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When an invasive plant fails to invade

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In 2012, much of the US Midwest was gripped in one of the most severe droughts on record. While conducting experimental fieldwork at a site in Nebraska during June of that year, I noticed a single musk thistle (*Carduus nutans*; Figure 1) that appeared to be in the bolt or early flowering stage, which is typical for the species at that time. Here, however, two things were unusual: this plant was less than 1 meter tall (with adequate moisture and light, musk thistle typically grows to heights of 1–2.5 meters before flowering), and was only 3 months old (the bolt stage, when it would produce a flowering stem and set seed, typically occurs during the thistle's second year). Interestingly, this plant died less than 3 weeks later, without producing flowers or seeds. Apparently, this plant was unable to successfully spearhead an invasion in this field because it could not complete its normal life cycle during a period of drought.

First introduced into the US from Eurasia in the 1800s (Russell *et al.* 2007), musk thistle has become established in Midwest prairies and can occur as dense monocultures or scattered individuals in open fields (including meadows) or wooded areas. Typically, the species is a short-lived biennial. During its first year, musk thistle develops from seed into a large rosette that remains vegetative throughout the summer and fall and overwinters in a dormant stage; later, in the early spring of its second year, the plant resumes growth, with bolting soon afterwards. The single reproductive stem produces one or more terminal flowers in early to mid-summer and then releases seed through late summer, and afterwards begins to senesce.

So why would there be a single thistle plant – one that appeared to be in the early summer of its first year – close to flowering in the middle of this grassland at this particular time? This question is similar to others that have been asked by invasion biologists, yet to have it play out in the field in real time is truly a rarity and a learning opportunity. By attempting to understand why invasive plants like musk thistle are present in natural areas, we will have a better chance of determining what actions (if any) are necessary to improve their management.

Much is known about the life cycles of plants, including musk thistle. Numerous stress factors – like weather conditions, neighboring plants, and insects – can cause musk thistle to shift from a biennial to an annual, thus altering what would be considered normal growth and development. This change in phenotype due to differing conditions is expressed by a single genotype and is referred to as phenotypic plasticity. The complexity of phenotypic plasticity makes studying the phenomenon a challenge.

Although many would not think an unsuccessful invasion to be important, it was puzzling why a musk thistle would attempt to establish in the midst of such severe conditions and with access to only limited resources. Toward the middle of 2012, as the drought conditions intensified, reduced growth of perennial grasses created canopy gaps, which allowed the early germinating musk thistle to grow, but then to die prematurely later on. There was no evidence of insect feeding and the microclimate conditions (such as soil moisture) were uniform throughout the area. Was this an instance of an invasive plant species adapting to extreme climate events, evidence of phenotypic plasticity, or both?

With adequate light and enough early spring moisture, the musk thistle plant in Figure 1 was able to quickly germinate and emerge, but it is unknown what triggered the plant to bolt without having the physiological capacity to cope with the extreme drought conditions that were progressively worsening. Phenotypic plasticity is an important trait because it allows one or a few newly introduced invasive plants to acclimate in previously unoccupied and competitive habitats (Sultan 2003). In addition, phenotypic plasticity may arise in response to new selection pressures (eg extreme drought events) in a particular range of introductions (Hierro *et al.* 2005; Chun 2011). Under intense conditions, the individual musk thistle was exhibiting phenotypic plasticity, but its failure to flower and set seed likely meant it had not acquired the proper traits to successfully reproduce.

In general, grasslands of the Midwest have been less susceptible to invasion by non-native plants than grasslands in arid western regions due to excessive perennial grass biomass accumulation under prevailing temperate climate conditions (hot, humid summers with cold winters; average annual precipitation ~762 mm). Because the climate of many western US states mimics that of the Mediterranean region, western grasslands are more prone to invasion by plants of Mediterranean origin. With increasing frequency of extreme drought due to climate change, conditions that promote invasion might be exacerbated in the western US and for the first time become a concern in the Midwest.

Within Midwest grasslands, musk thistle can change growth patterns in response to perturbations such as drought; in this case, however, it resulted in a failed attempt to establish in a Midwest short-grass prairie. Most failed attempts at invasion and establishment by non-native plants are undocumented. Bradley *et al.* (2010) suggested that invaders will have an advantage under extreme drought conditions if the resilience of native communities is impaired. Yet those same conditions could also lead to reduced fitness in the invading species.

More research is needed that addresses why many invasions are unsuccessful and what changes in the natural landscape, including severe drought, could be contributing to these failures. Using several examples, Zenni and

Figure 1. Carduus nutans *growing among perennial grasses of the US Midwest during the early onset of an extreme drought.*

Nunez (2013) discussed reasons for a species failing to naturalize or failing to invade after naturalization; yet much is still unknown and such instances are often difficult to detect. I would advocate for more detailed studies on invasion failures – perhaps this musk thistle example could contribute. One thing that we can learn in the near term is which invasive plant characteristics can be targeted for improved management; in some cases, however, such as musk thistle during extreme drought, perhaps we don't need to do anything at all.

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