Domestication of *Gleditsia triacanthos*

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Gleditsia triacanthos, also known as the honey locust, is a tree famed for living a double life. Commonly found in urban landscapes and along city streets, it is characterized by a narrow trunk with light grayish brown bark, tiny delicate green leaflets, and a pleasing pyramidal shape (See Figure 1).

Figure 1

Source: Clean Cut Property Services, Inc.

But in the wild, it is defined by the presence of massive thorns with long snake-like seed pods that hang from its branches (See Figure 2).

Figure 2

Source: Murray State Honey Locust Info Page (Matthew Richardson)

Native to the forests of central North America, the honey locust is typically found in moist bottom lands or limestone soils (Blair, 358). It is a woody, long-lived, legume with deeply fissured dark gray or black bark. The leaves are alternate and pinnately compound with leaflets ranging in color from light to dark green. Flowering occurs from early May to mid-June with flowers appearing in dense bunches about 2-5 inches long, ranging in color from white to pale yellow (See Figure 3) (Blair, 360).

Figure 3

Source: Jim Peterson Gallery

Large red thorns grow along the trunk and branches of the tree, with a definite thornless region on the upper reaches of trees over 10 years old (Blair, 361). The thorns typically grow in bunches of three, but they can be larger, especially on the trunk (Figure 4).

Figure 4

Source: Mounds Park Trees

The thorns tend to reach about 2-3 inches in length with the largest thorns near the bottom of the trunk and the smallest on the mature upper branches. The tree also produces long twisting purplish brown seed pods that can reach up to a foot or longer in length (See Figure 5) (USDA Plant Fact Sheet). Although thornless individuals do appear in the wild, it is relatively uncommon.

Figure 5

Source: New England Wild Flower Society

When compared side by side, it is difficult to believe that these two trees are members of the same species. Given the characteristics of the wild honey locust, it seems odd that it would end up being a tree we plant in our yards and along our streets. So why then was the honey locust selected as an ornamental tree and how was it modified to become the tree we see on streets today? To begin, it is useful to consider why the honey locust looks the way that it does. Connie Barlow explores this topic in her book The Ghosts of Evolution: Nonsensical Fruit, Missing Partners, and Ecological Anachronisms. In evolutionary theory, an ecological anarchism is defined as a trait that evolved in response to a partnership with a species that is now extinct. Barlow suggests that the seed pods of the honey locust are an ecological anachronism because they most likely evolved as a result of a relationship with megafauna. This is evidenced by the size of the seed pods. As Barlow points out, “there is no point in building a fruit larger than the gape of one’s intended partner” (41). Because there are no animals in the native range of the honey locust with mouths large enough to consume the entire fruit, we can assume that the primary consumers of honey locust pods are extinct (Barlow, 41). This is further evidenced by the presence of honey locust in river floodplains. This indicates that the seeds no longer have an efficient mode of dispersal to get uphill, and therefore have to settle in lower ground (Barlow, 43). This conclusion is supported by the hard coating that surrounds the seed. This coating retards germination unless it is significantly damaged. However, if this seed casing were to pass through the digestive tract of say a Wooly Mammoth, it would most likely dissolve preparing the seed for germination wherever it might land (Barlow, 44). The final piece of evidence that Barlow identifies is the sweet pulp found inside the pods; she asks “why waste energy manufacturing a sweet, protein-rich pulp unless that pulp is meant to attract an animal?” (44).

The challenge to this theory is that there are no written records from the time when megafauna roamed North America, so Barlow has no conclusive evidence to substantiate her claims. This is further emphasized by our inability to explain why the honey locust developed such aggressive thorns. Although clearly a defense mechanism, it is unclear what the tree was defending itself from. In addition to these objections, in order for a fruit to be considered anachronistic its seeds can no longer be dispersed through natural means, but the seeds of the honey locust are still dispersed through natural forces. In her book Barlow admits that the seed pods can be spread via waterways or by wind. It is also possible that once the seed pods fall to the ground they are consumed by deer or rabbits (46). Barlow argues that while these methods do work, they are feeble at best. Despite having a large range, the honey locust is remarkably rare in the wild. Although we cannot prove that the honey locust evolved in response to North American megafauna, this still the most likely explanation for the distinctive features of the honey locust today.

