possessed the common white ray florets and yellow disc florets that make up the flower head in this section of the Asteraceae. On starting his business in California, Burbank imported this species and began in 1884 to work in earnest on enhancing the flower size (ray florets) within the species. He first sought, as he did with many other crops, to improve the species through mass selection of OP seed. Unsatisfied with the results, Burbank crossed his best selections with the "English daisy," probably *L. maximum*, a species with larger but coarser flower heads than *L. vulgare* (Hall, 1939). These hybrids, although improved over the parental species, were "too rank for beauty, a tendency to run too much to foliage, and finally a blossom that left too much to be desired in purity and waxiness" (Hall, 1939). To rectify this, Burbank next crossed the best advanced hybrids with the Portuguese oxeye daisy, *L. lacustre* (Fig. 28), and further refined his hybrids over five or six generations; however, he was still

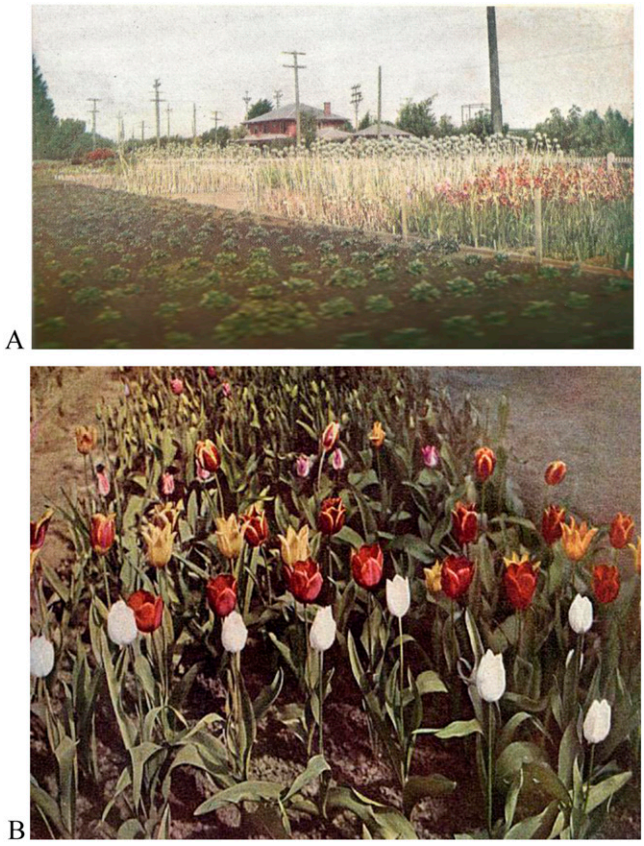

Fig. 22. "Many plants in small spaces" demonstrating the (**A**) tightly spaced crossing setups that Burbank often used and (**B**) subsequent clones or seedlings of variations (*Tulipa*) efficiently planted close together for ease of selection once they came into flower (Burbank, 1914–15).


Fig. 23. Seed packet of 'Mayflower' fragrant *Verbena* hybrid offered for sale in 1899 (Burbank, 1899).


Fig. 24. Fragrant *Zantedeschia* (= *Richardia*) 'Burbank's Scented' (**A**) and 'Lemon Giant' (**B**) (Burbank, 1914–15).

unsatisfied with the whiteness of the ray florets (Hornback, 1982; Howard, 1945).

Burbank was told of a Japanese species of oxeye daisy (*Nipponanthemum nipponicum*) that possessed ''small and inconspicuous'' flowers but with ''a pure waxy white color'' (Hall, 1939). He insourced seed from Japan and made repeated attempts over five or six seasons (Howard, 1945), finally selecting a single plant that combined all the desired flowering characteristics and habits he sought. From this he raised an additional five or six generations of seedlings, selecting for seed-bearing as well as adaptability, precocious flowering, and large flowers on leafless stems (Hall, 1939). In 1901, Burbank introduced his ''Shasta Daisies'' (Table 1; Fig. 28), named after the eponymous snow-capped California mountain nearby.

The number of species used to create shasta daisies, often described by Burbank as three (*L. vulgare*, *L. maximum*, and *N. nipponicum*) (De Vries, 1907; Hall, 1939) or four with the addition of *L. lacustre* (Fig. 28) (Hornback, 1982; Howard, 1945) may be debated; however, their hybrid nature is not. Botanists and horticulturists have ascribed the shasta daisies to the cultivated hybrid *L.* ×*superbum*, a hybrid between *L. lacustre* and *L. maximum* (Kent, 1990). *Leucanthemum maximum*, a true species from the Pyrenees, has apparently been rarely cultivated in the United States with most forms assigned to this species (e.g., *L. maximum* ''of gardens'') really attributed to the hybrid, *L.* ×*superbum* (Ingram, 1975). The hybrid species, along with the common species *L. vulgare*, are naturalized in California (Hickman, 1993) and, taken together, may give credence to the belief that Burbank simply improved on the naturalized form of *L.* ×*superbum* found in California (De Vries, 1905; Howard, 1945). The confusion persists to this day in horticulture with the recent proposal of grouping cultivated forms of shasta daisy under the

Fig. 25. Ornamental vegetable example, *Zea mays* 'Rainbow' (Burbank, 1914–15).

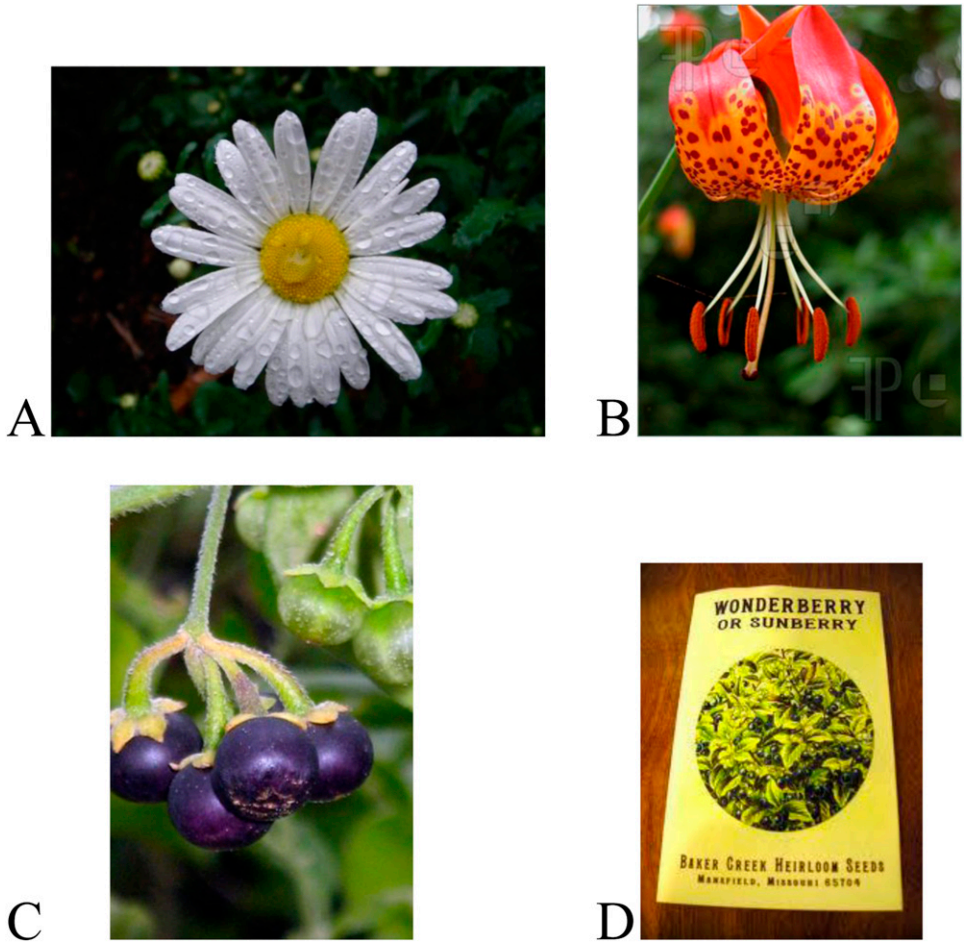


Fig. 26. Three of the four flowering plant species named after Luther Burbank include: (**A**) *Chrysanthemum* × *burbankii* Makinoi (Asteraceae), (**B**) *Lilium* ×*burbankii* (*L. pardalinum* × *L. parryii*), (**C**) *Solanum* ×*burbankii* Bitter (*S. villosum* × *S. guineense*), which was (**D**) introduced by John Lewis Childs as 'Wonderberry' (Burbank, 1914–15).


Fig. 27. The creation of the first 'Shasta Daisy' hybrids (**A**) in 1901, (**B**) descendents still flowering outside of Luther Burbank's home in Santa Rosa, CA, (**C**) a closeup of the single-duplex daisy flowers with white ray florets (petals) and central yellow, disk florets, (**D**) an early 1919 advertisement of 'Shasta Daisy' was on the front cover of Burbank Seeds catalog (Burbank, 1919).

*Leucanthemum* Maximum Group, which would encompass the former *Chrysanthemum* ×*superbum* and *C. maximum* cultivars and some cultivars of the parental species (Hatch, 2013).

Regardless of parentage, the "Shasta Daisies" as a group are of significant value to the ornamental nursery industry, as evidenced by a recent plant evaluation of 36 cultivars for northern gardens performed at the Chicago Botanic Garden (Hawke, 2007). Burbank continued to release cultivars up until the year before his death; the first three selections, 'Alaska', 'California', and 'Westralia', were introduced in 1904 (Table 1; Burbank, 1904) as clonal selections propagated through root cuttings. In subsequent breeding efforts, Burbank selected forms with even larger flowers ('Shasta Giant'), double or fluted florets ('Double Fluted Shasta'), serrated florets, and cream to yellow ray florets (Fig. 29; Table 1) (Hall, 1939; Howard, 1945). All are prolific producers of cut flowers, as exemplified by the rows of shastas grown in 1912 for the National Federation of Women's Clubs (Fig. 30). Today's plant breeders are building on Burbank's initial breakthroughs, best exemplified by the Realflor Collection of *L.* ×*superbum* offered by PlantHaven International, Inc. (Santa Barbara, CA), which includes cultivars with yellow ray florets ('Real Dream'), fringed florets ('Real Galaxy'), anemone-flowered forms ('Real Glory'), and fluted florets ('Real Neat').

*"The spineless opuntia: an established fact."* Cacti were another area of selection and breeding by Burbank. He released a few flowering ornamental types such as *Opuntia basilaris*, *Cereus chilensis*, and *Echinopsis mulleri* (Table 1). However, most of his work concentrated on spineless forage types. Although Burbank's shasta daisies represent a lasting success, his spineless prickly pear (*Opuntia* subgenus *Opuntia*, Cactaceae) project, although not an abject failure, encapsulates at once the shortcomings of his methods and the fine line between noble vs. financial pursuits in plant improvement. The rise and fall of Burbank's spineless *Opuntia* introductions has been well covered by Smith (2010) and to some degree in Benson (1982). In short, Burbank fell prey to both his own legend and the media hype that surrounded him, which posited him in the upper echelon of innovators at the beginning of the 20th century and the center of speculative and unscrupulous business ventures seeking to profit from this fame and, ultimately, led to a very public clash and crash because the market and taste for prickly pears never materialized.

Cacti were a major focus of Burbank, specifically the improvement of prickly pears, which he saw as the ideal solution for crop-poor marginal agricultural land in the arid regions of the world. Burbank was introduced to spineless *Opuntia* sometime after arriving in California, where spineless forms of the Indian fig (*O. ficus-indica*), like 'Marin', had already been introduced and cultivated (Burbank, 1907; Griffiths, 1912, 1928). "Spineless" is a relative term, referring to the true spines (modified leaves) and the minute glochids ("spikules" or modified, barbed hairs) born in areoles (modified axillary buds) in *Opuntia* (Fig. 31A) (Benson, 1982). Essentially spineless forms were already known, mostly forms of the widely cultivated *O. ficus-indica*, which originated in central Mexico and were disseminated by the Spanish for use in climatically suitable areas of their empire (Griffith, 2004; Russell and Felker, 1987). The cultivation of *Opuntia* and several other genera of cactus by indigenous peoples in the Americas predated the arrival of the Spanish, where it was grown

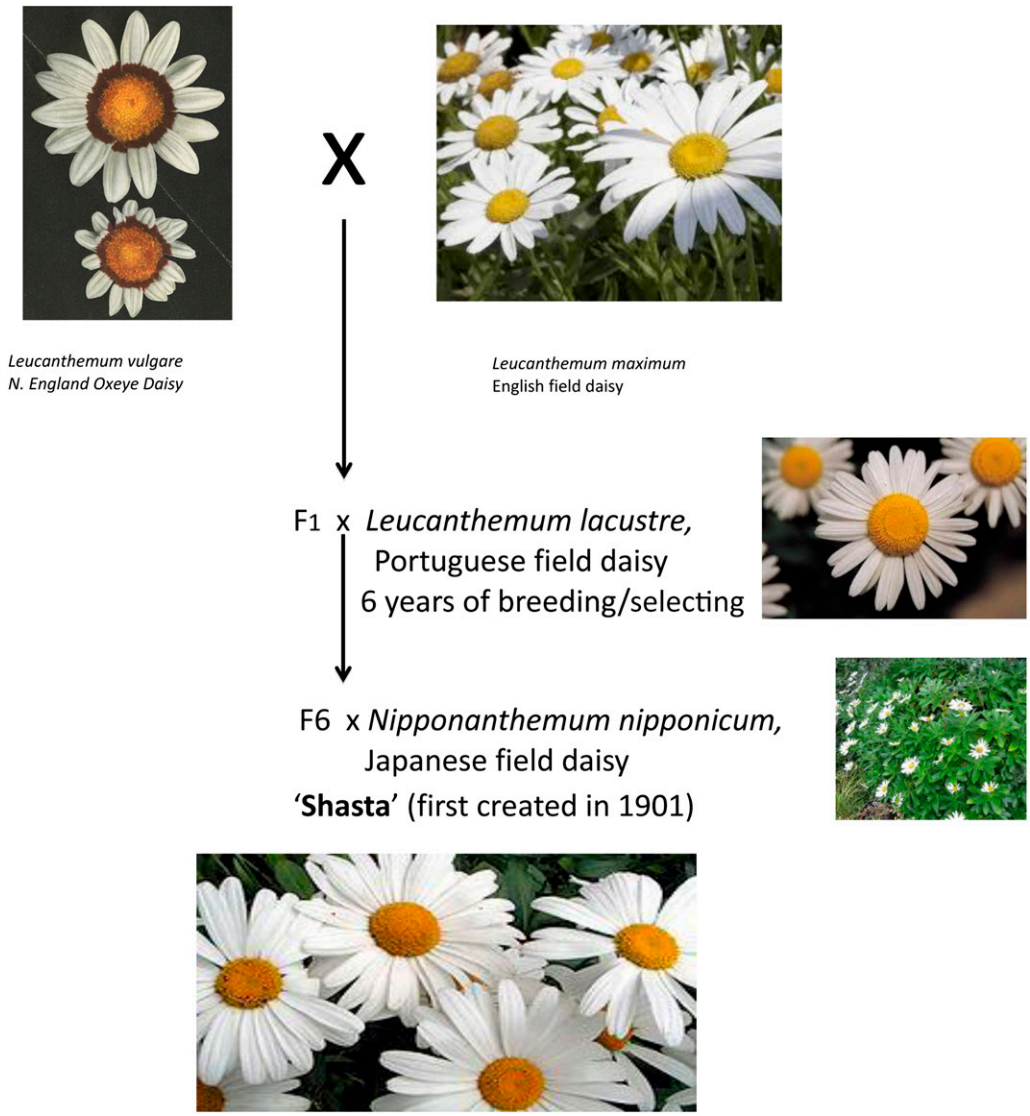


Fig. 28. The evolution of 'Shasta Daisy', named after Mount Shasta, located nearby the Sebastopol Farm (Burbank, 1914–15).

for both its edible fruit (*tuna*) and pads (*nopales*) as well as for other economic uses, like the important cochineal dye industry (Benson, 1982; Russell and Felker, 1987). By the end of the 19th century, prickly pear cultivation for agronomic and industrial use was established in most of the arid regions of the world, including the Mediterranean, northern and southern Africa, India, and Australia (Burbank, 1907; Griffiths, 1912, 1928; Russell and Felker, 1987).

The use of prickly pear as a forage crop began with the introduction of cattle to the New World by the Spanish to their territories in Mexico and the southwestern United States where *Opuntia* and their relatives are native. David Griffiths, an agrostologist or grass researcher within the Range Investigations Unit of the Bureau of Plant Industry at the USDA, published the results of massive surveys in this region on the extent of *Opuntia* forage or fodder use by ranchers (Griffiths, 1905, 1912, 1928). Forage and fodder use was documented in all regions where cattle and prickly pears overlapped, from southern California to Colorado and down through Texas, where the most extensive use of *Opuntia* was recorded. In general, the native prickly pears were prepared for foraging by removal of the main spines, either through singeing with brush fires or special "pear-burners," then chopped with machetes for direct foraging or through special "pear handling machinery" for fodder production (Griffiths, 1905). Here Burbank saw an opportunity to apply his breeding prowess toward generating a new race of "spineless" *Opuntia* that required no pre-processing to remove spines and yielded more tonnage in pads and fruit per acre with greater adaptability (Burbank, 1907). For example, 'Melrose' (Table 1) was one cultivar Burbank released that after less than 4 years from transplanting was estimated to produce 1 t fresh weight/day (Fig. 32).

Burbank's foray into cactus breeding began in the mid-1890s, when he began amassing a germplasm collection of cacti, including the native, hardy forms of the southwestern United States as well as the cultivated "spineless" forms already in cultivation, like 'Smith' (north Africa, 1893; from E.E. Smith), 'Skelley' (Sicily, 1895: from E.R. Skelley), and the aforementioned 'Marin' (may have been introduced as 'Marine' by Don Francisco de Paula Marin, ≈1791; Table 1) (Burbank, 1907). Burbank augmented his collection with those of the USDA's PI program, which beginning in 1898, started to collect both fruiting and forage types from around the world. In 1899, David Fairchild and W.T. Swingle with the USDA procured or collected many cultivated and wild forms from the Mediterranean and South America, including PIs 3422 and 3423, spineless forms from Argentina that Fairchild recommended to "be used in cross-breeding with other prickly pears." Burbank was not satisfied with these forms of "spineless" *Opuntia*, because they produced


Fig. 29. Example flower types of 'Shasta Daisy' created by Burbank's interspecific hybridizations: (**A**) single or simplex daisy (lower right), duplex daisy with long ray petals (lower left), and fringed types (upper right); (**B**) Anemone flower type in a simplex daisy; (**C**) fringed petal types; (**D**) spoon single daisy type (Burbank, 1914–15).

