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Paradoxes of Survival

A study of populations of wild lilies
in St. Lawrence County, N.Y., 2018-22

By Paul Siskind

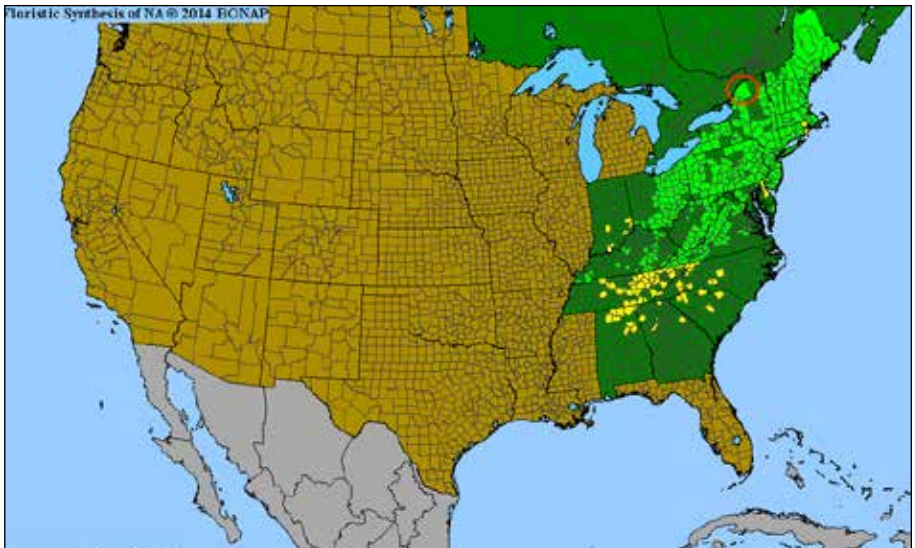
In spring 2019, I received a grant from the NALS Research Trust Fund to conduct a longitudinal study of the level of infestation of the invasive lily leaf beetle on wild populations of lilies (primarily *Lilium canadense*) across St. Lawrence County, N.Y. I described the project and offered some preliminary observations in an article in the June 2020 *Quarterly Bulletin* titled “Adventures in Stalking the Lily Leaf Beetle in the Wild.” This article summarizes the findings of my five-year study, and describes a paradoxical survival strategy of *L. canadense* and related species.

St. Lawrence County is at the northern edge of New York state. It covers 2,840 square miles, making it the sixth-largest

county east of the Mississippi River. The northwestern half of the county are lowlands of the St. Lawrence River watershed, whereas the southeastern half of the county rises into the Adirondack Mountains.

Through historical records, word of mouth, and personal searching, I found about 40 wild populations of lilies stretching across 60 miles of the county’s lowlands. The main types of environments that I found the lilies in were wet meadows, stream banks, and roadside drainage ditches. Almost all of the populations were *L. canadense*, which is the only lily historically listed as native to the county. Two of the populations were nonnative *L. lancifolium* that had become

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Figure 1. Distribution of *L. canadense*.

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naturalized, probably escapees from old farmstead gardens. One population (and possibly a second) contained lilies that appear to be *L. michiganense* or perhaps a hybrid with it. This was discussed in my June 2020 article in the QB.

Lilium canadense

L. canadense is the most widespread native lily in northeastern North America. (Figure 1) As with many species of lilies around the world, *L. canadense* isn't especially rare, but it's usually found in scattered, sparse populations. Indeed, a number of populations that I found had fewer than a dozen plants (although there are numerous challenges in getting an accurate count of lilies in the wild, as described in my previous article).

It takes five to 10 years for *L. canadense* to grow to mature, flowering size, depending on the growing conditions, developmental setbacks, etc. The bulbs of *L. canadense* are much smaller than Eurasian species or garden hybrids. I rarely found any that were more than 1 inch in diameter. The bulb is covered with many scales about the size of a grain of millet. These scales are brittle, and they easily detach from the bulb.

