Allelopathy: plant chemical warfare

by Kyra Clark

Our native Lupine wages chemical warfare on other plants by releasing alkaloids that inhibit germination or growth.

How does one plant out compete another? How can invasive species so quickly take over well-established areas? Some plants have specialized physiological adaptations that allow them to better access resources, some have unique germination cycles that allow them to sprout earlier than others, while many nonnative invasives take advantage of not having natural predators in their new environment. There are countless ways plants compete with one another, but one of the most interesting ways plants can compete in this battle for survival is with chemical warfare.

Several native plants and numerous invasive plants are allelopathic. Allelopathy describes the process whereby plants, algae, bacteria, coral, or fungi produce and release an "allelochemical", which positively or negatively influences the germination, growth, survival, or reproduction of a neighboring organism. Although allelopathy has a broad definition, it is generally used when one plant negatively affects nearby plants. This process is different from resource competition, but it does lead to reduced competition from nearby plants.

Allelopathic plants vary in the chemical compounds they use, how these compounds are formed, where they are stored, how they are released, and their modes of action in target plants. All allelochemicals, however, are secondary metabolites (not required for growth, development, or reproduction) and once released affect the survival or health of neighboring organisms. Allelochemicals are rarely auto-toxic, mean-

ing plants do not release enough toxic compounds to negatively affect its own growth.

Plants store allelochemicals in a single location, multiple locations, or throughout the entire plant. They are often found in the roots, leaves, pollen or buds. Allelochemicals are introduced into the environment by being exuded (released) from roots, released from decaying plant matter, leached from the plant, or volatilized (become a gas).

Allelochemicals can be classified under several groups of compounds. These groups describe an infinite number of compounds found in plants but only a select few within each group are actually allelopathic. Over the years there has been a lot of research on allelochemicals, but because they can be difficult to isolate and may have several functions, it is hard to determine if a compound is truly allelopathic.

Here in Alaska, there are both native and invasive allelopathic plants. Lupines (*Lupinus* sp.) are a familiar plant to most Alaskans and all lupine species release an alkaloid allelochemical. The alkaloid group includes recognizable compounds like morphine, nicotine, and caffeine. Allelopathic alkaloids can target multiple sites that inhibit seed germination or growth by impeding certain enzyme functions, photosynthesis, respiration, or DNA/RNA processing enzymes.

The highly invasive Spotted Knapweed (*Centautea stoebe*) uses an allelochemical within the flavonoid group of compounds. Allelopathic flavonoids generally inhibit seed germination and limit root or shoot length by blocking the H+-ATPase enzyme, the electron transport chain, or oxygen uptake by mitochondria. Spotted Knapweed exudes this flavonoid from its roots, which then leads to death of the root systems in nearby plants.

Another invasive plant that exudes allelochemicals from its roots is Garlic Mustard (*Allaria petiolafa*). Garlic Mustard releases a type of glucosinolate compound that, once released, becomes volatile and fills soil pores as a gas where it then acts on neighboring seeds. Glucosinolates can either be volatile or nonvolatile but, either way, they inhibit seed germination by targeting the enzymes necessary for glycolysis and respiration.

Quackgrass (*Elymus repens*), a common grass, releases a hydroxamic acid. Hydroxamic acids are usually exuded from roots (which is what quackgrass does) or released from degrading plant parts. These compounds inhibit seed germination and growth by blocking H+-ATPase enzyme and root growth. Hydroxamic acids often work with phenolic compounds, another group containing allelochemicals. However, phenolic compounds may not be true allelochemicals as they have a generalized cytotoxicity when in mixtures, but individual phenolic compounds are poorly cytotoxic when isolated.

The last three common groups of compounds that contain allelochemicals are quinones (e.g., Black Walnut), terpenoids (e.g., Rosemary) and polyacetylenes (e.g., Russian Knapweed). All of these groups use different modes of action to inhibit seed germination or growth.

One invasive species that has notoriety in Alaska is Orange Hawkweed (*Hieracium aurantiacum*). This hawkweed is pollen-allelopathic, meaning that allelochemicals are carried in wind-dispersed pollen and fertilized seeds, a strategy that allows it to rapidly establish in new areas. Meadow Hawkweed (*Hieracium caespitosum*) may also be pollen-allelopathic and/or may release allelochemicals in their decaying leaves. Our native Cottonwood is also allelopathic, releasing allelochemicals in decaying leaves that inhibit herbaceous seed growth nearby.

Both native and nonnative invasive species use allelopathy to their advantage. Because native plants co-evolve, the effects of native allelopathy seem to be more limited, perhaps because immunity or resistance becomes a rapidly-selected trait. On the other hand, when nonnative invasive allelopathic species enter a new environment, they quickly spread as native plants have not adapted to counteract these new allelochemicals.

The fact that certain plants produce specific compounds with the sole intention of harming neighboring plants for their own gain is both ruthless and fascinating. Occasionally the plants that appear the most robust and best suited for an environment are not the ones that survive—sometimes survival of the fittest come down to the production and release of tiny compounds. That's right, plants just got a little more interesting.

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