Fig. 30. Rows of 'Shasta Daisy' growing on the Sebastopol Farm, 1912, grown for the National Federation of Women's Clubs Meeting, San Francisco, CA (Burbank, 1914–15).

little to no spines or glochids, but rarely both, and Burbank sought a "perfectly" spineless form. However, in Burbank's initial offering of 19 new and improved *Opuntia* (1907; Table 1), seven were USDA PIs (e.g., 'Anacantha') and several more were likely the same germplasm independently obtained by Burbank from Walter Bryant ('Blanco', 'Morada'), Don Francisco de Paula Marin ('Marin'), and Frank Meyers ('Meyers') (Table 1). Interestingly, eight of these existing cultivars were being sold as the best, despite not having set fruit for him, so determinations as to quality were not based on his first-hand observations. In the same catalog, Burbank introduces the first of his completely novel introductions, consisting of seven cultivars and two hybrid mixes. 'Santa Rosa' (Table 1), an Indian fig type, was apparently the star of the class with "no thorns and no bristles. The first of its kind…" (Burbank, 1907) (Fig. 31B). Again, the rapid pace of introduction by Burbank can be seen, because the new clones were only 3 years old from seed and had not produced fruit, but based on their initial habit and spinelessness, were released. These and other selections later fruited (Fig. 31C), allowing Burbank to evaluate flavor in fresh and preserved fruits.

Collecting OP seed from his cacti germplasm and making crosses between nearly spineless types created immense populations for mass selection of spineless types (lacking both spines and glochids) at early stages of development of seedling development. He created a meticulous seedling screening method to undertake selection in the "true leaf" or pad stage after the cotyledonary stage (cotyledons are usually 100% spineless). He often sowed the large seeds individually (singulation) in wooden flats, which, after germination, percent germination and initial screening could begin (Fig. 33). Seeds were planted in a 10 × 10-row/column grid systems using a dibble board, which resulted in a flat of individual seedlings in a "plug tray" configuration of 100 seedlings (or a 100-plug tray). Such regular planting instead of in-row flats made for easier transplanting, screening for spinelessness in seedling Stages II to IV (McDonald, 1999) and is the configuration later used in modern 10 inch × 20-inch plug trays after the plastics


Fig. 31. The spineless cactus (*Opuntia*): 15 years of breeding and selection to produce nearly and/or completely spineless forms (Burbank, 1914–15). (**A**) A closeup of the flowers, fruit, and spineless pads (Note: the recessed nodes on each pad from whence spines would normally be produced). (**B**) Burbank sitting near an early accession with reduced frequency of spines, most likely 'Santa Rosa', and (**C**) a Luther Burbank postcard displaying the fruits on a field of spineless cacti.

Fig. 32. Spineless cactus 'Melrose' growth in less than 4 years from transplanting of rooted pads. Luther Burbank estimated that 'Melrose' produced 1 t weight/day in June (Burbank, 1914–15).

revolution in the 1980s (Konjoian, 1999). When he had larger populations, they were often broadcast sown in outdoor coldframes (Fig. 34A).

Although modern-day breeders easily select in plug trays for high germination (%) and yield potential (percent of transplantable seedlings), Burbank selected strictly for spinelessness. This phenotypic selection would closely match what is done by commercial stock (*Matthiola incana*) producer firms and/or pre-finisher growers by growing seedling flats at high temperature (4.4 °C) for 1 week after radicle emergence to rogue out undesirable single-flowered types (dark green cotyledons) in double-flowered (pale green cotyledons) hybrid seed (Takii Seed Company, 2014). After rogueing out spined seedlings, the remaining spineless types could be left to grow for greater than 1 year to select for competitive (vigorous) "giant" seedlings among "dwarf" types (Fig. 34B). In Years 2 to 3, seedlings and/or vegetative pads were transplanted into long rows for subsequent evaluations (Fig. 34C). Rogueing continued in this phase, a rather precarious job balancing on a board above the primary spineless seedlings (Fig. 34D)!

Like the majority of his introductions, ornamental or otherwise (Table 1), Burbank provides little to no parentage information, invariably using the terms "selected hybrid," "crossbred," "developed", or, once, "second-generation" to describe their origins (Burbank,

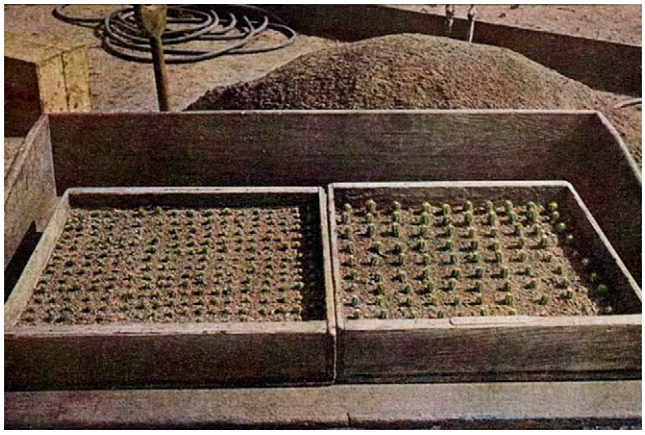

Fig. 33. Stages I to II of cactus seedling germination. Seeds were either sown spaced out as shown (left) to subsequently grow, appearing as modern-day "plug trays" of seedlings! Screening for lack of spine production could be accomplished at this early phase (Burbank, 1914–15).

1907; Howard, 1945). Of the ≈63 cactus introductions attributed to Burbank (Table 1), at least 18 are seedlings or clones of germplasm assembled from his contacts, like 'Smith', named for E.E. Smith who collected it in north Africa in 1893, and 'Anacantha' PI 3423 introduced by Fairchild and Lathrop from La Plata, Argentina, in 1899 (Table 1). Both cultivars happen to be the most frequently mentioned parents in Burbank's hybrids. Only six introductions have both parents listed such as 'Actual' ('Anacantha' × 'Smith'), whereas another seven are described as hybrids but with no pedigree information (e.g., 'Fresno'). Eight of Burbank's introductions appear to be OP seedlings (e.g., 'Banana' and 'El Dorado' derived from 'White Fruit'), whereas the remaining 24 are of unknown origin, including 'Burbank Standard', introduced in 1911 (Table 1), as the product of 14 years of breeding (Howard, 1945).

In simple terms, Burbank was a thrifty and savvy plant breeder–nurseryman–businessman, assembling the best germplasm, growing out large numbers for evaluating, and selecting the best to breed the next generation while selling off the surplus stock. After the initial offering in 1907, when 27 varieties were introduced (Table 1), two-thirds of which were germplasm, the remainder of his introductions was presumably hybrids or selections thereof. From 1909 to 1925, Burbank introduced 30 more selections, which coincided with the peak of the "great cactus boom and bust" at the start of the 20th century (Table 1) (Benson, 1982).

Burbank was not the first to recognize the potential of spineless cacti, although he was likely the most personally invested. According to Burbank, there were numerous spineless cactus qualities that would make this an outstanding forage (animal), food (humans), and industrial crop (Burbank, 1907, 1914–15):

> *"Supply abundant quantities of fresh fruit which ship excellently (eaten fresh or as jams, jellies, juices);*
>
> *Slabs supply an unprecedented amount of forage for stock and poultry;*
>
> *Young slabs make excellent pickles, good….when fried like eggplant, …also boiled and used as greens; may be prepared with sugar to produce a sweetmeat …like citron;*
>
> *Leaves used…as poultices;*
>
> *Abundant plant juices contain a mucilaginous substance that is used to fix pigments;*
>
> *Thorny varieties are used as hedges to protect the thornless types;*
>
> *Fiber of the plant makes an admirable stock for the manufacture of paper;*
>
> *Adaptability to arid regions."*

At the turn of the 20th century, the USDA, encouraged by reports of prickly pear use as forage and fodder in the southwestern United States, began a systematic investigation of the extent of use and potential of *Opuntia* for regular stock raising (Griffiths, 1905, 1912, 1913, 1928). Griffiths' publications bolstered, at first, the potential contributions a spineless *Opuntia* would make to ranchers and farmers in the southwestern United States. By 1912, Griffiths had overseen a massive distribution of spineless forms to 2000 interested farmers (Griffiths, 1912). The distribution program by the USDA, combined with Griffith's less than favorable statements (backed up with data) that no spineless forms, not even the ones sold by "nurserymen" (e.g., Burbank), are "perfectly so" and that it "is improbable that any of the spineless forms if completely neglected would succeed under conditions prevailing in this country" (Griffiths, 1912) was an attack on Burbank's brand. Ultimately, Griffiths concluded that the future of prickly pear as a forage crop lay in the encouragement of maintaining the native, spiny forms for use in times of drought with the spines removed when needed; otherwise, planting and protecting spineless forms from browsing until needed were rarely justified (Griffiths, 1928).

Unfortunately for stakeholders and ranchers, the USDA reports were too late to prevent the spineless cacti bubble. Beginning in 1905, speculation on the financial windfall resulting from development of another new agricultural crop for California and the rest of the world began with John Rutland's (Australia) purchase of one 'Santa Rosa' pad for a $1000 (Burbank, 1907). He paid less for 'Chico', 'California', 'Fresno', and 'Sonoma' (Table 1) and purchased the privilege of selling these in the southern hemisphere. To the best of our knowledge, this is the first example of exclusivity for ornamental crops in particular areas of the globe. Later, Burbank sued an express company for $10,000 for a shipment lost in transit to Australia. The Thornless Cactus Farming Company of Los Angeles formed in 1907 and purchased the rights to sell all seven of Burbank's new spineless *Opuntia* for the staggering sum of $27,000 (Smith, 2010). Railroad companies saw an opportunity to plant the unproductive lands they owned with the lucrative spineless *Opuntia* crop and land developers joined in, parceling land with the promise of riches for property owners who planted the miracle crop (Smith, 2010). Demand for spineless *Opuntia* continued to climb, yet the Thornless Cactus Farming Company was not meeting payment deadlines for Burbank. Seeking to boost sales, Burbank continued promoting himself (Fig. 31C) and the cacti through a litany of mass media outlets, speaking engagements, and biographical works (Smith, 2010). In 1913, the Luther Burbank Company formed, to consolidate controlling interests and marketing of all of Burbank's plant introductions, including the spineless *Opuntia* for $30,000 (Smith, 2010). Bad business decisions doomed both the Thornless Cactus Farming Company and later the Luther Burbank Company, both of whom focused on marketing, selling shares, and taking orders, but not production. To meet demand, the Luther Burbank Company removed the spines from wild-type *Opuntia* and sold them off as the Burbank's spineless introductions, the fraud ultimately leading to bankruptcy in 1916 (Smith, 2010).

## THE BURBANK LEGACY: FINAL SYNOPSIS

"What makes Burbank's work entirely different from that of other plant breeders is the immense scale on which his selecting is made…in his work, Burbank is guided by a special gift of judgment" (De Vries, 1905). Indeed, he was excellent at mass selection (pollen roulette) with a keen eye for selection and produced an array of beauty with wide adaptability, although there were only tested in one to two locations (Santa Rosa and Sebastopol, CA). His "rush to market" products were often fraught with disasters leading to bankruptcies. Although most of Burbank's ornamental cultivars have been lost, their numerous descendants have forever sealed Luther's reputation as the Father of American Ornamental Breeding, admirably from critics and devotees alike.

Throughout the past century, multiple ornamental plant breeders and public/private

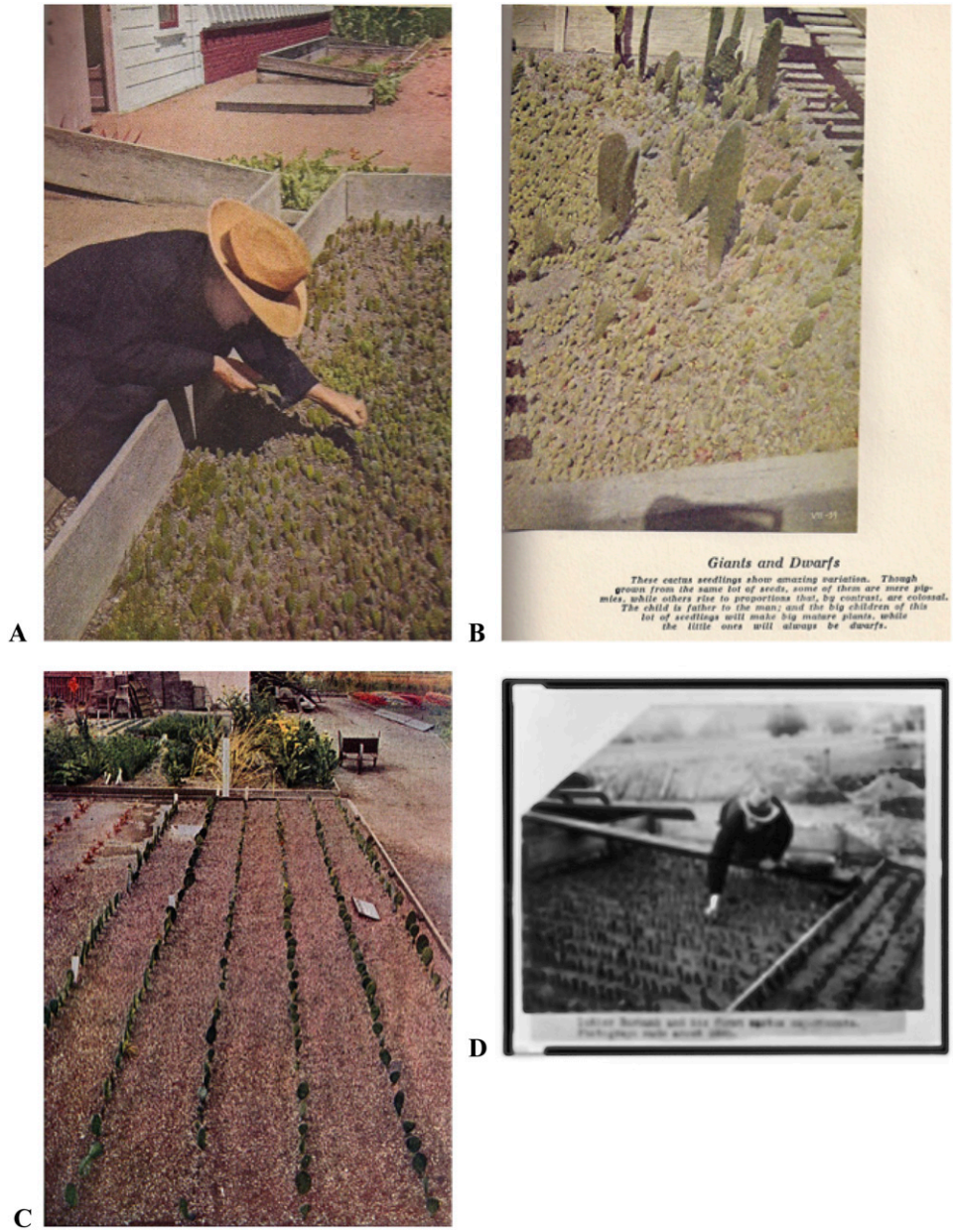


Fig. 34. Cactus selection procedures for "yield potential": (**A**) a broadcast-sown outdoor coldframe for selecting segregating and heterotic seedlings ready for transplanting (Stage IV); (**B**) a non-selected flat left to grow out; (C) rouging and selection of large beds of transplants involved precarious balancing on wooden planks placed above the frames, and (**D**) rows of transplanted seedlings and pad propagation after initial selections (Burbank, 1914–15).

programs have used many, if not all, of Burbank's techniques albeit along with his mistakes. Secrecy continues to pervade breeding programs because market value is derived from process, germplasm ownership of inbred parents for hybrid seed production, etc. Only in instances of scientific or popular press publications, U.S. Plant/Utility Patents, and Plant Breeders' Rights (in the rest of the world) is pedigree information ever revealed to the public domain. Otherwise, the proprietary breeding records and germplasm (carefully preserved in vaults for orthodox seed or clonal stock plant repositories) remain unknown and continue the mystique of flower breeders.

Modern-day marketers, salespersons, breeders, distributors, and retailers alike would do well to reread Burbank's accomplishments lest they unknowingly resurrect taxa such as *Osteospermum*, trailing (wave™) *Petunia*, red *Iris*, or white or crimson *Eschscholtzia* as "new crops." As history continues to demonstrate, 50 to 100 years after crops disappeared from market favor, they are "rediscovered" anew. Our richness of ornamental products is the direct result of modern-day breeders working contextually within the wealth of science and the undiscovered germplasm bank of previous breeders such as Luther Burbank.

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# Luther Burbank's Plums

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***Abstract*. The 113 named varieties of plums introduced by Luther Burbank (1849–1926) were by far the most numerous and arguably the most significant of his horticultural accomplishments. He began by importing 12 seedlings from Japan in 1885, including 'Abundance' and 'Satsuma' (*Prunus salicina*). The cultivars he released in the late 19th and early 20th centuries played a crucial role in developing commercial cultivation of Asian-type plums in California, the United States, and much of the world; they also served as founding clones for later breeders. His crowning achievement was 'Santa Rosa' (introduced 1906), which in 1945, 'Santa Rosa' accounted for 36% of the California plum harvest. Many of Burbank's other cultivars of primarily *P. salicina* ancestry were extensively cultivated in California in the early and middle 1900s, including 'Beauty' (introduced 1911), 'Burbank' (1888), 'Duarte' (1911), 'Eldorado' (1904), 'Formosa' (1907), and 'Wickson' (1895). His most important introductions of European plum (*P. domestica*) were 'Improved French' prune (1898), 'Sugar' prune (1899) and 'Standard' prune (1911). Some of Burbank's more obscure introductions never received general distribution and have disappeared; others such as 'Santa Rosa', 'Shiro' (1899), and 'Elephant Heart' (released posthumously in 1929) still are commonly cultivated today in home gardens and for sale at local markets.**

In the history of horticulture it is rare to find an individual who almost single-handedly created a new commercial industry based on a novel fruit type as Luther Burbank (1849–1926) did for Asian-type plums (*Prunus salicina*) in the United States. The 113 named varieties of plums and prunes that he introduced in the late 19th and early 20th centuries were by far the most numerous and arguably the most significant of his horticultural accomplishments. They played a crucial role in developing commercial cultivation of Asian-type plums in California, the United States, and much of the world; they also served as founding clones for later breeders.

Plums are native throughout the northern hemisphere, primarily in the temperate zones of Asia, Europe, and North America. *P. salicina* is native to China, where it has been cultivated since antiquity; *P. simonii* is another species native to China (Ramming and Cocui, 1990). For millennia, Native Americans harvested indigenous wild plums, which generally grow on shrubs or shrub-like trees. Compared with modern commercial cultivars, most native plums are small and tart and have astringent skins (Bailey, 1906). Settlers in the United States imported plums from their homelands, mostly *P. domestica*, which includes prunes, greengages, and egg plums, and *P. insititia*, which includes damsons and bullaces. The first named cultivars of plums were brought to California in 1851. Until 1870 only European and American plums were grown in California (Butterfield, 1938).

## EARLIEST ASIAN PLUMS BROUGHT TO CALIFORNIA

In that year a Mr. Hough of Vacaville, which was then one of the leading plum-growing areas of the state, imported plum trees from Japan through the U.S. consul, paying $10 each. A nurseryman in Berkeley, John Kelsey, bought the stock in 1874 and fruited the variety in 1876 and 1877. When the variety started to be widely propagated in the 1880s, another nursery, W.P. Hammond Co. of Oakland, named the variety 'Kelsey' (Butterfield, 1938). It was large and heart-shaped with skin that ranged from green to yellow or red when fully ripe (Fig. 1), a small pit, and firm yellow, juicy flesh.