Given these features, what makes this tree attractive to landscapers? This question can be answered by observing the traits of Gleditsia triacanthos var. inermis, or the domesticated variation of the honey locust. First and foremost, the tiny leaflets of the honey locust make it ideal for urban streets because it does not require intensive clean up when the leaves begin to fall, they simply wash away into the storm drains (Barlow, 12). Second, the honey locust is a particularly hardy species with resistance to drought, pollution, and disease (Blair, 358). And finally, its deep root system ensures that it will never buckle the surrounding pavement and makes it an ideal candidate for erosion control (Barlow, 13). In addition to these practical benefits, the honey locust is a beautiful and unimposing tree that offers an aesthetically pleasing addition to any urban landscape. The real question is how these traits became visible to landscapers. Beginning in the 1920’s American farmers began to plant honey locusts in their fields and pastures. According to Spencer Chase, “the shade cast by its feathery foliage is heavy enough for livestock and still light enough to permit good grass growth. In addition its pods have value as feeding supplements.” However, he also indicates that “despite these good qualities, farm use of honeylocust has been limited because of the dangerous thorns it produces” (Chase, 715).

Chase’s article “Propagation of Thornless Honeylocust” provides a comprehensive overview of the research conducted on honey locust domestication. According to his research, the first recorded efforts to select for specific traits on the honey locust tree occurred in 1926. These early experiments attempted to propagate trees with smaller fruits and a higher sugar concentration (715). Two years later, in 1928, the American Genetic Association sponsored a nationwide competition “to locate superior pod-producing trees” (715). The winning tree produced 58.3 pounds of the seed pods with an average of 36.65 percent sugar content (715). In the wild, honey locust seed pods can have a sugar content as high as 35 percent. By the 1940’s, one experiment determined “that honey locust pods grown on a single acre were equivalent in overall nutrition to 105 bushels of oats” (Barlow, 44). Shortly after the first experiments with selecting for higher sugar content in seed pods, researches began experimenting with breeding thornless honey locust to try to produce thornless trees.

The researchers found that only 60-65% of the seedlings from this pairing would develop into thornless trees (Chase, 715). This was neither an economically viable option nor a practical solution to the problem. It wasn’t until a 1939 study on grafting that an effective method for producing thornless trees was developed. The researcher took samples of scionwood from 15 honey locusts ranging from thorny to thornless and grafted the stems onto nursery stock. According to Chase, “the results indicated that thornless scionwood collected from branches which had definitely ceased thorn production would produce thornless trees” (Chase, 716). However, scionwood taken from trees that has only recently ceased thorn production still sometimes produced trees with thorns. Thorny scionwood produced a tree with thorns every time, and the scionwood taken from naturally thornless trees invariably produced thornless trees (716). The results are summarized in Figure 6.

Figure 6

TABLE 1.—THORNINESS OF GRAFTED TREES PROPAGATED WITH THORNY AND THORNLESS HONEYLOCUST SCIONWOOD

Parent tree	Type of scionwood selected	Number of grafts	Number of surviving grafts: Thorny	Number of surviving grafts: Thornless
	Thorny and Thornless Scionwood from Same Tree			
Torbett	Thorny	8	5	0
"	Thornless	29	0	23
Cluster	Thorny	10	9	0
"	Thornless	40	1	36
Goldworth	Thorny	6	6	0
"	Thornless	40	33	3
Gadsden	Thorny	5	5	0
"	Thornless	27	20	1
Lake	Thorny	6	3	0
"	Thornless	10	0	9
	Scionwood from Thornless Trees			
Penn	Thornless	11	0	10
Orr	Thornless	10	0	8
Ward	Thornless	26	0	18
	Various Scionwood Sources			
Calhoun	Thorny	11	9	0
Millwood	Thorny root-sucker	21	16	3
Torbett	Thorny root-sucker	3	2	0
Lake	Thornless root-sucker	6	5	0
Lowland	Thornless	8	0	7
Morrow	Thornless	23	0	21
Tony	Thornless	10	3	5
Hartselle	Thornless	7	0	7
Smith	Thorny	10	5	0
Gadsden	Thornless terminal of shoot thorny at base	6	3	0

Source: Propagation of Thornless Honeylocust

This experiment was replicated by Chase in 1940. He took samples from seven honey locust. One tree was entirely thornless while the other six varied in thorniness, but “had developed definite thornless regions” (716). From each thorny tree Chase collected three samples of scionwood: one from a thorny branch, one from a partially thorny branch, and the third from the thornless region. The results from this study are summarized in Figure 7.