An interesting aspect of *L. canadense* is that, after sending up its stem, the original bulb becomes depleted and the plant rebuilds a new bulb for the next year at the end of a short rhizome, 1-2 inches away from the previous bulb. (Photo 1) While various species of lilies around the world, especially in North America, creep by rhizome, it's uncommon for most species to totally deplete its previous bulb and regrow a new one on an annual basis. The plant also uses its rhizome to adjust the depth of the bulb. If the bulb or rhizome gets



Photo 1. *L. canadense* grows a new bulb every year at the end of a short rhizome.

disturbed (e.g., eaten by a rodent), scales that get detached can grow into a separate clonal plant. Sometimes a bulb will send out two rhizomes instead of one, creating two smaller clonal plants the next year.

Each bulb normally sends up only one stem per year. The stem of a young plant often browns out by midsummer, earlier than mature plants. But even with mature plants, if the stem gets broken (e.g., knocked down by wind, trampled by deer or ATVs, etc.), the plant usually goes dormant early rather than growing a new stem. This means that it can only rebuild a smaller bulb for the next year. The same thing happens if the plant gets defoliated (e.g., by deer or lily beetles). Thus, in any population of *L. canadense*, the number of visible green plants dwindles over the course of a summer, and only a small percentage of the plants will be large

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enough to flower in any given year.

The fragile life cycle of the lily suggests that individual populations would be highly vulnerable to extirpation, especially with large-scale disturbance like infestation by the lily leaf beetle or human activities.

Lily Leaf Beetle (*Lilioceris lili*)

Lily leaf beetle is a well-known scourge for many lily gardeners across North America. Even though much has been written about its impact on lilies in gardens, little work has been done on studying its impact on wild populations of lilies in North America. This article focuses on aspects that relate to lily leaf beetles' impact on our wild lilies.

LLB feeds almost exclusively on *Lilium* and *Fritillaria*, and *Lilium* is the only known host for successful reproduction.



ANDREA BRAUNER

Photo 2. *Tetrastichus setifer* laying eggs in a lily leaf beetle larva.

Because there are no known predators of LLB in North America, its presence could pose a significant threat of extirpation of wild populations of native lilies.

There are some studies that report that LLB prefers to feed on Eurasian species over North American species, and that it's less prolific when raised on North American species (possibly due to a chemical difference between the species). Indeed, in my own gardens and in the wild, I've observed that LLB rarely infests native lilies as densely as Eurasian species and hybrids. However, this also could be due to the fact that lilies are often grown more densely in gardens than they grow in the wild, and the concentration of feeding and breeding sites supports higher levels of infestations. Regardless, even if the beetle is less prolific on native species, the availability of Eurasian lilies in nearby gardens potentially increases the threat of the beetle extirpating populations of wild lilies.

The larvae of LLB cause more extensive leaf damage to lilies than do adults and in a shorter span of time. However, even modest leaf damage from adults early in the season can cause a lily to go dormant early because of desiccation.

LLB is reported to be strictly univoltine (one cycle of egg production per year) in its native Eurasia, with mating and egg laying occurring only in early to midsummer, which potentially mitigates its impact on lilies. However, there are confirmed reports of late-season mating by the beetles in North America, and even unconfirmed reports of late-season egg laying. Whether the beetle has become multivoltine in North America is unknown. It's also unknown whether adults live more than one year, and precisely when and how often in

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their life cycle they migrate to new plots.

Biological Controls

In its native Eurasia, infestation of LLB is naturally controlled by six species of small wasps and flies that lay their eggs in beetle larvae. (Photo 2) Starting in 1996, three of these have been released as biological controls in North America since: *Tetrastichus setifer*, *Lemophagus errabundus*, and *Diaparsis jucunda*. These imported parasitoids have been very successful at controlling LLB in North America, with infestation levels being reduced by 30-100%.

However, the parasitoids establish and spread only about half as quickly as the LLB spreads. As of 2023, the parasitoids had only been released in sites in New England; Ithaca N.Y.; and Ottawa, Ontario. They hadn't yet arrived in St. Lawrence County. (The parasitoids also have been recently released in Michigan, Winnipeg, Saskatoon, and Edmonton.)