In the late 1870s M.A. Chabot of Oakland started importing Japanese plants, including a plum cultivar that was round or heart-shaped with red skin over yellow ground, mottled with russet, and golden yellow, very juicy flesh. Luther Burbank, who arrived in California in 1875, obtained this cultivar and introduced it as 'Chabot'; different sources give the date of this introduction as 1881 (Butterfield, 1938) or 1885–86 (Hedrick, 1911).

One other Asian plum cultivar was present in California by the time that Burbank began breeding plums, the 'Simon' (*P. simonii*) or Apricot plum. This was obtained in China by a French consul, Eugene Simon, and sent to Paris in 1867; it was offered for sale by eastern U.S. nurseries as early as 1881 (Burbank, 1914; Hedrick, 1911). Burbank later described it as "a large, flat, tomato-shaped plum, with dark brown, hard flesh, purplish-red skin, and a small stone…sometimes eatable and sometimes classed as good when grown in the hot, dry climates of the interior valleys of California." It was not a "perfect fruit to begin" but valuable as a breeding parent because of its "small stone, delightful aroma, and desirable tree characters" (Burbank, 1914). [It also seems to have contributed firm flesh to its progeny, a characteristic exemplified by later cultivars such as 'Friar' (1968) and 'Blackamber' (1980).] Burbank said he used 'Simon' to breed many plum cultivars including 'Bartlett', 'Chalco', 'Challenge', 'Climax', 'Combination', 'Eldorado', 'Late Shipper', 'Maybard', 'Royal', 'Santa Rosa', and 'Wickson' (Howard, 1945).

## HISTORY AND METHODS OF BURBANK'S PLUM BREEDING

Burbank moved from Massachusetts to California in 1875 and in 1878 opened a small nursery business in Santa Rosa, 50 miles north of San Francisco. He first took a serious interest in plums in 1881, when he propagated 20,000 trees of the recently introduced 'Agen' prune (Smith, 2009). Only two or three named cultivars of Asian plum were present in California at this time and, as described previously, Burbank bought or traded for these. He had read of a blood plum in Japan, and in 1883, he had Isaac Bunting, a dealer based in Yokohama, ship him a dozen Japanese plum trees. He was hoping to find a novelty that he could market profitably, but all trees of this first shipment arrived dead. He tried again in 1885 and on 20 Dec. of that year received "12 sturdy, healthy Japanese plum seedlings." Two of them, 'Burbank' and 'Satsuma,' were of such exceptional quality that he sold buds and trees within a few years. The others, of varying quality and importance for the future, included 'Berckmans', 'Chase', 'Heikes', 'Late Blood', 'Long Fruit', 'Maru', and 'Willard', which were also sold under various synonyms. In 1887 Burbank sent fruits from the original trees to H.E. Van Deman of the U.S. Department of Agriculture, to local and national newspapers, and to be exhibited at a fruit growers' convention that met in Santa Rosa. In addition, he offered the new

Fig. 1. 'Kelsey' plums grown in Dinuba, CA.

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Japanese plums in his nursery catalog, charging $1 dollar per tree or 75 cents for dormant buds (Burbank, 1914; Butterfield, 1938; Dreyer, 1993; Smith, 2009).

Burbank began breeding plums, he wrote, because he "was impressed with the demand all about me for better varieties of plums and prunes, especially for drying and shipping purposes." He started gathering a collection of Japanese plums with desirable characteristics: "rapid growers, with early and abundant bearing qualities, and unusual adaptability to wide ranges of climate" and fruit "large in size, with a high percentage of flesh to stone, and with both skin and flesh of high color." His basic method was to "take the characteristics from the plums…and combine them in different varieties; to eliminate the faults as far as possible; to select and test the best among the millions of seedlings produced from the various combinations." To accelerate his progress, he used the original seedlings as stocks for grafting the scions of new seedlings, as many as 20 sets of grafts per tree (Burbank, 1914).

Burbank visited A.D. Pryal's nursery in Oakland, where he learned about pollination. A little more than a week later, after the first shipment of Japanese plum trees arrived, he purchased an 18-acre property in Sebastopol, near Santa Rosa, which he called the Gold Ridge Farm. As soon as the new Japanese plum trees flowered, he started making crosses with other Japanese, European, and native plums and growing seedlings of his own. As these seedlings started to produce fruit, he offered stock and control of the most promising selections in his nursery catalogs. The first of his plum creations to go on the market, in his catalog named *New Creations in Fruits and Flowers*, issued in June 1893, included 'Perfection' (which would later be renamed 'Wickson'); 'Hale' ('Kelsey' × 'Satsuma'); and 'Juicy' ('Robinson' × 'Abundance'). Burbank continued making crosses until his death in 1926 (Burbank, 1914; Butterfield, 1938; Dreyer, 1993; Howard, 1945). In all he released 113 cultivars of plums and prunes, accounting for more than half of his fruit introductions (Howard, 1945).

Burbank's Asian-type plum introductions had larger fruit size, better shipping qualities, and showier appearance than the European cultivars previously grown in California, and they rapidly displaced them in plantings for fresh market. His crowning achievement was 'Santa Rosa' (introduced 1906), which appears to have derived its reddish flesh from 'Satsuma'; firmness and acidity from the apricot or 'Simon' plum (*P. simonii*); and a rich, wild aroma, very likely from *P. cerasifera*. The American species used by Burbank in breeding plums contributed disease resistance, tough skin, and aromatic quality (Okie and Ramming, 1999).

As of 1914, Burbank estimated that he had devoted approximately one-tenth of his experimental work to plums, accounting for as much time any other crop; only the spineless cactus took more labor. At that time, he claimed that his plums accounted for one-third of the plums exported from California and also one-third of the "commercial value" generated by his breeding efforts (Burbank, 1914).

In 1945 his cultivars accounted for seven of the top 10 cultivars grown primarily for fresh fruit in California, including 'Santa Rosa' (36%), 'Beauty' (14%), 'Duarte' (10%), 'Wickson' (5%), 'Giant' (4%), 'Burbank' (2%), and 'Formosa' (2%), adding up to an astounding 73% of the market (Faust and Surányi, 2011). None of Burbank's plum cultivars are grown commercially on a wide scale in the United States today, but several such as 'Santa Rosa' and 'Shiro' are still important for local and home garden use. Some, like 'Inca' (1919) and 'Elephant Heart' (1929), are much appreciated by fruit connoisseurs, although they have significant flaws (both have gum pockets and ripen over an extended period; 'Elephant Heart' tends to have astringent, tart skin unless perfectly ripe) for commercial production.

Burbank also devoted serious attention to breeding *P. domestica* selections for the drying and fresh markets, beginning with 'Splendor' prune (a seedling of 'Agen') and 'Long-leaved Wonderful', both introduced in 1893, and 'Giant' ('Agen' × 'Pond') in 1894. The historical record is not complete, but a seedling of 'French' ('Agen'), which Burbank named 'Miller' and sold in 1898 to a nurseryman in Morgan Hill, appears to have been the cultivar later known as 'Improved French', which accounts for nearly the entire commercial prune industry in California today. Several of the other cultivars he introduced over the years were planted with great hopes, but none were ultimately successful as drying prunes; 'Sugar', a seedling of 'Agen' introduced in 1899, was the most widely planted, being grown on 4228 acres in 1949, although many of the shipments were as fresh plums. 'Standard', a cross of 'Sugar' and 'Tragedy' introduced in 1911, was widely planted in the beginning but disapproved for drying within a decade (Hansen, 1951; Howard, 1945; Wickson, 1921).

One of the oddest and most intriguing of his introductions was 'Miracle', a cross of *P. institia* × *P. domestica* released in 1901, which was almost seedless and was widely planted as a curiosity. In 1911, after several generations of crosses, he introduced 'Conquest', which had an even smaller rudimentary seed and was widely planted by amateurs as a plum but never dried as a prune (Howard, 1945). Although these two cultivars are no longer available, germplasm undoubtedly derived from Burbank's program still exists and is being used currently by researchers to fulfill Burbank's vision of a stoneless or seedless plum (Callahan et al., 2015).

Burbank made use of at least 11 plum species, including hybrids and selected seedlings of such native species as *P. maritima* ('Improved Beach', 1897; 'Maritima', 1899; 'Peach', 1901), *P. subcordata* ('Nixie', 1911), and *P. munsoniana* ('Juicy', 1893; 'America', 1898; 'Victory', 1911) (Howard, 1945).

Until recent decades, when studies of molecular markers became possible, the pedigrees of virtually all of Burbank's plums could not be affirmed with confidence, because he kept most of his records of crosses in his head rather than making meticulous notes. In addition, his technique for hybridizing consisted of waving blossoms of the pollen parent next to the flowers of the seed parent, but did not involve emasculating the flowers of the female parent or sequestering them from insect pollinators that could bring foreign pollen. He or his representatives claimed that several of his introductions such as 'Honey Moon' and 'July Fourth' involved hybrids of the diploid species *P. salicina* with the hexaploid *P. domestica* (Butterfield, 1938), a cross that subsequent generations of breeders have found does not result in adequate fertility.

However, the broad outline of his claim to have introgressed the genes of multiple species in his plum introductions was verified by a modern study. In an analysis of the random amplified polymorphic DNA markers of five typical California cultivars of Asian-type plums (including 'Eldorado,' which was bred by Burbank, and four others that were in large measure bred from his cultivars), Boonprakob et al. (2001) concluded that *P. salicina* contributed 36% of their genetic ancestry; *P. cerasifera* contributed 28%; *P. simonii* contributed 26%; and *P. americana* contributed 10%.

Burbank offered stock and control of his prized cultivars to private owners such as 'Golden' plum for $3000 in 1893 and 'Perfection' (later called 'Wickson') for $2000 in 1895. He eventually realized that he could greatly increase his earnings if he were able to charge a royalty for each tree rather than making a one-time sale, and a letter that he wrote to nurseryman Paul Stark shortly before his death helped persuade the U.S. Congress to pass the Plant Patent Law of 1930, which for the first time made possible the protection of rights for plant breeders (Dreyer, 1993). Sixteen patents were awarded to Burbank posthumously, and many plums were among the earliest awards, including numbers 12, an unnamed variety with crimson skin and light golden yellow flesh; 13, 'Great Yellow'; 16, 'Mammoth Cardinal'; and 18, an unnamed variety with yellow skin and flesh (Brooks and Olmo, 1997).

The following sections list and describe the plum cultivars introduced by Burbank, which were of greatest significance, either because they were widely planted in the United States or other countries or because they played a key role as founding clones for later breeders. This includes cultivars obtained either through importation or breeding and collates and updates the information found in the leading primary (Burbank's writings and nursery catalogs) and secondary sources. The cultivars are described in approximate chronological order, although it is not possible to be completely consistent, because in some cases, only the date of crossing is known, whereas in others, just

the date of introduction is available. Descriptions include the pedigree, history of introduction, tree and fruit characteristics, season, history of cultivation, and availability of germplasm and nursery trees.

## ASIAN-TYPE PLUM CULTIVARS IMPORTED BY BURBANK

'Burbank' was a seedling of 'Wassu' imported by Burbank from Japan in 1883 (Hedrick, 1911) or 1885 (Howard, 1945), named in 1887, and introduced in 1888. The tree is vigorous, spreading, a precocious bearer, and self-sterile. Fruit are almost globular; skin is cherry red over deep yellow ground, dotted with yellow spots; flesh is golden yellow, juicy, very sweet, but not intense in flavor; it is clingstone; and the pit is very small. The season is late June and early July with a relatively long ripening period. It is an excellent shipper (Allen, 1929). In the first half of the 20th century 'Burbank' was one of the most popular cultivars for both commercial and home use (Allen, 1929; Hedrick, 1911; Wickson, 1926). In 1938 171,000 crates were shipped, but by 1945, it accounted for only 2% of shipments from California. Today it is no longer grown commercially, germplasm is not available from the National Clonal Germplasm Repository for Tree Fruit, Nut Crops and Grapes at Davis, CA (NCGR-Davis), and nurseries no longer carry this cultivar.

'Abundance' was imported from Japan by Burbank in 1884 (Howard, 1945) or 1885 (Butterfield, 1938) and introduced by John T. Lovett of Little Silver, NJ, in 1888. It was originally known as 'Botan' (Howard, 1945). The tree is large, vigorous, and hardy. Fruit are medium size and globular or irregular ovoid with a pointed apex; skin is cherry red over a yellow ground, covered with white bloom; it is clingstone; and flesh is yellow, juicy, and rich (Allen, 1929; Hedrick, 1911; Waugh, 1901; Wickson, 1926). Its season is early. Multiple strains of different appearance were sold under the name (Waugh, 1901). 'Abundance' was adaptable to a wide diversity of soils and, as its name indicates, was a prolific bearer (Hedrick, 1911). In 1910 it was popular for shipment from early regions (Wickson, 1910), but it was a poor shipper, susceptible to brown rot, and by 1926, it was disapproved for shipping (Wickson, 1926). In 1945 it was still "perhaps planted more widely than any other Japanese plum, although others, because of their shipping qualities, [had] a much larger acreage, especially in the South and on the Pacific Coast" (Howard, 1945). It is not grown commercially today. Germplasm is available from NCGR-Davis, where the accession number is DPRU 919. This cultivar currently does not appear to be available from nurseries. It was a parent of 'Climax'.

'Satsuma' came from a tree received by Burbank from Yokohama, Japan, in Dec. 1885 and was first named "Blood Plum of Satsuma" after a province in Japan (Hedrick, 1911). Buds were sold under the original name in 1887, and the trees were first sold in 1889. The tree medium to large, upright-spreading, vigorous, moderately productive, bearing heavier crops as the tree becomes older. Fruit are small to medium, round, or slightly flattened; skin is mottled dull red and green (Fig. 2), somewhat tough, and bitter (Ashton, 2008); it is semiclingstone; flesh is deep red, firm, juicy with a rich almond-like flavor (Hedrick, 1911). The season is mid- to late July to early August. It is partially self-fruitful, adapted to areas with low winter chill, and so popular in southern California; it is a probable parent or ancestor of 'Mariposa'. It is never much cultivated commercially but important for local markets and home plantings; it is primarily used for cooking, canning, and preserves rather than fresh shipments (Allen, 1929). It is not represented at NCGR-Davis but widely available from nurseries.

## ASIAN-TYPE PLUM CULTIVARS BRED BY BURBANK

'Wickson' resulted from a cross made by Burbank ≈1887 of 'Burbank' (*P. salicina*) × 'Simon' (*P. Simonii*) (Howard, 1945) or 'Kelsey' (Hedrick, 1911). Introduced in 1895, and first advertised for sale as 'Perfection', it was renamed after the eminent pomologist Edward J. Wickson. The tree vigorous, productive, upright, not very cold-hardy, and self-sterile. Fruit are very large for its era, heart-shaped like 'Kelsey', but more symmetrical; skin ripens to yellowish red or solid red (Fig. 3); the pit is small and clingstone; flesh is coarse, amber yellow, translucent, tender, and juicy; flavor is good but not the best (Allen, 1929; Hedrick, 1911; Howard, 1945). Season is mid-July in Fresno. In the 1910s and 1920s, it was one of the most important cultivars shipped from California (Allen, 1929; Hedrick, 1911); by 1940 it was still the fifth most important Burbank plum cultivar in California (after 'Beauty', 'Duarte', 'President', and 'Santa Rosa'), but starting to decline, as some 2,000 acres were grown and 186,000 crates were shipped (Howard, 1945–46). By 2008 just 4000 packages were shipped, and today 'Wickson' is little grown commercially but still popular for farmers' markets and home gardens. Germplasm is available from NCGR-Davis (DPRU 2135); trees are widely available from nurseries.

Fig. 2. 'Satsuma' plums grown in Littlerock, CA.

'Shiro' was said to be a seedling of 'Wickson', representing "a combination of Robinson (*P. munsoniana*), myrobalan, and 'Wickson'" (Howard, 1945). It was developed in 1889 and introduced in 1898 (Butterfield, 1938) or 1899 (Ashton, 2008). The tree medium–large, moderately vigorous, hardy, and productive. Fruit are small to medium size; skin is light to deep yellow with a pale blush and numerous very small, inconspicuous dots (Fig. 4); it is clingstone; flesh is light yellow, semitransparent, juicy, sweet, and mild; flavor lacks character, and the skin is quite tart (Hedrick, 1911). The season is mid-June (San Joaquin Valley); early July (coastal valleys); or late July (mid-Atlantic). It can be shipped but quickly breaks down after ripening. It has been widely planted, but mostly for home and local markets (Howard, 1945); it is common in the Northeast and Midwest. The germplasm was formerly at NCGR-Davis (DPRU 2132) but is no longer present; trees are widely available from nurseries.

'Climax' was a cross of 'Simon' (*P. simonii*) × 'Abundance', originally called 'Royal', introduced in 1899 (Hedrick, 1911). The tree is a precocious and prolific bearer, spreading, vigorous, thrifty, and self-fertile. Fruit are large, heart-shaped with a pronounced apex; skin is deep red; it is clingstone; flesh is yellow, juicy, subacid, somewhat fibrous, tender, and melting (Hedrick, 1911; Wickson, 1926); it tends to crack and ripens rapidly at the apex. It is very susceptible to brown rot and poorly adapted to Eastern conditions (Hedrick, 1911). The season is the second half of June (Allen, 1929). Widely planted in the early 20th century, it is still growing in favor in the late 1920s (Allen, 1929; Wickson, 1926), but in

Fig. 3. 'Wickson' plums grown in Kingsburg, CA.

Fig. 4. 'Shiro' plums grown in San Luis Obispo, CA.

decline by 1945, when there were ≈1000 bearing acres in California (Howard, 1945). Germplasm is not currently available at NCGR-Davis (was DPRU 1501, 2119); trees are not available from nurseries.

'Gaviota' was said to have originated in 1900 as a cross of *P. salicina* × *P. americana*, although Howard wrote that it "probably contains admixtures of other species"; first named 'Rice Seed', it was introduced 1909 by Fancher Creek Nurseries of Fresno (Howard, 1945) or in 1907 (Butterfield, 1938; Hedrick, 1922). However, from an analysis of its molecular markers, Boonprakob et al. (2001) concluded "it appears that 'Gaviota' has *P. simonii* in its background." The tree is variously described as vigorous (Allen, 1929) or weak (Howard, 1945) and prolific, tender to cold, blooming late, and self-sterile. Fruit are very large for its time; it is oval, dark red over yellow ground color; flesh is yellow, firm, sweet, with a distinct, characteristic flavor; seed is small; it shipped and stored well for its time (Allen, 1929). The season is late July and early August (Allen, 1929). It has been increasing in popularity since 1922 (Hedrick, 1922); shipped from the Vacaville, CA, district (Wickson, 1926); 44,000 crates marketed from California in 1940; was grown in Australia and South Africa; and is no longer grown commercially (Howard, 1945). 'Gaviota' was used by John Weinberger for size and is in the parentage of 'Friar' (= 'Gaviota' × 'Nubiana'). Germplasm is not present at NCGR-Davis; it does not appear to be available from nurseries; it may be available through rare fruit collectors (Mariani, 1994).