Figure 7

TABLE 2.—THORNINESS OF HONEYLOCUST SCIONWOOD AND OF GRAFTED TREES, 1940-1946

Parent tree	Type of scionwood selected	Character of grafted trees[1]: Trees produced in nursery 1940	Field planted trees[2]: Thorniness of shoot growth, Set 1941	Set 1944	Set 1946[3]
		Number of trees			
Torbett	Thorny	14	4	4	2
		3	3	3	2
"	Partly thorny	33	4	2, 2	2
		29	4	4	2
"	Thornless	14	4	4	2
Cluster	Thorny	2	2	2	1
		2	2	2	1
"	Partly thorny	15	4	4	2
"	Thornless	19	4	4	2
Goldworth	Thorny	8	4	4	1, 1
"	Partly thorny	29	4	4	2
		24	4	4	2
"	Thornless	5	4	1, 3	2
		43	4	4	2
Calhoun	Thorny	39	4	2, 2	2, 1
		8	4	4	2
"	Partly thorny	13	4	1, 3	2
		37	4	4	2
"	Thornless	19	4	4	2
Tony	Thorny	5	3	2, 1	2
		1	1	1	1
"	Partly thorny	23	4	1, 3	2
		12	4	4	2
"	Thornless	8	4	4	2
Bessemer	Thorny	9	4	4	2
"	Partly thorny	1	1	1	1
		9	3	2[4]	2
	Thornless	9	4	4	2
Penn[5]	Thornless	10	4	4	2

[1]Thornless trees and thornless shoot growth shown by bold numerals.
[2]When available 4 trees of those produced by each type of scionwood were field planted in 1941.
[3]Approximately one-half the trees were removed February, 1945.
[4]One tree died.
[5]Thornless parent tree.

Source: Propagation of Thornless Honeylocust

The thorny scionwood produced 77 thorny trees and 14 thornless trees. The partially thorny scionwood produced 99 thorny trees and 120 without thorns. From the thornless scionwood, 113 thornless trees and 5 thorny trees were produced. Chase suggests that "it is probable that the thornless region of this parent tree was not clearly developed or precisely determined as all 5 of the thorny trees produces come from 3 shoots out of a total of 16 collected" (719). After observing the trees for 6 years, Chase concluded that "thornless trees grafted from thornless scionwood from all sources were still thornless in 1946" (719). However, he noted that "in lieu of thorns some trees produced short vestigial shoots which were semi-persistent and not objectionable." These shoots were not present on any of the thorny trees (719).

Chase does not offer any indication of why these growths occurred on the thornless trees nor why the shoots from thorny trees that had ceased producing thorns were able to produce thorness trees. He does caution that there needs to be "a clear definition of the thornless region of the parent tree" but that "the propagation of thornless honeylocust with selected scionwood is relatively simple and practicable" (719). The only issue Chase encountered in his study was that the seed pods with the highest sugar concentration tended to come from thorny trees. While this presented an issue for farmers, it was of no concern to landscapers who would eventually select for fruitless varieties of the tree anyways. To return to the original question of why the honey locust selected as an ornamental tree and how was it modified, the history of the plant tells us that it was first used as a shade tree on farms given cattle's proclivity for the fruits, and then later developed for city streets. The research on grafting thornless trees and the subsequent production of these varieties made the characteristics of the honey locust visible to landscapers, but it doesn't explain why it was selected as a tree to be planted on city streets across the nation. The answer to this question lies in the story of the American Elm.

Ulmus americana, or the American Elm, is native to Eastern North America. It is a long-lived tree with long branches that drape out from a tall central trunk (Figure 8).

Figure 8

Source: An Introduction to American Elms

The umbrella like canopy filters light through an arrangement of alternate, doubly serrate leaves. These leaves tend to be dark green in color with a glossy texture (Figure 9).