Thus, many individual populations of wild lilies across the country remain at potential risk of extirpation by LLB until the parasitoids arrive in each area. By tracking the levels of infestation by LLB in numerous plots spread across a large area over a five-year period, the goal of this study has been to help us understand the risk that LLB

poses to our native lilies until the biological controls become established.

Survey Methodology

I surveyed about 40 wild populations of lilies across the county in May-September of 2018-22. Because some populations weren't found until later years, those sites have data from less than the full five years. Similarly, a few of the populations were extirpated (fully or partially) during the survey years, so those populations don't have five years' span of data either.

Because the number and the size of the lilies that grow (or are visible) within a single area varies greatly over the course of a season and from year to year, the size of each survey plot was estimated and generalized into three categories:

- 1-10 plants = small**
- 11-30 plants = medium**
- Greater than 31 plants = large**

Any plant that was large enough to grow

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Photo 3. Separate plots of lilies in a large field.

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a whorl was counted. Single-leafed young plants weren't counted. Plants within 50 feet of each other were considered to be in the same plot unless they were separated by a road. Plots were demarcated with bamboo stakes and flagging tape so that I could keep track of them, and to also try to prevent trampling or mowing. (Photo 3)

I surveyed each plot on a rotating but variable basis, every two to four weeks during the growing season. This depended on the weather, growing conditions, driving distance, etc. During each visit, I counted the number of plants and noted their general sizes. The number of adult beetles, larvae, and eggs found on the plants was noted, as well as other signs of LLB presence (such as leaf damage, scat droppings, etc.). I also took notes about

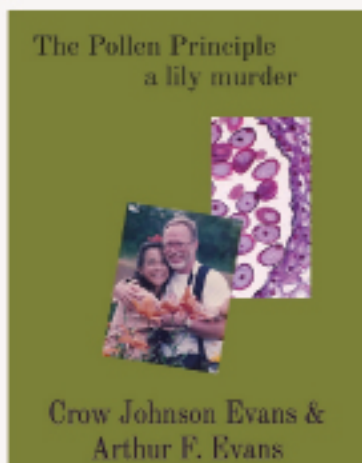
the general health and level of damage to the plants.

These data were approximate, because a number of factors of the life cycle of both the plants and the LLB make it impossible to collect strict quantitative in a large-scale in situ longitudinal study like this. I also added notes about other factors that might influence the data, such as:

- If the owner of the plot had picked off beetles or sprayed with insecticide.
- If the area had been mowed down, foraged by deer, trampled, graveled over, etc. (Photo 4)
- If the lilies were hard to find because they had become overgrown by surrounding vegetation.

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THE POLLEN PRINCIPLE A LILY MURDER



There's been a murder on day one of the annual International Lily Society meeting. The local Chief of Police convinces Kristina—an attractive former escort service owner—to turn sleuth. Disguised as a passionate *Lilium* grower, she attends the conference and has four days to figure out the mystery.

"... A hoot, a howlingly funny mystery for anyone who has played in the garden dirt, hybridized, or admired with amazement the power of lilies..."

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■ When the lilies browned out for the season.

When I compiled the data, I generalized it into broad categories of infestation levels:

- 0 = No clear evidence of presence of LLB.
- 1 = LLB present, but sparse damage.
- 2 = Medium infestation.
- 3 = High infestation.

If two survey plots were very close to each other and showed similar levels of infestation over the years, I combined them into a single population point on the map of the results. However, if nearby plots showed significant differences in levels of infestation, those populations are indicated separately on the map (but appear to be much farther apart than they actually were).

Extirpations and Replantings

Many of the populations of lilies that I found were growing in precarious places, such as roadside drainage ditches, or meadows that were sometimes used as farming fields. And in a few cases, roads were widened and/or land was cleared for a new house in precisely the spot where a plot of lilies was growing. Furthermore, in 2020 a proposal for a new solar farm to be installed was announced, and one of the plots of lilies was growing in a roadside ditch right on the border of the project.

It seemed cruelly ironic to me that in a county that covers 2,840 square miles I would witness the extirpation of a number of plots of lilies measuring just a few square feet within a short span of five years. This presented an ethical conundrum: Should



Photo 4. A mature lily nearly graveled over by road widening.