'Duarte' originated as a cross of seed parent 'America' (*P. munsoniana* × *P. salicina*) and pollen parent 'Climax'; Burbank said it "owes its flavor largely to wild American ancestors." It was developed in 1900 and introduced in 1911 by Pioneer Nursery Company of Monrovia, CA (Howard, 1945). The tree vigorous and upright with numerous fruiting branches (Allen, 1929); it is self-sterile. Fruit are large with dark or dull red skin, thickly colored with large cream or brownish dots; flesh is dark red; it somewhat resembles 'Satsuma'; it is semifreestone; flavor is very good (Allen, 1929). The season is mid- to late July; formerly it was the earliest blood plum (Wickson, 1926). It was important in the leading shipping sections in 1929 (Allen, 1929); in 1940, 2,000 acres were grown in California, and 254,000 crates shipped (Howard, 1945); it is no longer grown commercially. Germplasm was formerly at NCGR-Davis (DPRU 2821) but is no longer available; trees of 'Improved Duarte' are available from nurseries.

'Eldorado', also known as 'El Dorado', originated as a cross of *P. salicina* × *P. simonii*, introduced 1904 (Howard, 1945). "Many years ago a small black Japanese hybrid plum was produced on my Sebastopol place...ripening early in July...but too small...at last in 1904 Eldorado appeared, just like the little purple All Summer, but about ten times as large" (Howard, 1945, citing Burbank catalog from 1918). The tree is medium–large, very upright, and self-infertile. Fruit are large; skin is reddish black (Fig. 5); it is clingstone; flesh is firm and amber yellow; it is said to store and ship well; it is good for canning (Facciola, 1998). It ripens midseason. It was grown commercially in California ≈1910–60; 36,000 crates were shipped in 1939 (Howard, 1945); by 1965, it accounted for 10% of commercial plum shipments, but this share had declined to 3% in 1988 (Faust and Surányi, 2011), and 'Eldorado' is no longer grown commercially. Germplasm is available from NCGR-Davis (DPRU 2122); trees are not readily available from nurseries but may be obtained through rare fruit groups.

'Santa Rosa' was described as "'a complex hybrid containing a mixture of *Prunus triflora [salicina]*, *P. Simonii*, and *P. americana*, with the salicina characters predominating.' The exact varieties will never be known, but the red flesh would indicate that the 'Satsuma' played a part" (Howard, 1945). However, Boonprakob and Byrne (2003) found that 'Santa Rosa' did not have *P. americana* in its parentage, but did have *P. cerasifera*. It was introduced by George C. Roeding of the Fancher Creek Nurseries, Fresno, CA, in 1906 (Howard, 1945) or 1907 (Butterfield, 1938). The tree is vigorous, upright, compact, and highly productive. Fruit set improved by cross-pollination; it is low chill (300 h). Fruit were large for its era (but small today) and roundish; skin is purplish red with conspicuous dots and whitish bloom; it is clingstone; flesh is yellow to dark red near the skin, rich, juicy and aromatic, and delicious (Allen, 1929); it is tart near the skin and pit. The season is 10 to 25 June in Fresno. It is Burbank's most celebrated and most widely grown plum introduction; it is among the top or a leading salicina-type plum in the United States, southern Europe, North Africa, South Africa, Australia, and New Zealand (Howard, 1945). For many decades it was the standard for the California plum industry; it was planted widely in the 1920s (Allen, 1929; Wickson, 1926); 5160 acres were grown in California in 1939 (Howard, 1945); it accounted for 36% of the California plum harvest in 1945, 35% in 1955, 31% in 1965, 20% in 1975, 10% in 1988, and 7% in 1994 (Faust and Surányi, 2011); by the mid-1980s it was considered too small and soft (Day et al., 2013), and today it is mostly grown for local sale and home use.

Fig. 5. 'Eldorado' plums grown in Visalia, CA.

Among the many cultivars developed as sports or mutations from 'Santa Rosa', or using 'Santa Rosa' as a parent or grandparent, were 'Bella-Rosa', 'Blackamber', 'Black Ruby', 'Casselman', 'Campagne', 'Explorer', 'Fire Queen', 'Fortune', 'Fresno Rosa', 'Gar-Rosa', 'July Santa Rosa', 'Laroda', 'Midrosas', 'Padre', 'Premier', 'Roysum', 'Queen Rosa', 'Queensland Bellarosa', 'Rosa Grande', 'Rosanna', 'Salsa-Pride', 'Santa Rosa-Two', 'Segundo', 'Showtime', 'Sierra', 'Star Rosa', and 'Weeping Santa Rosa' (Brooks and Olmo, 1997). Germplasm is available from NCGR-Davis (DPRU 2131); trees are widely available from nurseries.

'Formosa' was described as "a mixture of *triflora* [*salicina*] species and several others" (Howard, 1945). It was introduced 1907 by Fancher Creek Nurseries of Fresno, CA. Trees are thrifty but not always productive and are self-sterile. Fruit are large and heart-shaped; skin is smooth yellow with a pale bloom, turning cherry red as it ripens; it is nearly freestone; flesh is pale yellow, firm then melting, sweet and juicy, sweet with a rich apricot flavor (Allen, 1929; Wickson, 1926). The season mid-June with a relatively long harvest season; it ships and stores well for an older variety but shows bruise marks readily. It was already being discarded for shy bearing in 1926 (Wickson, 1926); shipments from California in 1940 amounted to 53,000 crates and 2,000 boxes (Howard, 1945); it is no longer grown commercially. Germplasm is available from NCGR-Davis (DPRU 924); trees do not appear to be available from nurseries.

'Beauty' was described as "the product of a very complicated heredity including several species" (Howard, 1945). It was introduced 1911 (Butterfield, 1938). Trees are self-fertile and bear prolifically. Fruit are medium size and heart-shaped; skin is crimson covered with white dots; flesh is amber streaked with scarlet (Allen, 1929). Fruits are very attractive; it was regarded in the 1920s as the best early plum for shipping (Wickson, 1926). Burbank considered it "perhaps the best of all" his plums (Burbank, 1914), and it is still appreciated by connoisseurs. Beauty is one of the earliest ripening of Burbank's releases, ripening 1 to 15 June in Fresno, 7 to 10 d before Santa Rosa. In the early 1940s, 200,000 to 250,000 crates were shipped annually from California (Howard, 1945); it is no longer grown commercially but is a home garden favorite. Germplasm is available from NCGR-Davis (DPRU 2120); trees are available from nurseries.

'Inca' was introduced in 1919, but no information about its pedigree is available (Howard, 1945). The tree is low chill. Fruit are large, oval, tapered toward the blossom end; skin is golden yellow with magenta specks (Fig. 6); it is clingstone; flesh is apricot-colored, very sweet, rich-flavored, juicy, and tender; a gum pocket is typical (Mariani, 1994). The season early August in Fresno and mid-August in Santa Clara Valley (personal observation). It is never commercial because of the gum pocket problem, but

it is a singularly beautiful and delicious cultivar with a cult following among fruit collectors (Mariani, 1994). It is a parent of 'Sierra'. Germplasm is no longer at NCGR-Davis (formerly DPRU 2820), but trees are available from nurseries.

'Elephant Heart' is of unknown pedigree, but 'Satsuma' appears likely to have been a parent or ancestor. It was selected ≈1920 and introduced in 1929 by Stark Brothers Nurseries, Louisiana, MO (Brooks and Olmo, 1997). The tree is vigorous, hardy, and prolific. Fruit are large and heart-shaped; skin is thick, mottled purple, brown, and green with heavy bloom (Fig. 7); it is freestone; flesh is blood red, juicy with a rich, distinctive flavor (Brooks and Olmo, 1997; Facciola, 1998); when underripe, however, the fruit has a grassy aroma. The season is the first half of August. 'Elephant Heart' was grown commercially on a small scale from the 1940s; just 4000 cases were shipped in 2008, but the cultivar is popular at farmers' markets and home gardens and a favorite among fanciers of heirloom fruits. Germplasm is available from NCGR-Davis (DPRU 2123); trees are available from nurseries.

## EUROPEAN (*P. DOMESTICA*) PLUM CULTIVARS BRED BY BURBANK

'Splendor' prune was a seedling of 'French' ('Agen') pollinated by 'Pond' ('Hungarian'); it originated in 1886 and sold as 'Cross-bred Prune A.P.-318' to Stark Brothers in 1893 and renamed by them and introduced as 'Splendor' in 1894 (Howard, 1945). The tree is partially self-fertile. Fruit are medium to large, larger than 'French' prune; the shape is oval with a distinct neck; skin is dark purple with small russet dots and a heavy bluish bloom; it is freestone; flesh is yellowish, translucent, meaty, rich, and sweet (Howard, 1945). The season a week earlier than 'French'; it ripens its crop all together. It is considered unsatisfactory as a prune because it clings to the tree after ripening (Wickson, 1921). It is a successful plum but not extensively planted (Howard, 1945; Wickson, 1926). It is not available from NCGR-Davis or from U.S. nurseries; trees are available from Australian nurseries (Woodbridge, Yalca).

'Giant' prune was a cross of 'French' ('Agen') × 'Pond' ('Hungarian'), exhibited in 1888, and introduced in 1893 (Howard, 1945). Trees are vigorous and productive and self-fertile. Fruit are large, intermediate in size between its parents, long, oval, and the shape is slightly necked; skin is light to dark purplish red covered with numerous russet dots and a bluish bloom; it is freestone when ripe; flesh is light golden yellow, firm, dry, coarse, fibrous, and of very mild or insipid flavor (Allen, 1929; Hedrick, 1911; Wickson, 1926); it resembles 'Pond' in quality. The season is the first half of August; in its day, it was among the later varieties grown for fresh shipments. It was originally called a prune but rarely used as such. It was widely, but not extensively, planted as a shipping plum (Howard, 1945); it is not grown commercially today. It is not available from NCGR-Davis or from U.S. nurseries; trees are available from a few English nurseries.

'Improved French' appears to have originated from a seedling of 'French' ('Agen'), which Burbank named 'Miller' and sold in 1898 to Leonard Coates, a nurseryman in Morgan Hill, CA. Coates first called it the 'Improved French' prune and later 'Morganhill' (Howard, 1945). The cultivar resembled the original 'Agen' but was reported to be somewhat larger and more uniform in fruit size (Doyle et al., 2012). The tree upright and vigorous, self-fertile, with average precocity with a moderate tendency to alternate bearing; fruit matures uniformly throughout the tree. Fruit are medium-sized, ovate, and slightly necked; the skin is reddish purple to full purple with light grayish bloom; it is semifreestone; flesh is yellow to amber, typically ranging from 22 to 24° Brix; drying ratio commonly averages three to one (Doyle et al., 2012). The season is the second half of August in the Fresno area. It accounts for the great majority of the prune orchards grown in California today. Germplasm is not currently available at NCGR-Davis; trees are widely available from nurseries.

'Sugar' was a seedling of 'French' ('Agen') and an unknown pollen parent introduced in 1899. The tree upright and can grow quite large; it is a heavy producer, but because of brittle wood, trees require annual pruning (Howard, 1945); it severely alternate bears (Hansen, 1951). Fruit size is medium to large, larger than 'French'; shape is oval and slightly flattened; skin is dark reddish purple covered with thick white bloom (Fig. 8; Hedrick, 1911; Howard, 1945); it is freestone; flesh is golden yellow, juicy, tender, sweet, and mild; high in sugar content both fresh and dried (Howard, 1945; Wickson 1926). It tends to dry into a somewhat coarse, stringy product; it is not of highest quality as a cured prune (Wickson, 1926). It is used fresh and for canning. The season is 1 week to 10 d earlier than 'French' prune (early August in Fresno). It quickly assumed commercial importance in the Californian prune districts (1903); was extensively shipped as a plum (Howard, 1945); grown on 4228 acres in 1949 (Hansen, 1951); no shipments were reported in 2009 and little grown today. 'Sugar' is the seed parent of 'Sutter' prune bred at UC Davis and released in 2000 (Doyle et al., 2012). It is not available from NCGR-Davis; trees are available from U.S. nurseries (Bay Laurel, Pacific Groves).

'Standard' prune was a cross of 'Tragedy' × 'Sugar' made ≈1897 and introduced in 1910 (Burbank, 1914) or 1911 (Howard, 1945). Fruit are large; skin is purple–black with blue bloom; flesh is amber, fine-grained, melting, juicy, and sweet; seeds are very small; it is freestone (Wickson, 1926). It is used for both drying and shipping; it is best sulfured before drying (Mariani, 1994). Burbank claimed that 'Standard' was the "the first prune ever produced that combined superior qualities of flesh" with a fully free stone (Burbank, 1914). It "ripens with the French prune in September" in Sonoma County (Burbank, 1914). It was disapproved for shipping by 1921 (Wickson, 1921) but still widely planted in plum-growing regions; it is more successful as a plum than as a prune, even in California (Howard, 1945). It is not available from NCGR-Davis (formerly present as DPRU 2610); trees are not available from nurseries but available from fruit collectors.

Fig. 6. 'Inca' plum grown in Morgan Hill, CA.

Fig. 7. 'Elephant Heart' plums grown in Dinuba, CA.

Fig. 8. 'Sugar' prune plums grown in Dinuba, CA.

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# 21st Century Approach to Improving Burbank's 'Stoneless' Plum

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***Abstract*. The theme running through many of Luther Burbank's breeding programs was to make plants more tailored to human uses. Mr. Burbank thought that the stone in plum fruits was unessential to a tree that was propagated vegetatively, so he chose stoneless plums as a breeding goal. He made two releases, 'Miracle' in 1903 and his final and almost perfect 'Conquest' in 1916, which he considered one of his best accomplishments in plum breeding. 'Conquest' had only a grain of stone and flavor and size comparable to the best French types of the time but was not commercially successful. In view of the current desire for convenience food such as seedless fruit (citrus, grapes, watermelon) and advanced knowledge of genetics and breeding technologies, we have taken up where Mr. Burbank left off in the production of a better than "almost perfect" stoneless plum. We began by locating what were most likely remnants from Mr. Burbank's breeding program and we are now using 21st century technology to achieve a completely stoneless, high-quality plum fruit. These technologies include molecular markers, genetic engineering, and accelerated breeding cycles (FasTrack). Initial experiments had characterized the stoneless trait as a decrease in the number of endocarp cells that form the stone. We defined the time critical to the formation of endocarp by analyzing gene expression of a number of transcription factors involved with determining endocarp cells. We identified genes that were expressed differently during this period between normal stone cultivars and one of the stoneless cultivars. In addition, we targeted genes for genetic engineering to reduce the lignification in endocarp and to reduce or convert endocarp cells to non-lignifying cells. A system, FasTrack, using a flowering gene from poplar, has been incorporated to reduce the juvenility period and eliminate the seasonal aspect of fruiting to see the results of the breeding as well as the genetic engineering approach much faster. The combination of these approaches is now in place to attempt to improve on Mr. Burbank's stoneless plum.**

## HISTORY OF THE STONELESS PLUM

Luther Burbank was heralded in his day as a genius in breeding (New York Times, 30 Sept. 1906), especially in the area of practical breeding (Jones, 1928). One theme that ran through his breeding approach was to select and improve plants that had lost certain characteristics that were of no use to people. To this end, Luther Burbank thought that the plum stone that surrounds the seed was not necessary. The plum was not seed propagated, hence protecting the seed was not important. "But a moment's reflection makes it clear that the plum stone serves man no useful purpose, while the inconvenience it gives us is obvious" (Burbank, 1914a). So he began a breeding program to obtain plums without stone through his project "*An Experiment in Teaching a Plant Economy*" (Fig. 1).

Part of Mr. Burbank's success as a breeder was his choice of germplasm. He believed in incorporating germplasm from wide-ranging sources. There existed a so-called stoneless plum, 'Sans Noyau', in France that Luther Burbank used as the source of his stoneless trait. "There has been known for several hundred years, a wild plum, an unproductive, thorny bush, which bore insignificant, acid, bitter, wild berry-like fruits with only half or two-thirds of a stone" (Burbank 1914c). He imported this plum from Transom Freres Nurseries in France and began to cross it beginning in 1890 to his high-quality 'Agen' or French-type germplasm (Fig. 2). From these seedlings he was able to select better quality and nearly stoneless germplasm, from which he could backcross to the 'Agen' plum. He made his first release of 'Miracle' (Fig. 3A) (Burbank, 1903) as a beta-version

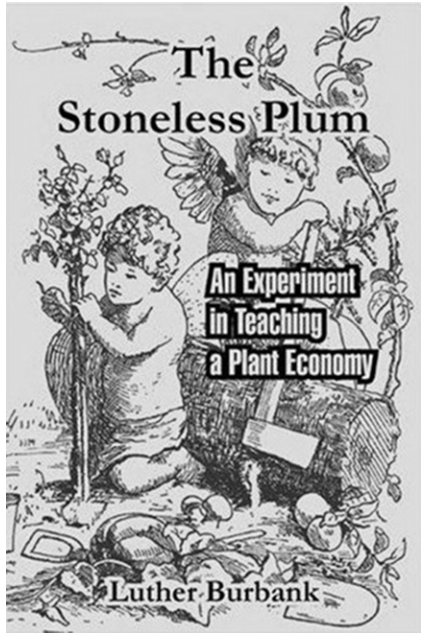


Fig. 1. Cover of Luther Burbank's re-publication of the stoneless plum bulletin: "The Stoneless Plum: An Experiment in Teaching a Plant Economy." <http://www.amazon.com/The-Stoneless-Plum-Experiment-Teaching/dp/141470125X>.

Fig. 2. A picture taken from *Burbank Methods and Discoveries* (1914a) entitled "Three Stages of Development." At the left is the original wild French plum, called the 'San Noyau'—of insignificant size and practically inedible. It is almost stoneless. Mr. Burbank improved the plum by hybridizing it with cultivated varieties, retaining the stoneless condition and introducing the qualities that make a commercial fruit. The central figure shows the plum at an intermediate stage of development; at the right the improved stoneless descendant a generation or two later.

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Fig. 3. A composite of pictures taken from *Burbank Methods and Discoveries* (1914a): (**A**) 'Miracle', the first stoneless release; (**B**) typical stoneless seedlings showing a sliver of stone. (**C**) 'Conquest' and (**D**) typical stoneless plum showing the complete lack of stone surrounding the seed.

stoneless plum, because it still had a crescent of stone and not quite the flavor and size of the French-type plums. "A representative of the Oregon Nursery Company, on a visit to my Sebastopol grounds in 1903, was greatly pleased with this variety, and at once purchased it……At the time it was the best stoneless plum in existence. But its chief merit was that it was the forerunner of a race of stoneless plums and prunes which will in time be grown wherever these fruits are raised" (Burbank, 1914c). Mr. Burbank had grand plans for this program. He released a second stoneless plum, 'Conquest', in 1916 (Fig. 3B) (Burbank, 1914a, 1914b, 1914c). He has included this plum in his four favorite plums. "The stone has been eliminated wholly with the exception of a tiny speck. The fruit is so very valuable and the tree so very productive that I have consented to introduce it this season" (Burbank, 2014c). He goes on to say that the quality of the fruit and size are similar to the French prune.