Figure 9

Source: Carolina Nature

In the spring the tree produces small purplish brown flowers, and the fruits, colloquially described as helicopter seeds, are samara with a deeply notched tip (Michigan Trees, 191). The American Elm is tolerant of a variety of soil conditions making it an ideal candidate for urban landscaping. Given its graceful form and patriotic connotations, it was selected as a tree to be planted on the streets of most northeast and midwest neighborhoods (Bey). During the 19th and early 20th century, the Elms established themselves as an urban monoculture. But disaster struck in the 1940's when the Elms established themselves as an urban monoculture. But disaster struck in the 1940's when the Dutch elm disease reached America and began infecting trees from New York to Chicago. According to a 1989 article in the New York Times, "of the estimated 77 million elms in North America in 1930, over 75% had been lost by 1989" (New York Times). Dutch Elm diseases is a fungal infection that causes a tree to block its own xylem, preventing water and nutrients from reaching vital parts of the organisms. It spreads rapidly and the results are devastating, leaving streets filled with dead or dying trees (US Forest Service). One way to combat the spread of the illness is to alleviate the strains of a monoculture. This means planting other species of trees along streets to prevent the fungus from moving from one tree to another through close proximity (D'Arcy). The honey locust was one of several native trees to be selected to replace the beloved American Elm (Blair, 362). The success of the experiments with grafting made it viable to produce thornless trees to plant on streets. The Horticulture page for Cornell University describes some of the advantages to grafting, which helps to explain the significance of these experiments in the domestication of the honey locust. The first advantage they cite is for "when a plant must be clonally propagated to maintain a select genotype, but it difficult to propagate vegetatively by cutting or other means" (Cornell University). In the case of the honey locust, the desired genotype is *Gleditsia triacanthos var. inermis*. As discussed above, the only way to achieve guaranteed thornlessness is through grafting. The second advantage Cornell cites is Economics. This is essential for urban landscaping because the ideal species for planting on a mass scale is cheap to produce and will live for several years. While these offer obvious benefits, the experiments with grafting also demonstrated the effectiveness artificial selection in changing the morphology of the species.

Artificial selection is broadly described as the intentional reproduction of desirable traits in a species. For the honey locust, thornlessness was the most desirable quality, but the natural genetic variation of the species made it possible to further manipulate the tree. This is evidenced by the abundance of variety available for urban landscaping. These varieties include the "Shademaster" which was selected for its height and long branches. The "Sunburst" which is a common tree in yards because it presents a beautiful yellow color almost all year. And the "Skyline" which is the variety typically planted on street. This tree is smaller than the other two varieties, has a narrower trunk, and a more definite pyramidal shape (US Forest Service). All of these varieties can be seen in Figure 10.

Figure 10

Source: USDA Plant Fact Sheets

Genetically, the diversity of *Gleditsia triacanthos* has been studied by Andrew Schnabel and J.L. Hamrick in their article "Organization of Genetic Diversity Within and Among Populations of *Gleditsia triacanthos* (Leguminosae)." The researchers conclude that "the most recent review of allozyme diversity in plants, conclude that high levels of variation are most strongly correlated which a wide geographic range, outcrossed mating system, and long generation times. All three traits are characteristic of *G. triacanthos* and help explain the high levels of allozyme diversity found in our study" (Schnabel & Hamrick, 1065). What this means for landscapers is that the species offers a wide range of traits from which the most desirable can be selected for an propagated on a large scale. This quality is also explored in Arthur Ghent's article "A Possible Mode of Induction of Pinnateness in Honey Locust, as Implied by Consistent Gradients of 1, Mixed, and 2Pinnate Leaves." Although this article does not deal explicitly with genetic variation, the author indicates that honey locusts are highly sensitive to manipulations, suggesting that phenotypic variation is both common and a source for a diversity of traits from which the most desirable can be selected. As discussed above, the honey locust naturally possesses many desirable qualities, but this qualities can be modified or enhanced through artificial selection.