I allow some populations of lilies to get mowed down every year, just to protect the purity of my data? Similarly, if a culvert project would disturb a small population for just one summer, should I wait to see if they survive and bounce back from the disturbance because not moving would yield valuable data (but at the risk of them being extirpated)?

I decided to make decisions on a case-by-case basis, balancing scientific observations with practical considerations as well as my desire to preserve the lilies. For example, one of the largest populations of lilies that I found in 2018 was historically significant, having been noted in the flora atlas of the county. It was in an area that spanned three different microenvironments: a shrubby riparian slough along

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a creek; a wet meadow (that had been cleared as farmland in the past); and a roadside ditch. I counted about a dozen large plants in the slough and in the meadow, but there were more than 200 stunted plants growing in the drainage ditch, getting mowed down each year. Photos 5 and 6 show what the meadow looked like in 2019 and 2024.

I called the highway superintendent to suggest that his crew should avoid mowing that ditch, but he didn't agree to it. Because of this, I decided to dig out as many of the small/stunted bulbs from the roadside ditch as I could find. I then replanted those bulbs in a variety of places. I replanted some of the bulbs to augment other smaller populations in my survey, but I also replanted some of the bulbs in areas of the county where I hadn't found any lilies. (These are indicated in purple in Figure 2.)

Then, in spring 2020, a farmer plowed up the meadow for planting. On top of that, to get from the road into the field, he drove through the patch of mature plants. I decided that I should remove the rest of the lilies/bulbs from the roadside ditch for replanting, but I should leave the mature lilies in the slough and at the edge of the meadow/field, because that particular meadow/field seems to have historically alternated between being farmed versus fallow; and at the very least the lilies at the riparian edge were partially protected from plowing. I think that I made the right call, because when I revisited the population this summer (2024) the field had been plowed again, but the patch of mature lilies at the riparian edge had recovered and were blooming. (Photo 6)

Ironically, the solar farm that had been proposed (about 400 feet up the road from

this site) was never built, but most of that population of lilies seem to have been extirpated when they filled in the drainage ditch and cleared the hedgerow to prepare for the construction. I found only one lily growing there this summer.

Results

The results of the study are summarized on the map in Figure 2 on Page 13.

Observations and Discussion

By tracking the levels of infestations, this study generated some generalized observations about the impact of LLB on these wild populations of lilies.

- LLB doesn't infest wild populations of native lilies as completely, nor as heavily,

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as it does Eurasian hybrid lilies in garden settings. This corroborates previous ex situ host suitability and preference studies. This difference could be due to the fact that wild lilies don't grow in dense concentrations in the way that lilies are often planted in gardens, or it's possible that chemical differences between North American species versus Eurasian hybrids make them less attractive or effective as feeding/breeding sites to sustain heavy infestations of LLB.

- Even within a heavily infested population, some plants will sustain little damage. (Photo 7) Similarly, nearby plots might not be infested or only lightly infested.
- The level of infestation in a population doesn't necessarily increase in a consistent fashion. It may wax and wane within a season, or between seasons.
- In both the wild and in gardens, the

adult beetle rarely feeds on small plants, and it doesn't lay eggs on short/young plants. This is presumably because a short plant doesn't provide enough foliage to feed the larvae through their development into pupae. The fact that North American lilies generally have less foliage than many Eurasian species, and that they also grow more slowly than Eurasian hybrids, means that North American species can persist as short plants with just one or two whorls of leaves for a number of years. This feature seems to play a large role in our native lilies' ability to withstand infestation by LLB (as well as human disturbances, such as trampling or mowing).