These two releases appear to be the only commercial cultivars from Mr. Burbank's very large stoneless program (Fig. 3C and D). He had several thousand stoneless seedlings planted and had generated hundreds of thousands of seed, but he had a hard time preserving them as a result of higher levels of rot and consumption by pests resulting from the lack of stone. Mr. Burbank states that in one experiment to test the preservation of seeds, he began with 100,000 seeds stored in several manners. He was able, however, to plant out several thousand seedlings to evaluate but none of those seedlings had the required combination of stoneless and commercial fruit quality. "Every color of plum now appears in these stoneless hybrids—white, pale yellow, orange, scarlet, crimson, violet, deep blue, almost black, striped, spotted, variegated, and mottled in every way imaginable" (Burbank, 1914c). Neither 'Miracle' nor 'Conquest' appear to have been a success in the marketplace although they had great publicity (New York Times, 1906, 1912; Burbank, 1903). It could be because the growers were paid by the pound and these stoneless plums weighed less without the stone (L.J. Rombough, personal communication).

In teaching plums to be stoneless, Mr. Burbank did not feel he had actually achieved his goal.

"So my ideal of an eatable plum having no stone about its seed was almost achieved. I say almost achieved because there still remained, in the case of the plums of best quality, a fragment of shell which varied from a small crescent about on side of the kernel to an almost invisible granule. There were some individual plants among the numberless seedlings that bore fruit in which the stone was absolutely eliminated and, in some cases, the seed also" (Burbank, 1914a).

Burbank felt he did all the pioneering work, "Even though the fruit should not be of better quality than that which it supplants, the fact that the elimination of the stone permits an increased abundance of fruit, to say nothing of the value of the stoneless fruit itself, will offer an inducement that the progressive fruit raiser will find conclusive" (Burbank, 1914a). He did believe that he had not reached the plants limit, but that with more crosses and screening of seeds that he already had, he would find the perfect stoneless and seedless, high-quality plum (Burbank, 1914a). Mr. Burbank found that it was much easier to combine stoneless with poor-quality fruit than it was to obtain a high-quality fruit with a stone (Burbank, 1914b). We look at his results as a proof of concept in that he was able to obtain fruit that were completely stoneless and even seedless. This accomplishment suggests that it is possible to accomplish his goal but that it just needed more combinations to combine the required fruit quality traits with stoneless and even seedless. We have picked up Luther Burbank's goal of stoneless plums 100 years later. We believe the time is now ripe for accomplishing this because of the gain in knowledge and technology over the last century. When 'Miracle' and 'Conquest' were being released, Gregor Mendel's work was just being rediscovered and was not accepted by everyone, including Mr. Burbank, who still believed that acquired traits could be inherited (Stansfield, 2006). Today there is a better understanding of genetics and what influences traits. There are also the techniques of molecular biology, which allow us to introduce traits not in the germplasm as well as manipulate specific genes rather than recombine two genomes from the two different parents. For plum, there is now a FasTrack breeding system, which is able to shorten the generation cycle from 4 to 7 years to 1 year and the ability to breed year-round in the greenhouse rather than seasonally (Srinivasan et al., 2012). Using this new knowledge and techniques, we have begun a program to produce a high-quality fruit that has no stone (and in the future no seed). We are using breeding in much the manner of Mr. Burbank but with not only a goal of stoneless combined with quality fruit, but with understanding the genetics of the trait. We are using molecular biology to also understand the trait and identify genes that could be manipulated to obtain the stoneless phenotype. Lastly we are using our FasTrack system of breeding that reduces the generation time in plum to 1 year from seed to fruiting plant for both the breeding and the genetic engineering approaches.

## 21st CENTURY BREEDING

We chose as a goal for modern breeding a completely stoneless plum not only for the reason of no useful purpose that Mr. Burbank used (Burbank, 1914a), but for several additional reasons. First, the removal and detection of stone and stone fragments is a

large expense for the processed food industry; next, that the production of the energy-dense stone could be limiting to fruit production; and lastly, that the creation of a novel fruit could stimulate the public to increase consumption of a healthy food. The idea that a plum or any stone fruit could be consumed without having to carefully eat around the stone is very appealing. It also could allow for smaller fruit, even grape-sized, to be desired. Ideally the fruit would be completely pitless—no stone and no seed—but our focus is initially on the stone because that is a major focus of all *Prunus* processing industries.

The first thing we set out to do was to obtain some of Mr. Burbank's germplasm with which to study and proceed. It would be a lot quicker starting with the fruit quality of 'Conquest' and only a speck of a stone. Because Mr. Burbank's two plums were not successful, they appeared to have been lost from nursery catalogs and we were unable to locate them. Plums with the name of 'Stoneless' and 'Sans Noyau', one of which was a bush like the originally described 'Sans Noyau', were available from a number of sources including the USDA National Clonal Germplasm Repository, Davis, CA, the University of California, Davis breeding program, the USDA-ARS program at Parlier, CA, and from a private owner, Lon Rombough, who had a stoneless breeding program as a hobby (Fig. 4). These sources were budded to rootstocks and planted in the fields of USDA-ARS–Appalachian Fruit Research Station, Kearneysville, WV. The first trees that bloomed and fruited were the 'Stoneless' from ARS. After several seasons of fruiting, it was noted that in some years it had a nearly complete, albeit soft stone (Fig. 4E), and in others, it had almost no stone at all, only a speck at the funiculus (Fig. 4C). The degree of stone formed appeared to correlate with the temperature around pollination and early fruit development in that when it was warm after pollination, there was more stone tissue. This plum, in its best years, resembled the description of 'Conquest' because its size was similar if not larger than the French types and fruit quality was good (Fig. 4).

Next, we wanted to know something about the genetics of the trait so that we could potentially mark the gene(s) with molecular markers to aid in its incorporation into high-quality germplasm.

Mr. Burbank, unfortunately, did not keep good breeding records for the stoneless plum project so little has been known about the genetics of the stoneless trait—whether it is a single gene and whether it is a dominant gene. First, we found out that the parental 'Stoneless' was self-incompatible, that is, it could only be pollinated with pollen from other plums. Mr. Burbank had mentioned that 'Miracle' is an uneven fruit bearer and that may be because it needed an appropriate pollenizer (Burbank, 1914c). Our 'Stoneless' flowers were pollinated by a mixed collection of pollen from forced flowers from other plums as well as any plum trees that flowered in overlapping times. Fruit was harvested and seeds germinated. The first-generation seedlings were planted and began to flower and fruit 4 years later. There was considerable diversity in terms of leaf size and shape, tree size and shape, and fruit size and shape that may reflect the recent introduction of the small fruited, bush-like 'Sans Noyau' in the heritage of 'Stoneless'. After 6 or 7 years, less than half of the seedlings had fruited. Of those that had, ≈50% had a stone defect, either a partial stone or a stone thin enough to cut through with a knife (Fig. 5).

That 50% of the fruiting seedlings in the $F_1$ generation had a stone defect suggests that at least part of the trait of stonelessness is dominant and segregates as a single gene. It also suggests that the parent 'Stoneless' is not homozygous for the stoneless trait because half the $F_1$ fruiting seedlings had what appeared to have been a normal stone.

The future goal for breeding is to generate molecular markers for the putative single-dominant stoneless gene. To this end, the whole genome of 'Stoneless' and a number of normal stone cultivars have been sequenced. There are over 1,000,000 differences in single bases, small insertions and small deletions between 'Stoneless' and 'Improved French', a normal stone cultivar also resulting from Mr. Burbank's breeding program. These will be analyzed further to pick out appropriate polymorphisms to use as molecular markers to map the $F_1$ population, looking for linkages to the stoneless trait that can be used in furthering the breeding effort.

## MOLECULAR STUDIES

Armed with information about segregation and expression of genes, we wanted to further understand the stoneless trait. This knowledge could give us targets for looking at the molecular control of that process. A careful study of the growth and size of the different tissue layers, exocarp (skin), mesocarp (flesh), endocarp (stone), and seed tissue was undertaken to determine if the same amount of endocarp was formed in 'Stoneless' (Callahan et al., 2009). Using dry weight measurements and lignin stains with phloroglucinol, we determined that there were fewer endocarp cells in 'Stoneless' than in a normal stone cultivar. RNA levels for enzymes involved in the hardening of the stone were also measured and found to be similar in endocarp (the little that was made) for both 'Stoneless' and for the normal stone cultivar (Callahan et al., 2009). A finer level examination of the cells that form the mesocarp and the endocarp of 'Stoneless' and of a normal stone cultivar, Cacanska lepotica, showed that there are many fewer layers of endocarp cells being formed in the 'Stoneless' confirming the conclusion that 'Stoneless' has little or no stone because it has far fewer endocarp cells that differentiate into the stone (Fig. 6).

This study then gave us a target process to evaluate that of endocarp formation. RNA accumulation levels were measured in peach to look at gene expression associated with endocarp formation. From these studies it was found that there were specific genes involved with lignification that were expressed in endocarp and then only at specific times in development (Dardick et al., 2010). Genes responsible for formation of endocarp and the resulting lignification had been previously identified in *Arabidopsis* (Ferrandiz, 2002; Irish, 2010). These were also tested to see if a similar process took place in peach. Results showed that for a number of transcription factors, *SHATTERPROOF* (*SHP*), *SEEDSTICK* (*STK*), *FRUITFULL* (*FUL*) *ALCATRAZ* (*ALK*), and *INDEHISCENT* (*IND*), patterns of expression, particularly in endocarp tissue, were similar to that seen in *Arabidopsis* (Dardick et al., 2010). These genes were analyzed in a plum series of tissues from initial floral bud set

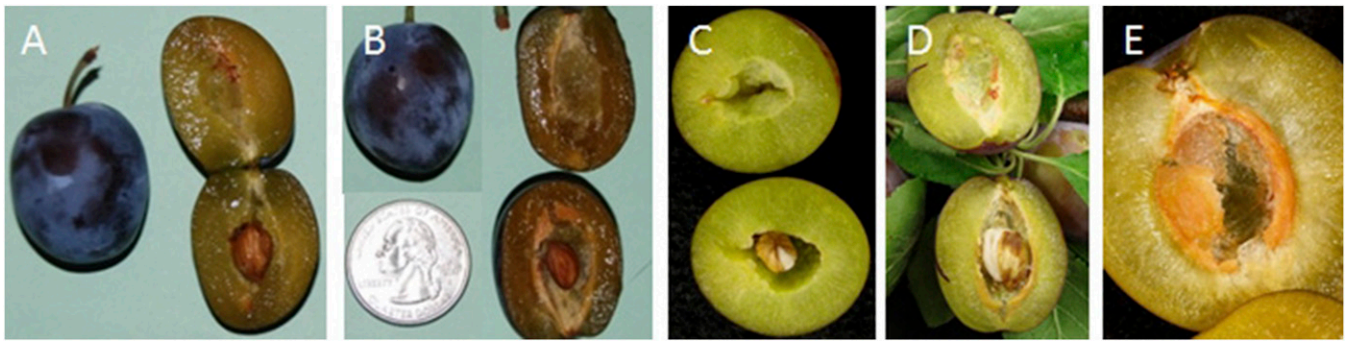


Fig. 4. Various sources of plums without stones: (**A**) fruit from 'Sans Noyau'; (**B**) fruits from 'Stoneless' from the USDA National Clonal Germplasm Repository (NCGR), Davis, CA. (**C**–**E**) 'Stoneless' from ARS in Parlier, CA, grown in Kearneysville, WV. Each picture represents a different year, demonstrating the variation in the amount of stone obtained depending on the environmental conditions around pollination.

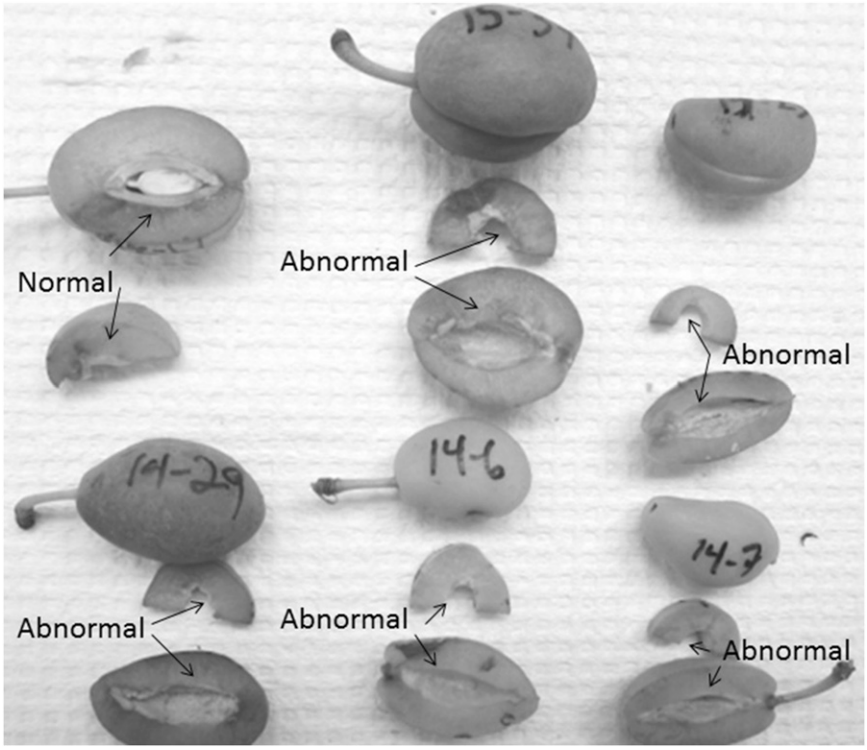


Fig. 5. Fruit derived from $F_1$ seedlings of 'Stoneless' grown in Kearneysville, WV. The fruit in the upper left corner has a complete stone formed (Normal), whereas the remaining five fruit have partial or almost no stone at all (Abnormal) demonstrating the dominance and variation of the stoneless trait.

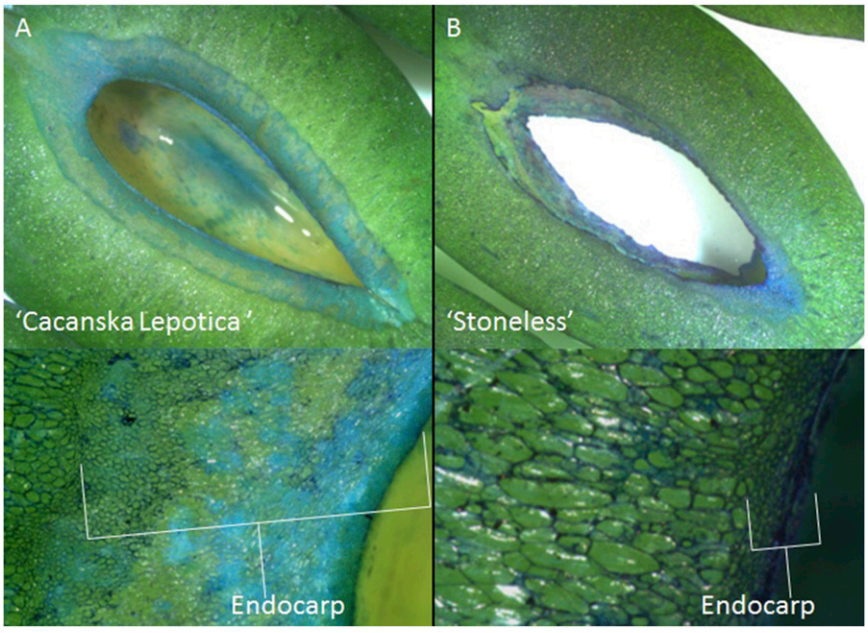


Fig. 6. Fruit cross-sections from a normal stone cultivar, Cacanska lepotica (**A**) and from 'Stoneless' (**B**) stained with 0.025% Toluidine blue O. The blue is the result of the interaction with lignin, which is beginning to be formed in endocarp cells surrounding the seed cavity. The number of cell layers forming the endocarp in 'Stoneless' is only a fraction of that seen in the normal stone cultivar Cacanska lepotica.

in early summer to May samples taken the next year, when the stone began to harden at ≈252 d after the first collection in July. The accumulation patterns of the RNAs again showed that plum fruit development was similar to that of *Arabidopsis* with flower and carpel transcription factors being expressed before and up to pollination and the endocarp forming transcription factors being expressed around the time of pollination to shortly afterward (Fig. 7).

From expression profiles of these genes it appears that the time of endocarp formation is within 10 d after pollination. This is similar to the time when endocarp formation in 'Stoneless' is affected by temperature, resulting in more or less stone being formed. RNAs were sampled in the flanking time, from 10 d before pollination to 8 d past pollination for whole carpels and fruitlets as well as ≈25 d past pollination for endocarp tissue for both 'Stoneless' and two normal stone cultivars. This comparison of RNA expression has found over 2000 genes being expressed significantly different between 'Stoneless' and normal stone cultivars (data not shown). These differences are either at one time in development or in the overall expression of the RNA higher or lower in the 'Stoneless' fruit. It is not clear yet which of these differences are important to stone development. These data will be further analyzed and compared first to understand the gene activity necessary for making endocarp and second, to identify specific genes or pathways associated with the differences in 'Stoneless'.

To genetically engineer a stoneless plum, we could prevent those endocarp cells from forming the hardened lignin. Modifications of lignin in this manner have been used to modify wood formation with goals for making low pulp wood or easier to extract biofuel (Boerjan et al., 2003). This could then be used to manipulate only those processes in an otherwise high-quality fruit cultivar to obtain a soft and potentially edible stone. Alternatively, we could change the formation of the endocarp cells that eventually lignify either by eliminating them like in the stoneless mutant of Mr. Burbank or changing them into mesocarp cells. This also has precedence in the literature because there is a natural mutation in oil palms that has no endocarp layer of cells as a result of the absence of a functional transcription factor *SEEDSTICK* (Singh et al., 2013). When one copy of the gene is present, a thin endocarp is formed and when two copies are present, a normal hardened endocarp is present. There are also mutants in the dehiscent fruit of *Arabidopsis* that eliminate or convert the endocarp to mesocarp tissue (Ferrandiz, 2002). These examples can also be considered as a proof of concept for the molecular aspect of making a stoneless plum through genetic engineering.