The evidence presented above leads to the conclusion that the honey locust was first selected as a tree for farms. Once the desirable traits of the honey locust become visible and the need for new tree species in urban landscaping emerged, the honey locust was selected as a tree to be planted in streets all across America. Artificial selection for the most desirable qualities and the success of grafting of thornless individuals made it possible for the honey locust to firmly establish itself in the urban landscape. However, I must caution that these conclusions are tentative. A majority of my research was taken from a single article, "Propagation of Thornless Honeylocust" by Spencer Chase, and while his methods are thorough they do not entirely explain the results. For instance, why is it that a scionwood that has ceased producing thorns, but that is on a thorny tree, can produce a thornless individual? I was not, in any of my research, able to answer this question. There are also gaps in the historical narrative of the honey locust such as how the fruits were breed out of *G. triacanthos var. inermis* and whether the tree was popularized first on streets or in yards. Assuming that landscapers drew inspiration from the presence of the honey locust on farms, who was the first landscaper to propose that they be used in cities? And more broadly, was the decision to plant to honey locust in streets made by a single individual or was it a decision that was made and then replicated?

While all of these questions warrant further research, there are a few questions raised by this study that ought to be expounded on. The first is what benefits are there to a species that is domesticated for urban landscaping? In terms of the evolutionary success of a species, the honey locust demonstrates how humans have expanded the native range of the species. Because the honey locust is so adept at adapting to a variety of conditions, in regions where it was introduced as landscaping tree, it has often become nativized (Blair, 358). In addition to the expansion of the range, humans have also contributed to propagating the genes of the species, albeit artificially. Nonetheless given the challenges the honey locust's faces in distributing its seeds, as addressed by Connie Barlow in *The Ghosts of Evolution*, humans have provided an alternative method to natural reproduction that ensure large populations of the honey locust persist into the future. It could also be argued that by domesticating the honey locust humans have become more familiar with the species and are therefore more willing to protect it if it were ever to come under threat.

But there appear to be disadvantages embedded in the domestication of the honey locust as well. For example, it the wild honey locust were to come under threat of extinction, would we be willing to contribute time and money to saving this variety given that the domesticated version is so prevalent on our streets? It would be unfortunate to lose the rich biological history of the honey locust's anachronistic fruits and thorns, not to mention that the forest would become far less interesting without the wild honey locust. That being said, in terms of evolutionary success, does it matter that the domesticated version has lost its distinctive traits? This segues into the second set of questions that require further explanation and analysis. Given that the wild and domesticated honey locust look so different from one another, why aren't they considered separate species?

David Michener explores this question is his brief article "Phenotypic Instability in *Gleditsia Triacanthos* (Fabaceae). He claims that "thornless individuals have long attracted taxonomic attention across the range of the genus" (Michener, 360). He concludes that once it is demonstrated that "mature thornless trees can revert to producing thorns there can be no biological basis for recognizing any infraspecific thornless taxon" (361). So while the domesticated honey locust is signified with the addition of "*var. inermis*" it is not a taxonomically recognized species. Returning to the issue of conservation, this means that the wild tree could go extinct without technically losing the honey locust species. This raises a number of philosophical concerns relating to the validity of taxonomic boundaries, but for this purpose of this study I will limit my analysis to a few brief comments. Because the function of the wild honey locust is so distinct from that of the domesticated version, it seems necessary to distinguish to two in nomenclature merely to ensure that each is preserved for its given purpose. In other words, by dividing the honey locust into two distinct species, although their may not be strong biological evidence to support this division, we could ensure that the wild tree is adequately protected while continuing to propagate the domestic species for aesthetic purposes. Although it is not desirable for a tree that we plant in our yards and on our streets, in is desirable to maintain genetic diversity on the planet. This is essential not only to protect the earth's ecosystems, but also for the purpose of expanding our knowledge about the world.

My final comment in respect to the topic of the domestication of the honey locust is that the wild version offers just as fascinating a story as the narrative of how the wild honey locust became a tree common on our streets. Although only touched on briefly in this paper, the evolution of the honey locust offers fascinating insight into the North American landscape pre-humans. The transformation of the honey locust also offer some clues into to the nature and desires of humans in regards to our interaction with the natural world. While it makes sense that we would want to eliminate any quality that poses a risk to our well-being, the sight of the honey locust in the wild is far more mesmerizing than the version that appears on the streets. While the honey locust is an attractive addition to any sidewalk, it is important to consider how the distinction between the wild and domesticated trees influences our conception of what a species is and how it functions in relation to our society and to ourselves as individuals.

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