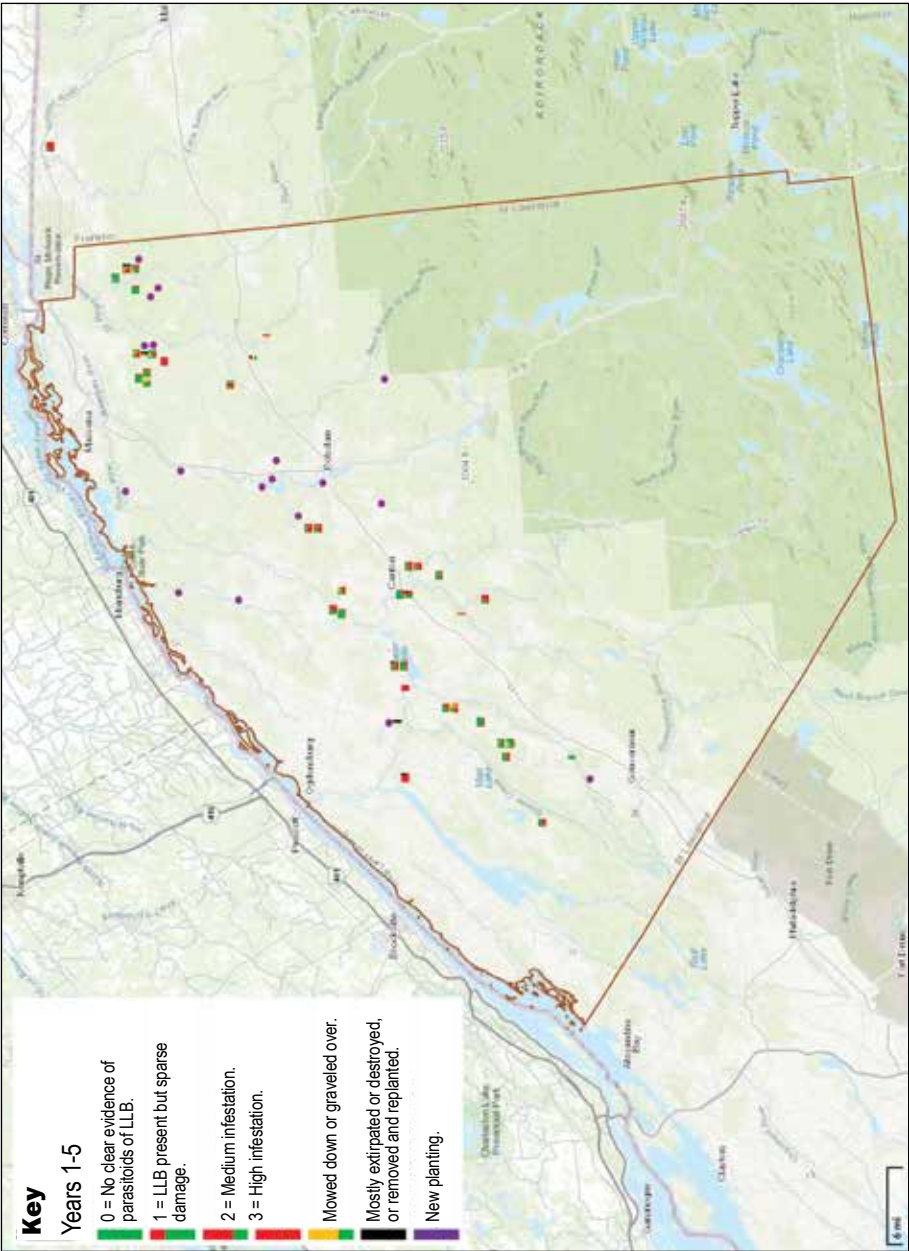
- Weather conditions appear to affect levels of infestation in both short and long term. For example, cold and snow in late spring delays the emergence of the beetle more than it delays the sprouting of the lil-

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Photo 5 (left) and Photo 6. The same meadow in 2019 (left) and 2024. A farmer plowed the field in 2020, and in 2024 it had been plowed again, but a patch of mature *L. canadense* plants at the riparian edge had recovered.

Figure 2. Levels of infestations of LLB in populations of *L. canadense* in St. Lawrence County, N.Y., from 2018-22.



ies; this allows the plants to grow bigger before the season's cycle of infestation begins, which then affects the level of infestation later in the season as well as the size of the plants that will grow the next year.

■ Dry conditions appear to have a significant impact. A dry season, especially an early drought, causes plants to desiccate and go dormant earlier, providing less food to



Photo 7. Comparison of a defoliated lily (above) near an untouched lily (below).

support new broods of larvae, and less food for new adults to eat before overwintering.