## ACCELERATING TIME TO FRUITING

The approaches to perfecting Mr. Burbank's stoneless tree all require time to evaluate because of the necessary wait for the transition of non-fruiting juvenile trees to mature trees that will fruit. Our first $F_1$ population has not completely fruited even after 7 years. One approach that Mr. Burbank used was to continually graft seedlings onto mature fruiting trees, reducing the time to flowering to only a few years or even in the next season. Not only did he speed up the process, but he was able to minimize the space needed by grafting many seedlings on a single tree (Fig. 8A). We have taken a different tack by using genetic engineering to create a germplasm source that flowers and fruits continuously in the greenhouse (Srinivasan et al., 2012). The gene *FLOWERING LOCUS T* from poplar was introduced into plum, which caused the transformed plums to flower and fruit within

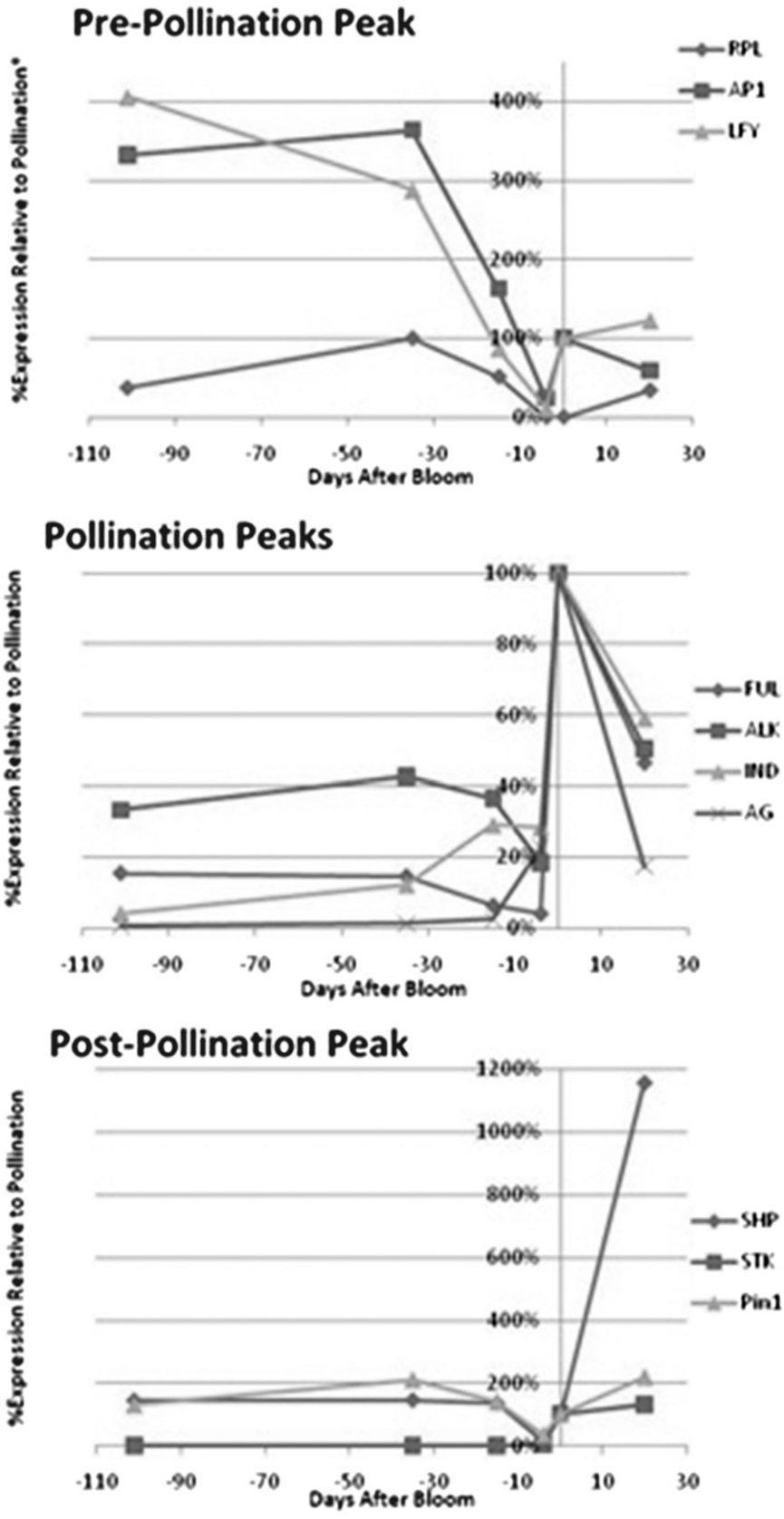


Fig. 7. Relative amounts of mRNA for transcription factors associated with floral bud formation, carpel formation, and endocarp formation during the time before (floral buds) and at pollination (carpels) as well as 20 d later in the endocarp tissue alone. There are three periods of peak expression: pre-pollination, pollination, and post-pollination. Ap1 = *APETELA1*; lfy = *LEAFY*; rpl1 = *REPLUMLESS*; FUL = *FRUITFUL*; ALC = *ALCATRAZ*; IND = *INDEHISCENT*; AG1 = *AGAMOUS*; shp = *SHATTERPROOF*; stk = *SEEDSTICK*; pin3 = Pin formed 3; NST = *NAC SECONDARY WALL THICKENING PROMOTING FACTOR1*. Results were obtained using quantitative polymerase chain reaction with triplicate samples and quantification by the ΔΔ Ct method using 26S RNA as the standard gene.

the first year. There is no juvenility period, no vernalization required, and no long-day, short-day effect resulting in the plums flowering all year-round in the greenhouse. We can then pollinate the early-flowering plums with 'Stoneless' pollen to move the system into a yearly breeding cycle. The early-flowering trait segregates as a single locus so half of the seedlings will flower early, and half (according to our genetics) will have the stoneless trait. The fourth of the seedlings that contain both can then be crossed with high-quality fruit cultivars to recombine in the fruit quality traits necessary. These crosses can be repeated as many times as necessary to obtain the necessary quality traits while still keeping only the stoneless and early-flowering seedlings. Then only those that are not early flowering (half stoneless and half normal) will be planted out and evaluated for combination of stoneless and high fruit quality.

## SEEDLESSNESS

In terms of convenience food, once the stone is gone, the seed itself presents a problem because it can be bitter as a result of the presence of varying amounts of amygdalin, which can be converted to cyanide on digestion (Bolarinwa et al., 2014). Future plans are to incorporate seedlessness to have a pitless fruit. Mr. Burbank mentioned that he was able to obtain pitless fruit, although not with the fruit qualities he desired (Burbank, 1914a) suggesting that it is possible to produce fruit that contain neither stone nor seed. The generation of seedlessness becomes another project with similar types of approaches as stonelessness, although in fact there are consumers who quite like the taste of the seed as is the case for this ice cream recipe (New York Times, 2000).

## CONCLUSION

Through standard hybridizations, Luther Burbank created a nearly stoneless plum with high fruit quality from a bush-like plum bearing fruit containing a partial stone with bad flavors and of very small size. This was an amazing feat, especially for the time because there was little understanding of the potential complexities of genetics (Stansfield, 2006). Mr. Burbank was able to coax a nearly complete stoneless phenotype from this partial stone and obtain good fruit size and flavors, traits that usually revert to the more wild-type phenotype of small and bad flavors. We have obtained what are most likely remnants of this breeding feat and have begun to implement both a traditional and molecular breeding program to ultimately obtain Mr. Burbank's goal of a completely stoneless plum with the high fruit quality traits. Having seen many seasons of fruit on the parent 'Stoneless' and now fruit on the first $F_1$ generation, this has become an even more incredulous accomplishment. The stoneless trait appears to be dominant, which certainly makes it easier to follow, but the degree of stoneless varies in the


Fig. 8. Both pictures represent techniques to accelerate the juvenility period of plums to allow fruiting sooner. (**A**) Picture of Burbank's "Many Plums on One Tree. ….Several hundred cultivars may be found growing from a single trunk" (Burbank, 1914a). (**B**) An early-flowering plum from the FasTrack system that is 1 year old and is fruiting and flowering in the greenhouse.

$F_1$ population making it difficult to score and varies by year. It is not clear if this is an effect of different backgrounds or modifiers of the stoneless trait. We also found out that the trait appears to be environmentally affected in its expression such that some years, it is not stoneless at all. For Mr. Burbank to follow that would have been extremely difficult. It also may be part of the reason his releases were not popular in that they may not have been stoneless every year depending on the climate.

Mr. Burbank had been known to have a keen eye in the selection of parents and progeny such as the breeding of the blue poppy from red poppies (Burbank, 1914d). We do not have that same eye; hence, we are incorporating a 21st century technique of molecular markers to identify traits invisible in the seedlings. To this end, the genome of 'Stoneless' has been sequenced to identify polymorphisms to use for those markers.

To speed up the breeding cycle, Mr. Burbank grafted seedlings on mature trees to get them to fruit faster. We have used a technology that uses a genetically engineered early and continually flowering plum. This will allow us to advance the number of breeding cycles for leaving behind possible negative traits, which Mr. Burbank said was harder to do than to obtain completely stoneless fruit. In our last approach to obtaining Mr. Burbank's goal, we are going totally 21st century in identifying targets at the molecular level to manipulate. Although we have not advanced the generation of Burbank's stoneless plum, we have now developed tools with which to attempt to improve on his amazing feat of a stoneless plum.

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# Luther Burbank's Contributions to Walnuts

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*Additional index words. Juglans hindsii*, *Juglans nigra*, *Juglans regia*, 'Paradox' walnut, walnut rootstock

***Abstract*. Luther Burbank began making controlled crosses between walnut species in the late 19th century after hearing about a "supposed natural European hybrid walnut." He crossed *Juglans hindsii* (northern California black walnut) × *J. regia* (Persian walnut) and produced progeny that he named 'Paradox' because of its extremely fast growth and other "anomalies." He also crossed two American species, *J. hindsii* × *J. nigra* (eastern black walnut), producing 'Royal' walnut progeny that were fast-growing and prolific nut producers. A third interspecific hybrid was a cross between *J. ailantifolia* (Japanese walnut) × *J. regia* that resulted in extremely vigorous progeny but was not named. He observed segregation in the $F_2$ populations and described giants and dwarfs as reversions to ancestral forms. Luther Burbank also made selections for walnut scion cultivars and was especially interested in thin-shelled nuts. He collected seeds from a *J. regia* growing in San Francisco because it produced regularly and had very high-quality nuts with relatively thin but poorly sealed shells. He selected one of its seedlings as 'Santa Rosa Soft-Shell' and described it as bearing large crops of nuts that were nearly white with thin shells and delicious white meat. Burbank's contributions to the walnut industry endure to this day, especially through the widespread use of seedling and clonal 'Paradox' walnut rootstocks.**

Luther Burbank's field notes published in a 12-volume monographic series (Whitson et al., 1914, 1915) covers 40 years of his plant breeding work. Based on the changes in Burbank's writings about Mendelian genetics in the walnut chapters in Volumes 2 and 11, the notes were likely published consecutively. He wrote that the paper by Mendel (1865) was forgotten for over 30 years (Whitson et al., 1914, 1915). By that time he had been breeding plants in California for more than 20 years. His understanding of Mendelian concepts, although murky, developed somewhat and he ultimately found it useful to explain the performance of his $F_1$ and $F_2$ generations.

In his field notes about walnuts published in 1914, Burbank showed that he was aware of Mendel's findings and mentioned "prepotency or dominance" when describing traits of one parent manifesting itself over those of the other in the walnut $F_1$ interspecific hybrids. When describing the segregation in the $F_2$ generations, he did not use the term "segregation," rather he called this a "mixture of racial strains."

After describing dwarf walnuts in $F_2$ populations generated from *J. hindsii* × *J. regia* (or *J. hindsii* × *J. nigra*) $F_1$ hybrids, Burbank mentioned that Mendel would call them "pure recessives" or homozygous. He followed this with: "The reader may or may not feel that the new terminology adds to our comprehension of the phenomena" (Whitson et al., 1914, 1915, p. 160). However, on page 150, Luther Burbank described the "dwarfs" in the $F_2$ generation as a "reversion to dwarfed ancestral strains." For the "giants" in the $F_1$ and $F_2$ generations, he wrote: "These, then are the remote ancestors ("colossal plants of the Carboniferous Era") that may be invoked in explanation of the rapid growth and relatively gigantic stature of our hybrid walnuts" (p. 164).

By the time that he wrote the field notes published in Vol. 11 of the same series (Whitson et al., 1914, 1915), Luther Burbank was applying Mendelian terminology to his walnut populations. At this time, he was using the term "segregation" and wrote: "It will be noted also that the distribution of these characters in the second generation was essentially that which has come to be familiar everywhere within recent years as the typical distribution of characters among second generation hybrids in what is now known as Mendelian heredity" (Whitson et al., 1914, 1915, p. 195).

The segregation that he observed in the $F_2$ generation from 'Paradox' was first described in his 1898 supplementary catalog (Whitson et al., 1914, 1915). In this catalog, he divided the offspring into three groups: one-third a new type of Persian walnut with broad leaflets, one-third a new type of California black walnut, and the remaining one-third had combined traits of *J. hindsii* and *J. regia*. Burbank wrote that these observations of segregation were obviously made before the catalog was published in 1898 "at a time, therefore, when no one living had the remotest knowledge of the discovery made by Mendel more than thirty years before" (Whitson et al., 1914, 1915, p. 196). At this point, he seemed defensive: "…the fact being quite overlooked that the essential principles involved had been discovered by me quite independently; exploited by me in connection with many hundreds of species; given publication by me prior to the rediscovery of Mendel's forgotten paper: championed by me against the opposition of all the leading authorities of the world; and that therefore the aspect of heredity in question might with full propriety have been named "Burbankian" instead of "Mendelian," were it not that Mendel's discovery had priority because it was published so long ago as 1863, whereas my independent discovery of the principle was not made until almost twenty years later. Even at that, however, I had had full twenty years priority over any one else except Mendel in the recognition of the principle" (Whitson et al., 1914, 1915, p. 199).

However, Burbank still believed that there was a "misapprehension as to the real significance of 'unit characters', and who, misguided by a narrow range of experiments, and lacking the breadth of view that comes with wider experience, have supposed that all heritable characters might be classified as fixed and unvarying entities that are transmitted in accordance with the Mendelian formula" (Whitson et al., 1914, 1915, p. 200). In this, he seems to be making a point about polygenic traits "that do not Mendelize in any tangible or demonstrable way" (p. 200). He also thought that Mendel's "unit characters" were composed of "subordinated characters" and that new "unit characters" appear at various times and that the old "unit characters" would then no longer follow Mendelian heredity. To follow this, he wrote: "So Darwinian heredity, which recognizes the heritability of whole coteries of characters that are too profoundly fixed to Mendelize, is again receiving recognition" (p. 202).

## INTERSPECIFIC HYBRID WALNUTS

"I had heard of a supposed natural European hybrid walnut, and I determined to make the experiment of fertilizing the flowers of the California species with pollen from the Persian" (Whitson et al., 1914, 1915,

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p. 138). The California walnut species has since been identified as *Juglans hindsii* (Lucker, 1996). Thus was born the idea leading to crossing *J. hindsii* with both *J. regia* and *J. nigra*. However, it was controversial when he first made the crosses.

Burbank stated that when his *New Creation in Fruits and Flowers* catalog was published in June 1893, the hybrid walnuts were 5 or 6 years old and the 'Royal' had borne fruit, but not the 'Paradox' (Whitson et al., 1914, 1915). Allowing time for stratification, the crosses were therefore made in 1886 or 1887. Howard (1945, p. 39) wrote that Burbank stated in this same catalog: "This hybrid originated in 1888 from a cross made the year before" corroborating the 1887 date. Therefore, it would appear clear when Burbank first hybridized walnuts. However, Howard (1945) wrote that the walnut interspecific crosses were made earlier, from 1878 to 1885, and that his first hybrid was in 1878 and was between *J. hindsii* × *J. regia* and the next year the first hybrid was obtained from *J. hindsii* × *J. nigra*. He further added that Burbank's mention of 1888 in his 1893 *New Creations in Fruits and Flowers* catalog was a printing error.

Dr. George H. Shull, a geneticist from Princeton University, spent from 1906 to 1911 in Santa Rosa, CA, as a representative of the Carnegie Institution of Washington, which had bestowed a large grant to Burbank. Shull's duty was to control the activities of Burbank and collect and record all of the information that he could gather on previous achievements. This was warranted because although Burbank's creations were valuable and famous, his notes were rudimentary (Janick, 2015) and deserved better documentation.

In a letter dated May 12, 1943, Shull quoted from his unpublished report on Burbank's activities: "In 1877 Mr. Burbank applied pollen of the Persian to a tree of California black; the nuts were stratified and planted (1878) with the result that among a very large number of obviously pure California blacks, "some 5 or 6" were plainly hybrids. There was some variation in size and vigor, and only the finest and largest one was retained for propagation, and this was the first Paradox. Two of the other hybrid seedlings were sent to the Sebastopol grounds where they served as stocks for numerous Persian grafts" (Howard, 1945, p. 40). Topworked walnuts can still be identified at the Gold Ridge Luther Burbank Experiment Farm (Fig. 1).

With such a contradiction among the dates reported by Burbank, Howard, and Shull, it is difficult to determine the exact timing of his first interspecific walnuts. One would think that Burbank would be correct, but because of his fractured notes, Dr. Shull may indeed have the real date. This seems corroborated by the sign (Fig. 2, inset) at the Gold Ridge Luther Burbank Experiment Farm in Sebastopol, CA, which states that the 'Royal' tree there was planted in 1885 meaning that the cross that resulted in this $F_1$ tree was made before or during 1884, before the 1887–88 dates reported by Luther Burbank.

## 'PARADOX' WALNUT

Burbank found that seedlings of a *J. hindsii* × *J. regia* cross were much more vigorous than seedlings of either species (Whitson et al., 1914, 1915; Fig. 3) and that this very rapid growth rate was sustained from year to year. For a walnut tree to grow to 18.3 m (60 ft) in 16 years was truly extraordinary because hardwood trees were known to grow slowly. A fast-growing hardwood was a paradox, and indeed this and the fact that the hybrid manifests several traits of one parent over the other, rather than a blending of traits, was why Burbank named his hybrid by this name.

'Paradox' is a shy producer of thick, hard nuts that resemble rough-textured Persian walnuts. Burbank was able to germinate enough of the few seeds that it produced to observe giants and dwarfs in the $F_2$ generation (Whitson et al., 1914, 1915)

Another anomaly of Burbank's 'Paradox' walnut is its very long leaves, some reaching 1 m (3 ft) long with an "apple-like fragrance" (Whitson et al., 1914, 1915). As first observed by Burbank, the leaves on 'Paradox' trees are similar to those on Persian walnut as is the bark. Burbank wrote about using 'Paradox' seedlings for rapid production of fine hardwood that could be used for cabinetry (Whitson et al., 1914, 1915), but this never caught on.

By 1912, Smith et al. (1912) had tested seedling 'Paradox' as walnut rootstocks. They were disappointed with the results of grafting onto $F_2$ 'Paradox' but were pleased with the "unusual" vigor of the walnuts grafted onto $F_1$ 'Paradox' rootstocks. They discussed the higher cost and care of producing the $F_1$ 'Paradox' seedling rootstocks compared with black walnut rootstocks or Persian walnut on its own roots. They and other pomologists of the time were testing 'Paradox' as a rootstock and that was the beginning of the use of what was to become the most popular rootstock in California. This is because of 'Paradox' vigor, some *Phytophthora* crown and root rot resistance, and some resistance to root lesion nematode (Fig. 4). The majority are $F_1$ hybrid seedlings of *J. hindsii* × *J. regia*. *J. hindsii* is the female parent used by modern nurseries for production of seedling 'Paradox' rootstock (Fig. 5). Seedlings that germinate from the stratified black walnuts are a mixture of 'Paradox' and pure *J. hindsii* that are easy

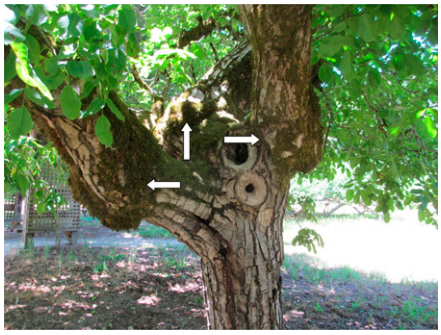

Fig. 1. Topworked walnut at the Gold Ridge Luther Burbank Experiment Farm. Luther Burbank topworked his walnuts to accommodate more *J. regia* nut cultivars for his crosses on fewer trees. A photograph of his much younger topworked walnuts appears in Whitson et al. (1914, 1915, p. 161).


Fig. 2. 'Royal' walnut tree on the grounds of the Gold Ridge Luther Burbank Experiment Farm in Sebastopol, CA, that was 128 years old when photographed in 2013. For scale, the fence is 6 feet (nearly 2 m) tall. Inset shows sign directing visitors to the 'Royal' Walnut tree with planting date.

Fig. 3. 'Paradox' walnut trees on the grounds of the Luther Burbank Home & Gardens, Santa Rosa, CA. When this photograph was taken in 2013, the older tree on the left was 99 years old its original top was no longer present. The 'Paradox' tree on the right (arrow) was ≈20 years old.

Fig. 4. A walnut orchard grafted onto 'Paradox' rootstock. The 'Paradox' manifests the dominant smooth bark trait from its Persian walnut paternal parent, making the graft unions (arrows) not as obvious as when grafted onto black walnut rootstock.

Fig. 5. The right scaffold of this tree was grafted with *J. hindsii,* whereas the left scaffold is *J. regia* in this commercial 'Paradox' seed orchard. Black walnut is used as the female parent to facilitate rouging nonhybrid walnuts from 'Paradox' seedlings in the nursery bed. It is necessary to have a few Persian walnuts in the seed orchard as pollen sources.

Fig. 6. This closeup of the 'Royal' tree in Fig. 2A shows its heavy production of nuts. This tree still produces nearly 907 kg (1 ton) of nuts each year (Wiesler, 2012).

to distinguish by leaf texture. If *J. regia* were used as the seed parent, it would be more difficult to visually separate from and rogue non-'Paradox' seedlings.

Three clonal 'Paradox' walnut rootstocks are available today through micropropagation. Two of the clonal rootstocks are traditional 'Paradox' $F_1$ hybrids of *J. hindsii* × *J. regia*: 'Vlach' imparts vigor to the scion and 'VX211' imparts vigor and lesion nematode tolerance. 'RX1' is a new type of 'Paradox' because it is an $F_1$ hybrid between *J. microcarpa* (Texas black walnut) and *J. regia* that has resistance to *Phytophthora*. 'Paradox' rootstock development is now focused on creating various *Juglans* interspecific hybrids to incorporate increased resistance to soilborne pathogens and adaptability to various soil conditions. Today superior rootstock genotypes can be cloned using micropropagation, ensuring a more uniform phenotype for the grower.

## 'ROYAL' WALNUT

At around the same time that Burbank created 'Paradox' walnut, he also made the *J. hindsii* × *J. nigra* cross that resulted in the 'Royal' walnut (Whitson et al., 1914, 1915; Fig. 2A). Similar to the 'Paradox' hybrid, this $F_1$ hybrid grew extremely rapidly and the $F_2$ generation segregated, producing both giants and dwarfs.

A striking difference between 'Royal' and 'Paradox' walnuts is that 'Royal' produces large seed crops. Burbank wrote: "At sixteen years of age one of these trees produced a harvest of nuts that filled twenty apple boxes, each about two feet long by one foot in width and depth. In one year I sold more than a thousand dollars worth of nuts from a single tree" (Whitson et al., 1914, 1915, p. 146). The 'Royal' tree, planted in 1885, continues to produce large seed crops at Gold Ridge Luther Burbank Experiment Farm in Sebastopol, CA (Figs. 2 and 6). The nuts are similar to black walnuts but bigger. Trees in the $F_2$ generation may not be good producers of nuts (Whitson et al., 1914, 1915).

Although California walnuts are not grafted onto 'Royal' rootstocks today, Burbank was a proponent of such use. He reported that Persian walnut grafted onto 'Royal' produced much larger nut crops and that blight was less of a problem when compared with Persian walnut on its own roots (Whitson et al., 1914, 1915). Luther Burbank recommended planting seeds of the 'Royal' hybrid and then selecting the strongest growers from the segregating $F_2$ generation. He then recommended allowing the rootstocks to grow for 4 to 5 years to a trunk caliper of 3 to 6 inches (7.5 to 15 cm) before grafting. Today, using modern nursery practices, $F_1$ 'Paradox' seedlings are grafted within the first 2 years onto trees with a 1-inch (2.5-cm) caliper.

## JAPANESE WALNUT HYBRIDS

Burbank crossed Japanese walnut (*J. Sieboldii*, now *J. ailantifolia*) with *J. regia*. Similar to his other walnut hybrids, this one grew rapidly (Whitson et al., 1914, 1915). It produced few nuts and the nuts were intermediate between the parents. The leaves were much larger and more pubescent than either parent and the bark was white. The nuts were very hard and the great-tasting meat was difficult to extract from the shell. This hybrid is no longer grown.

## SCION BREEDING

Similar to walnut breeders today, Luther Burbank selected for "early and abundant bearing, whiteness and palatability of meat, and absence of tannin—it being tannin which gives the brown color and bitter taste to the older and ordinary walnuts" (Whitson et al., 1914, 1915, p. 37). However, he also selected for thin-shelled walnuts, also known as soft shells or paper shells. He pointed out that shells of Persian walnut are already thin-shelled compared with the native black walnuts of North America, but sought to improve on this trait.

This included breeding paper-shelled walnuts that can be cracked with bare fingers, making them easy to eat. However, because of poor shell strength, they do not handle or ship well. Burbank developed a walnut that had such a thin shell that birds could easily peck through it (Whitson et al., 1914, 1915). He also mentioned a "nut that had a mere rim of shell, being thus comparable to the stoneless plum" (Whitson et al., 1914, 1915, p. 36). Because of predation and shipping problems, he returned to a somewhat thicker shell in his breeding.

He selected and named the 'Santa Rosa Soft-Shell' walnut. Mr. Alfred Wright told Luther Burbank about the parent tree that was growing in San Francisco (Whitson et al., 1914, 1915). Burbank said that the tree produced nuts of extremely high quality but with poor suture closure, leading to storage problems compared with nuts with sealed sutures. He collected nuts from the original tree shortly before it was destroyed to provide room for a street. It was from these seedlings that he selected 'Santa Rosa Soft-Shell.' This seedling was selected for cloning because although the nuts are medium size, they are ready for harvest ≈3 weeks earlier than other walnuts grown at the time in California (Whitson et al., 1914, 1915). The taste was said to be delicious and the meat of the nut white. He especially liked that it produced large crops, but it could be damaged by late spring frosts. This cultivar is no longer grown.

## CONCLUSION

Although Luther Burbank thought that 'Paradox' walnut was best grown for its wood, today it is the most used walnut rootstock in California. The use of the $F_1$ hybrids as rootstocks bypassed the variation and additional selection required of the $F_2$ generation. Therefore, nurseries have orchards, primarily of *J. hindsii* with a few *J. regia* interplanted or grafted onto the black walnuts. The black walnut seeds are collected, sown in nurseries, and the black walnuts are rogued, leaving the 'Paradox' to be used as rootstock. Micropropagation has allowed for commercial production of three clonal 'Paradox' rootstocks moving 'Paradox' in a direction unimagined by Luther Burbank. 'Royal' and Japanese × Persian walnut hybrids are not grown commercially. Although Burbank selected for many of the same traits as modern walnut breeding programs, the 'Santa Rosa Soft-Shell' has been replaced with improved walnut cultivars.

Burbank's contributions to walnuts are substantial and long-lasting. Walnut rootstock breeders especially stand squarely on his shoulders as they incorporate genes from walnut wild relatives into interspecific hybrids and select for tolerance or resistance to various soil conditions, including pathogens.

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# Luther Burbank's Best Berries

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*Additional index words.* blackberries, genetic resources, *Fragaria*, germplasm, raspberries, *Rubus*, small fruit, grape, blueberry, *Solanum*

***Abstract.*** **Luther Burbank, the quintessential nurseryman of the early 20th century, remarked that small fruit was the "Cinderella of the pomological family." He stated that although tree fruits had been improved to the point of an almost uncountable number of cultivars, it was the time and responsibility of his generation and those to follow to develop the small fruit for human consumption. Burbank had a penchant for detecting potential qualities of unusual plants and his broad association with plant explorers at the U.S. Department of Agriculture and elsewhere allowed him to examine diverse wild berry species. He obtained seeds of many small fruit species from throughout the world. He made wide crosses within and between these genera and species. Burbank selected and named many cultivars to be introduced through his nursery and elsewhere. He named and released ≈40 blackberries, raspberries (*Rubus* L.), and strawberries (*Fragaria* L.); four grapes (*Vitis* L.); and a hybrid *Solanum* that he named 'Sunberry'. He sometimes exaggerated their descriptions for promotion or public recognition. For example, *Rubus* ×*loganobaccus* 'Phenomenal' was, he stated, "far superior in size, quality, color, and productivity…" to 'Loganberry'. Unfortunately, this cultivar was not a commercial success. Burbank made a few crosses and sold what he considered to be improved species, e.g., 'Himalaya Giant' blackberry (*R. armeniacus*). He created new common names for foreign species, e.g., balloon berry (*R. illecebrosus*) and Mayberry (*R. palmatus*), to better market them. However, his amazingly keen observations of thornlessness, pigment diversity, and recognition of repeat flowering and fruiting in blackberries, raspberries, and strawberries, were insightful of the needs of future industry. Burbank was a disciple of Darwin and his theory of natural selection. Burbank's classic breeding approach, to make wide crosses, produce large numbers of hybrid seedlings, choose significant seedlings with his traits of choice, and backcross to the desired parent for several generations, was successful, although he did not know of ploidy or gene recombination. Unfortunately, the 'Himalaya blackberry', now ubiquitous in hedgerows and fields throughout the Pacific Northwest in the United States, is designated as a federal noxious weed. Although not presently in commercial production, three of his *Rubus* cultivars ('Burbank Thornless', 'Snowbank', and 'Phenomenal') are preserved in the U.S. Department of Agriculture, National Clonal Germplasm Repository, in Corvallis, OR.**

> *"The successful plant developer must be able to look beneath the surface of his [her] plants to discover and utilize the underlying harmonies."*—Luther Burbank (Burbank, 1914)

Luther Burbank (7 Mar. 1849 to 11 Apr. 1926) was an amazingly charismatic person with a reputation as the plant "wizard." He referred to himself as a "plant inventor," the equivalent in horticulture to what his friends and colleagues, Thomas Edison and Henry Ford, were in engineering.

Burbank was a focused plant breeder. He had a combination of rough-cut, dirt-under-the-fingernails knowledge of a horticulturist and the sharp eyes of a plant breeder who could instantly delineate the smallest difference in the color of a petal or width of a stem. He was so vigorous and energetic in selecting plants that his helpers could hardly keep up (Howard, 1945). His business strategy was to produce novel plants and sell them outright to plant nursery brokers such as John Lewis Childs and others. This allowed him to continue his favorite work: breeding and selection.

Although long-term recognition came from significant cultivar releases in many crops, he had a fondness for berries, calling them the "Cinderella of the pomological family." He made many forays into the development of berries from wild species from around the world. He educated and encouraged other breeders and nursery people to improve small fruits (Burbank, 1914). Burbank loved children and welcomed the opportunity to teach them about nature and the plant world. The breeding narratives of his 12-volume book, "*Luther Burbank: His Methods and Discoveries and Their Practical Application*" (Burbank, 1914), are intermingled with tales about and for children. He bred plants for the future of humankind.

Burbank was inspired by Darwin and became a literal disciple of his theory of variation of species and natural selection. Burbank realized that plants in nature were not fixed and could be manipulated by humans for improvement and use. Burbank's breeding protocol was to make wide crosses, including unusual intergeneric ones such as apples with blackberries or strawberries with raspberries. Next he produced millions of hybrid seedlings. With such great numbers of offspring, he then selected only a few having his traits of choice and discarded the remainder. He had only 20 acres of land including both his Santa Rosa and Sebastopol, CA, farms (Smith, 2009), so if seedlings did not perform, they were quickly pulled and burned. He backcrossed seedlings with desired traits to the parent for several generations, focused on his specific breeding objectives, and culling the rest (Howard, 1945). This recurrent selection proved successful with a broad array of plant genera, although Burbank had no clear knowledge of chromosomes, ploidy, or gene recombination. Not understanding genetics or mutation, he denied Mendel's theory throughout his career, although his results were supportive.

This article has two objectives. The first is to broadly summarize Burbank's work on small fruit and berry crops. The second is to emphasize his efforts on *Rubus* including his development of thornlessness, pigment mutation, and interspecific crosses. In addition, Burbank's efforts will be integrated into current work on small fruit and berry breeding and genetics.

## BURBANK'S BERRIES

Howard (1945) described Burbank's life work and compiled a summary of his releases.

Approximately 60 berry crop releases are noted (Table 1). In this article, we take a broad approach of this to include not only the

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Table 1. Number of named small fruit and berry cultivars, grouped by crop type, released by Luther Burbank (tabulated from Howard, 1945).

| Crop | Number | Crop | Number |
|---|---|---|---|
| Blackberries | 16 | Buffaloberry | 1 |
| Raspberries | 13 | Cape Gooseberry | 1 |
| Strawberries | 10 | Elderberry | 1 |
| Dewberries | 4 | Gooseberry | 1 |
| Grapes | 4 | Juneberry | 1 |
| Sunberry | 3 | Mulberry | 1 |
| Blueberries | 2 | Salmonberry | 1 |

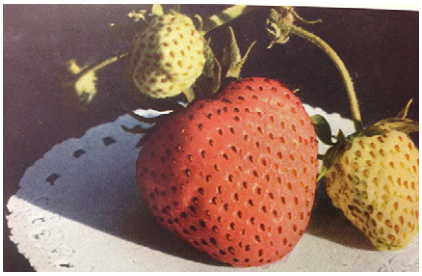

Fig. 1. Heart-shaped fruit of an unnamed strawberry cultivar. Image adapted from that in Burbank (1914).

horticultural small fruits, but a few botanical "berries" that Burbank worked on as well. Although Burbank mentions many additional species importations and crosses (Burbank, 1914), he did not maintain detailed written notes. When asked about pedigrees, he could verbally describe the parents because he recognized species and hybrids through traits. He did not keep a written log of his crosses nor were his crosses controlled in the sense of exclusion of unwanted pollen. He did not care as much about ensuring the occurrence of a specific cross, so he did not use cages; rather, he kept focused on the outcome of his breeding objectives. He selected one plant that matched his vision, with the right combination of traits, out of thousands of undesirable siblings.

His friend, U.S. Department of Agriculture (USDA) plant explorer David Fairchild, as well as many other contacts throughout the world, provided him with seeds of unusual small fruits (Burbank, 1914; Fairchild, 1944). He imported particularly unusual species from all around the world so that diversity was as broad as possible. He then performed intergeneric, interspecific, or other unusual crosses to obtain novel berries never seen before. The many sterile and undesirable seedlings were discarded at the earliest opportunity so that those of the next cross could take their place.

**Strawberry**

Burbank appreciated the diversity of strawberry species. He was unaware of ploidy levels, but obtained wild species from the United States and elsewhere to make broad crosses. Most of these crosses were not attempted anywhere before his efforts. Unfortunately, many produced non-fertile offspring. For example, he crossed *Duchesnea indica*, a plant with a similar appearance to strawberry but with yellow petals and inedible red fruits, with the common cultivated strawberry. No viable offspring were produced (Howard, 1945). Others have confirmed these results (Hughes and Janick, 1974).

Fig. 2. 'Sunberry' fruit. Image adapted from that in Burbank (1914).

Burbank discussed nature with a group of school children. He talked about seeds being the link between successive generations. To bring the illustration home, Burbank said that the seed is the very "heart" of the plant (Fig. 1). One youngster replied, "Then the strawberry wears its heart on its sleeve." Burbank liked that analogy. He remarked in his book (1914) that the ultimate of strawberry perfection would be seedlessness. He recognized that many clonally propagated crops such as banana, horseradish, pineapple, and even potatoes to an extent have eliminated or reduced seed production. Strawberries commonly propagate vegetatively by runners so that Burbank had no doubt that strawberry seeds could be eliminated through breeding once the perfect strawberry had been produced (Burbank, 1914).

Burbank made many wide crosses with strawberries. He crossed Chilean strawberries (species or forma unnoted) with the major strawberry cultivars of his day: 'Brandywine', 'Monarch', and 'Marshall'. He raised more than 500,000 strawberry seedlings in 40 years (Burbank, 1914). Although there were many seedlings of "a high order," each had imperfections that could be improved. Burbank discussed broadening the gene pool for the cultivated strawberry, defining a task continued by today's scientists and breeders. In fact, Hancock et al. (2010) are "reconstituting" the strawberry genome with wild collections from North and South America.

One of Burbank's breeding objectives was to get "a strawberry to bear the year around." Remontancy, or continuous blooming and fruiting, was one of his breeding objectives for strawberries. Regrettably, Burbank's explanation of continuous bloom in strawberry was conjecture rather than understanding. He described how the new hybrid strawberry combined ancestral strains from two hemispheres, North and South America. Thus, to him this was an illustration of the tendency for parents from both hemispheres to contribute summer bearing habit to produce a perpetual bearing trait in the seedlings (Burbank, 1914). Burbank did not live to see the development of remontant strawberries, but modern day-neutral cultivars that bloom throughout the growing season are a fulfillment of Burbank's vision and have proven invaluable to the industry. Burbank named 10 strawberry cultivars, although none have survived (Howard, 1945).

**Grape**

Burbank's efforts with *Vitis* species focused on table grape development. Burbank (1914) estimated that over 40 years he probably raised ≈100,000 seedlings from crossing the best table grape cultivars. He hybridized many genotypes including European and American and cultivated and wild. He also imported many wild species from Syria, Mexico, Australia, China, and Japan. Burbank released five grapes: four grape cultivars and one species introduction (Howard, 1945). Several were seedlings of 'Pierce', a sport of 'Isabella'. Burbank's goals were productivity, fruit size, pigments (including white, yellow, red, and purplish black), flavor, season, and seedlessness.

**Blueberry**

Burbank did not release any highbush blueberries (*Vaccinium corymbosum*); that achievement is credited to Dr. Frederick Coville, USDA plant breeder in Beltsville, MD. Burbank brought highbush blueberry to California and planted it in his yard. Burbank recognized that highbush blueberry could be selected for warmer climates and predicted that blueberry could be grown for production in California. Burbank brought in a species of blueberry from South Africa (likely to have been *Vaccinium exul*) and crossed it with the "coastal blueberry" (likely to be *V. ovatum*); both of these are diploid species. No hybrid cultivar survives today from this cross. Blueberries have now achieved major world status and are an important crop in California with a value of over $133 million.