■ Mowing, trampling, and browsing by deer and rabbits appear to impact levels of infestation similarly to drought, i.e., decreasing the foliage available for the beetles/larvae, and causing early dormancy.

Thus, the levels of infestation of a population are affected by the complex interactions of a combination of disparate factors:

- The slow and seasonal life cycle of the lilies.
- The ability of the lilies to persist over long periods as small bulbs and nonflowering plants.
- The compressed univoltine life cycle of the LLB.
- The amount and timing of migration of LLB away from their birth plots (which has not yet been studied).
- LLB's preference for tall plants for feeding and breeding.
- The impacts of dry conditions on the senescence of the lilies (i.e., whether they stay green long enough to support the LLB).
- Affects of other types of perturbances, including mowing, trampling, deer/rabbit browsing, etc.

Paradoxes of Survival

The interactions of these factors create an interesting paradox: Factors which appear to reduce the general health of a population of lilies also help to reduce the levels of infestation by LLB. For example:

■ A heavy infestation creates fewer tall plants for feeding/breeding, which leads to reduction of infestation in future years.

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■ Drought conditions, trampling, and deer/rabbit browsing also cause similar setbacks for lily health, but these setbacks also help reduce infestation by the LLB.

■ Mowing of roadside ditches and other not-lethal human disturbances present an extreme example of the paradoxes. On the one hand, mowing prevents the plants from ever growing taller than one or two whorls. This creates a dense colony of stunted plants (possibly clonal) growing from small bulbs. They'll never grow to flowering size if the mowing persists, but they also never grow tall enough to support an infestation of LLB. Furthermore, mowing probably also kills a lot of the beetles and larvae in a plot, lessening the likelihood of an infestation spreading to nearby populations. Thus, even though mowing might appear to be "bad" for a population of lilies, it might paradoxically protect it from heavy infestation (or even extirpation) by the LLB.

While these paradoxes might at first seem surprising, they actually reflect the typical dynamics of classic predator-prey cycles that have been understood by ecologists for many decades, e.g., a predator that feeds on a limited type of prey rarely extirpates it because as the prey becomes scarce the population of the predator declines, allowing the prey to rebound. We usually think of predator-prey cycles as applying to carnivorous animals, but they apply to herbivores as well. In this case, the predator-prey cycles play out rather slowly, primarily because of the slow life cycle of *L. canadensis*.

From a human perspective, we might consider a dense colony of short clonal plants that never grows to flowering size to be "unhealthy," but from an evolutionary

perspective it can be understood as an effective strategy for the lilies to bide time and continue to survive until the dangers of disturbances (whether brought on by infestations of LLB or mowing by humans) have passed.

I began this study because I thought that it might help us figure out ways to "protect" populations of our native lilies from extirpation by the LLB. The bad news is that I learned that some human activities present more of a danger of extirpation to individual populations of lilies than the beetle presents, and that human extirpations can happen a lot faster. The good news is that the paradoxical interactions of the variety of factors will likely allow wild populations of *L. canadense* to survive infestation by the LLB (and some human activities such as mowing) as colonies of small plants, long enough for the eventual spread and establishment of the imported parasitoid biocontrols to protect the lilies when their populations can rebound. **QB**

In spring 2019, Paul Siskind received a grant from the NALS Research Trust Fund to conduct two projects studying aspects of the ecology of the invasive lily leaf beetle in North America. An update was published in the June 2022 *Quarterly Bulletin* ("Adventures in Stalking the Lily Leaf Beetle in the Wild"). Siskind previously wrote a three-part series "Controlling Lily Leaf Beetle, an Integrated Pest Management Approach" published in the March 2017, June 2017, and June 2018 issues of the QB. Along with his primary career as a composer and teacher, he also is a Master Naturalist. Before his retirement, Paul was on the faculty of St. Lawrence University, Canton, N.Y. He lives in northern New York, about 20 miles south of the Ontario border. He grows his lilies in USDA Zone 4b. He can be reached at paul@paulsiskind.com.