**Sunberry**

Burbank was the subject of many controversies during and after his lifetime, but one of his creations, the 'Sunberry', or 'Wonderberry', caused particular disagreements. Although Heiser (1987) stated that Burbank himself gave different accounts of the origin of his 'Sunberry', Burbank claimed in his book, volume 6 (1914), that his 'Sunberry' (Fig. 2) was a product of more than 20 years

of crosses. Burbank described that he crossed the great African stubble-berry, *Solanum guinense*, and the little downy nightshade *S. villosum* many times. In 1905, a few seedlings from this cross that sprouted in the greenhouse were different. As the plants came to maturity, one seedling flowered and fruited quite abundantly (Burbank, 1914). The fruit was intermediate in size between the two parents but the quality was quite different from either. Rather than the vile-tasting fruit of *S. guinense* or the insipid fruit of the *S. villosum*, Burbank selected fruit from the offspring that excelled in "profusion, size, and flavor." He took the seed and multiplied them rapidly to produce two crops in a single season. He checked that the traits that he desired were "fixed" and gave the name 'Sunberry' to what he said was the $F_2$ of *Solanum villosum* × *S. guineense*.

Burbank was not in control of the cultivar after he sold it to John Lewis Childs. Childs changed the name to 'Wonderberry' and marketed it with superlatives including: "Luther Burbank's greatest and newest production. Fruit blue-black like an enormous rich blueberry. Unsurpassed for eating...in any form. The greatest garden fruit ever introduced.... Easiest plant in the world to grow, succeeding anywhere and yielding great masses of rich fruit." Because some customers interpreted the plant as being a selection of the common nightshade, *Solanum nigrum*, with inedible or even poisonous fruit, an anti-'Wonderberry' movement was started. Herbert W. Collingwood, president and editor of *The Rural New Yorker,* was vocal in the movement. Heiser (1987) describes the controversy in detail, including how Burbank accused Childs of distributing the common "huckleberry" (nightshade) as the 'Wonderberry'.

Heiser describes how Jorge Scoria, a graduate student at Indiana University, replicated the cross that Burbank had described and said that he had made. Now we know that *Solanum guineense* is hexaploid ($2n = 6x = 72$), whereas *Solanum villosum* is tetraploid ($2n = 3x = 48$). Because of the chromosome inequality, a sterile pentaploid offspring might be expected; however, Scoria observed no offspring. He considered that Burbank may have misidentified *S. villosum.* Heiser noted that Burbank's written description of *S. villosum* also did not match the species. Burbank may have used *S. sarrachoides*, a diploid ($2n = 2x = 12$) South American species that had been in California at that time.

Heiser crossed *S. guineense* and S. *sarrachoides* and obtained hybrids. These plants did not resemble pressed specimens of Burbank's 'Sunberry', although they produced seeds, so Heiser came to conclude that Burbank had not made the cross that was described.

Heiser heard about a *Solanum* called "*msoba*" grown in South Africa and ordered some seed from Gleckler's Seedmen of Metamora, OH. Information from Gleckler indicated that Burbank's 'Sunberry' was very much like the South African *msoba* with silver leaves and bluish berries. After growing this species from seed, Heiser (1987) gives two possible conclusions: the *msoba* may have been ancestor to the 'Sunberry' or vice versa. New plant samples made the former hypothesis seem more likely. This new information from South Africa led Heiser to conclude that the 'Sunberry' was definitely not black nightshade, *Solanum nigrum*; neither was it the hybrid that Burbank claimed. Whatever the derivation, the 'Sunberry' did not become a wide success in America or Europe, but this *Solanum*, or something very similar, is likely to be under cultivation in South Africa.

**Rubus**

Burbank was drawn to the simplicity of rosaceous flowers, including those of the plums, apples, peaches, pears, and mountain ash. He was especially intrigued with *Rubus*—raspberries, blackberries, and their relatives where he made wide crosses between species and between different crop groups. He examined and crossed many wild *Rubus* species (Table 2). He imported and improved what he called "races" of little known exotic species and sold many berry genotypes for cultivation in the United States. He brought in *R. hawaiiensis* from Hawaii, *R. idaeus* var. *strigosus* (American red raspberry) from Alaska, and many species from Asia, South Africa, Europe, and India. He created new common names for foreign species, e.g., balloon berry (*R. illecebrosus*) and Mayberry (*R. palmatus*), to better market them.

Burbank made good use of American raspberry species including the American black raspberry species, *R. occidentalis* of eastern North America, and its counterpart, *R. leucodermis*, native west of the Rocky Mountains. He also used the North American red raspberry, *R. idaeus* var. *strigosus*, in his crosses. He released 13 red, black, and purple (black × red) raspberry cultivars along with making broader crosses within the genus (Table 3).

**Blackberry**

In the 1880s Burbank imported blackberry seeds from India. He was unaware at the time that this was a European blackberry, *R. armeniacus,* which had been introduced into India. He grew the blackberry seedlings, made a few crosses, selected for large fruit and thornlessness, and sold what he considered was an improved species, e.g., 'Himalaya Giant' blackberry. He was not likely aware that *R. armeniacus* was pseodogamously apomictic and many of his crosses were likely in vain. Burbank released this blackberry clone with the best of intentions, but unfortunately it has become a noxious weed throughout Pacific Northwestern North America (McConahey, 2006). Birds enjoy eating the fruit and have ensured plant distribution along the West Coast. This blackberry has great genetic variability (McConahey, 2006). Seed of thornless, highly productive clones produced plants that vary in thorniness and productivity and have become invasively distributed throughout the Pacific Region. The thorny types appear to be the most vigorous.

*Thornlessness.* Burbank was quite excited about finding and selecting for thornlessness in blackberries. He predicted that the children of the next generations would be blissfully ignorant about thorny blackberries because of the introduction of the thornlessness. He invoked children's stories and poems about thorny briars and explained that this poetry would not be applicable in the future (Burbank, 1914). He was certain that his thornless types would be so popular as to take over the market. Although clonal propagation can maintain the genetic thornless mutants, seedlings will be predominantly thorny.

Table 2. Some of the *Rubus* L. that Luther Burbank crossed in his experimental gardens.

| Species | Species group/common name |
|---|---|
| *R. allegheniensis* Porter | Eastern American erect blackberry |
| *R. coreanus* Miq. | Korean black raspberry |
| *R. armeniacus, R. procerus, R. discolor* | European blackberry, Himalaya(n) blackberry |
| *R. canadensis* L. | Northeastern erect blackberry |
| *R. chamaemorus* L. | Cloudberry |
| *R. crataegifolius* Bunge | Siberian berry, Asian raspberry |
| *R. deliciosus* Torr. | Rocky Mountain raspberry |
| *R. hawaiiensis* A. Gray | Hawaiian raspberry |
| *R. idaeus* L. | European red raspberry |
| *R. illecebrosus* Focke | Balloonberry, strawberry raspberry |
| *R. laciniatus* Willd. | Evergreen blackberry, cut-leaf blackberry |
| *R. leucodermis* Douglas ex Torr. & A. Gray | Western black raspberry |
| *R. loganobaccus* L.H. Bailey | Hybridberry, Loganberry, Boysenberry |
| *R.* ×*neglectus* Peck | Purple raspberry |
| *R. occidentalis* L. | Eastern black raspberry |
| *R. odoratus* L. | Flowering raspberry |
| *R. palmatus* Thunb. | Mayberry, Japanese raspberry |
| *R. parviflorus* Nutt. | Thimbleberry |
| *R. phoenicolasius* L. | Wineberry |
| *R. pileatus* Focke | Asian raspberry |
| *R. rosifolius* Sm. | Cape bramble, Mauritius raspberry |
| *R. spectabilis* Pursh | Salmonberry |
| *R. strigosus* Michx. | American red raspberry |
| *R. trivialis* Michx. | Southeastern trailing blackberry, dewberry |
| *R. vitifolius* Cham. and Schldtl. = *R. ursinus* Cham. and Schldtl. | Western trailing blackberry, California dewberry |

Table 3. *Rubus* clones released by Luther Burbank.

| Crop | Cultivar name | Pedigree | Release yr | Extant in 2014 |
|---|---|---|---|---|
| Blackberry | Himalaya = Himalaya Giant | $F_2$ *R. armeniacus* | 1885 | Yes |
| | Autumn King | Lawton × Oregon Everbearing | 1893 | No |
| | Iceberg | $F_3$ (Crystal White × Lawton) | 1894 | No |
| | Red Hybrid Blackberry | Similar to Loganberry but larger and better quality. | 1897 | No |
| | Triumph | Unknown | 1914 | No |
| | Snowbank | Seedling of Iceberg | 1916 | Yes |
| | Superb | Seedling of Himalaya Giant | 1916 | No |
| | Santa Rosa | *R. armeniacus* selection (thornless blackberry) | 1920 | No |
| | Sebastopol | *R. armeniacus* selection (thornless blackberry, like above but later season and sweeter) | 1920 | No |
| Hybridberry (blackberry × raspberry) | Paradox | $F_4$ (Crystal White × Shaffer's Colossal raspberry) | 1893 | No |
| | Primus | *R. ursinus* × *R. crataegifolius* | 1893 | No |
| | Phenomenal | Aughinbaugh × Cuthbert (raspberry) | 1893 | Yes |
| | Cultivar synonyms = Hybrid 18234 Humboldt | | 1909 | |
| | Climax | Sibling of Phenomenal | 1914 | No |
| Raspberry (includes blacks and reds) | Mendocino | Selection of wild *R. leucodermis* | 1887 | No |
| | October Giant | Seedling of Eureka (large, primocane-fruiting black raspberry) | 1893 | No |
| | Eureka | $F_3$ (Gregg × Shaffer) | 1893 | No |
| | Hybrid E. 11,546 | $F_3$ (Souhegan × Gregg) | 1893 | No |
| | Hybrid S.S 147 | $F_3$ (Shaffer × Souhegan)? | 1893 | No |
| | Hybrid S.S. 6701 | $F_3$ (Souhegan × Gregg)? | 1893 | No |
| | Japanese Golden Mayberry | Yellow selection of *R. palmatus* | 1893 | No |
| | Dictator | Gregg × Shaffer | 1897 | No |
| | Sugar Hybrid | $F_2$ (Shaffer × Souhegan) | 1893 | No |
| | Rubus | Selection of *R. capensis* (synonym for *R. rosifolius*) | 1894 | No |

In Burbank's time, the objective of thornlessness was primarily of interest so that gardeners and commercial growers would be able to manage and manipulate the plant with less risk of personal injury. However, with the advent of the regular use of machine harvesters to harvest blackberries in the 1960s and 1970s, thorn contaminants in the harvested product became a serious issue. Although thorns may have just been a nuisance in the 1970–80s, they became a major focus of lawsuits in the 1980–90s. Consumers who say they were injured by thorns in processed berry product sometimes have resorted to litigation. Therefore, thornlessness is a major objective of blackberry breeding programs.

The first commercially important thornless blackberry was 'Thornless Evergreen', a sport of 'Evergreen' released ≈1926. The first commercially important thornless blackberries released to meet modern standards of fruit quality were 'Navaho', released for the fresh market in 1989, and 'Black Diamond', released in 2005, for the machine-harvested, processed fruit market.

*White-fruited Rubus.* Burbank assumed the challenge of developing a "truly white blackberry" without understanding the genetic background. Pure white blackberries were not recorded previous to his breeding efforts. Even today light-colored, i.e., yellow, mutants in *Rubus* occur but are infrequent across species with higher ploidy (Jennings, 1988).

Yellow color forms are not uncommon in diploid *Rubus* species and are documented in the raspberries, *R. idaeus*, *R. occidentalis*, and *R. phoenicolasius* and the blackberries, *R. trivialis* and *R. allegheniensis* (Jennings, 1988). Many light-colored *R. allegheniensis* have since been patented, including types such as 'Nettleton's Creamy White' (U.S. Plant Patent 20,234), which, although patented as a *R. fruticosus*, is a *R. allegheniensis* selection. However, colorless mutants in tetraploid or higher ploidy *Rubus* have not been reported (Jennings, 1988).

Light fruit color in *Rubus* is a recessive mutation, a "knockout" function of the anthocyanin pathway (Lee et al., 2012). For a white fruit to occur in tetraploid blackberries, all four loci would need to have mutated. Because mutations by their very nature are uncommon, inbreeding would be required for the complete homozygous recessive condition. In the case of a tetraploid, that means that only a 6.25% chance that any yellow-fruited seedling will occur from a parent carrying one copy of the mutated gene. With possible inbreeding depression in the early generations, such an occurrence at any of the higher ploidy levels is exceedingly rare unless it is deliberately selected for over several generations.

Many of the commonly seen pigment mutations in *Rubus* are orthologous, i.e., genes that have similar function for different species as in *R. phoenicolasius* and *R. idaeus*, but other mechanisms exist. The level of fruit flesh and skin color depends on where the pigment production pathway is disrupted (Lee et al., 2012). Lee et al. (2012) detected very low levels of cyanidin-3-glucoside and cyanidin-3-rutinoside in yellow forms of *R. occidentalis*, but the total anthocyanin concentration was less than 1% of normal. Red raspberry has a well-known common mutation that produces amber/orange-colored fully ripe fruit (*ppTt*). This, in combination with another, much less common mutation, produces a much lighter yellow and less orange-colored fruit (*pptt*). The orange-fruited form likely has low levels of anthocyanins similar in type to those of the black raspberry, whereas the other is completely devoid of them. Other chemicals produced in the fruit can provide a yellowish color even without any anthocyanins. The structure of the drupelet skin and its contents may mean that some are likely to be more translucent than yellow, but none are truly white.

Burbank mentioned that his white blackberry produced translucent drupelets, and the whitish cast was likely attributable more to glare off the drupelet surface reflecting light than from white pigment. For plants that have a chlorophyll deficiency, their leaves produced little or no chlorophyll and the unripe fruits, instead of being greenish as normal, were almost whitish. As the fruit ripened, they became nearly translucent and then accumulated some anthocyanins near the end of ripeness. Their translucence was likely a structural quality not seen in raspberry species, even when the same pigment genes were knocked out in blackberry.

Burbank described 'Crystal White' (Fig. 3) as having semitranslucent fruit with a yellowish tint. He said that he improved the fruit quality by crossing with 'Lawton' and then selected recombinants with less color. These statements are likely true, but the intriguing part is that 'Lawton' (Fig. 3) is a tetraploid, and 'Crystal White' and 'Snowbank' (Fig. 4) are diploids (Meng and Finn, 2002;



Fig. 3. (**A**) 'Crystal White'(diploid) and (**B**) 'Lawton' blackberry (tetraploid) fruit. Image adapted from that in Burbank (1914).

Thompson, 1995). His 'Crystal White' × 'Lawton' hybrids were likely to have been triploid with only a few tetraploids. He probably observed much more sterility than he mentions in his description, which merely says that they "were black." He described a few white-fruited types in the $F_2$ generation, as would be expected. 'Snowbank' is based on further crossing and selection from within this group. He was likely able to select recombinants that had less pigment, but probably had to produce huge populations to get these few.

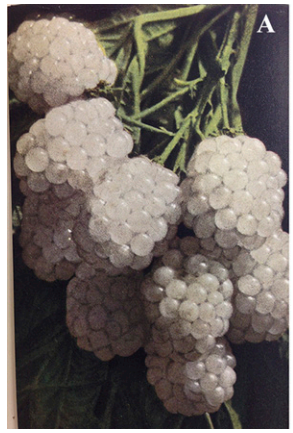



Fig. 4. (**A**) 'Iceberg' image adapted from that in Burbank (1914), and (**B**) 'Snowbank' blackberry fruit, photo credit to Rachael Spaeth of Luther Burbank Home and Gardens, Santa Rosa, CA.

Fig. 5. 'Phenomenal' fruit. Image from that in Burbank (1914).

'Snowbank' is diploid, so the probability of obtaining two homozygous recessive white mutant alleles is greater than for a tetraploid plant. The $F_1$s may have been triploids with two sets of chromosomes from 'Lawton' and one from 'Crystal White'. Then, in the $F_2$ generation, Burbank selected diploid recombinants that inherited two copies of the recessive mutation from 'Crystal White', whereas the third set of chromosomes dropped out during meiosis. This would have resulted in a white-fruited diploid like 'Crystal White', but with genetic contributions for improved fruit quality from 'Lawton'. Unfortunately, 'Iceberg', an offspring of 'Snowbank', no longer exists.

**Hybridberry—Blackberry × raspberry**

Since the 1883 discovery of 'Logan' (synonym = 'Loganberry'), by Judge James Logan of Santa Cruz, CA (Jennings, 1988), many *Rubus* breeders were interested in making blackberry by raspberry crosses. 'Logan' came from a cross of the octoploid *R. ursinus* 'Aughinbaugh' × diploid *R. idaeus* 'Red Antwerp' and is a hexaploid with 42 somatic chromosomes (Jennings, 1988). 'Logan' is likely the result of an unreduced pollen grain of the red raspberry that fertilized the octoploid blackberry.

Burbank also was interested in this type of cross. He crossed 'Aughinbaugh' with *R. idaeus* 'Cuthbert' to produce a second-generation seedling he called Hybrid berry V.C. 18,234, subsequently renamed 'Humboldt'. This clone was then sold to John Lewis Childs, renamed, and marketed as 'Phenomenal' in 1894. 'Phenomenal' proved to be Burbank's best-known berry cultivar (Fig. 5). He described it as "far superior in size, quality, color, and productivity…" to 'Loganberry'. Despite Burbank's claim, this cultivar was not as much of a commercial success as 'Logan' (Jennings, 1988).

'Phenomenal' became of interest to B.M. Young of Morgan City, LA. Young obtained plant material from Burbank and made a cross with the hexaploid 'Phenomenal' and the octoploid, *Rubus baileyanus* × *R. argutus* 'Austin Mayes'. The result was 'Young' (synonym = 'Youngberry'), a berry that was introduced in 1926 and rapidly became popular for its excellent flavor and large fruit. The fruit color is maroon, and the flavor is sweet. 'Young' was a parent of 'Olallie' and is in the pedigree of 'Marion', 'Silvan', and many other cultivars in the Oregon blackberry breeding program. Burbank's cultivar Phenomenal has contributed to more than 2400 ha of blackberries planted in the United States. 'Young' is also grown in New Zealand although it is marketed under 'Boysen' (H. Hall, personal communication).

## CONCLUSION

Of the crops of plants bred and released by Burbank, his small fruit genotypes have had less direct economic impact on the present commercial production than that of his potato or ornamental flowers such as the 'Shasta' daisy, yet his blackberries and hybrid berries, 'Burbank's Thornless', 'Snowbank', and

Fig. 6. Image of Luther Burbank selecting *Rubus* seedlings. Image adapted from that in Burbank (1914).

'Phenomenal', remain available through genebanks (at Sebastopol and Santa Rosa, CA, and the USDA-ARS National Clonal Germplasm Repository, Corvallis, OR), and these cultivars continue to have an impact on world berry production. 'Phenomenal' blackberry is a parent of 'Young', which became a founding clone for breeding programs in Oregon, New Zealand, Australia, and others around the world.

Burbank (Fig. 6), the plant inventor, was very foresighted in predicting the development and importance of berry crops to U.S. agriculture. He had a strong vision for novelty and correctly predicted traits that would be of high economic value. His innovative breeding approach has led the way for the generations of berry breeders now crossing and releasing the newest improved berries for consumers to enjoy.

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