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KEY FACTORS INVOLVED IN THE ESTABLISHMENT OF INVASIVE, NON-NATIVE WEED SPECIES IN THE UNITED STATES AND AUSTRALIA – WHERE WILL THE RESEARCH GO FROM HERE?

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Ecology of weed invasion.

Weeds have invaded both terrestrial and aquatic areas across Australia, with some dramatically reducing our productivity and quality of life. They have co-evolved with our systems of land use, and the methods we have developed for their management have proven to be major contributions to modern agriculture. Despite these developments, weeds continue to cost the global economy billions of dollars annually (Westbrooks 1998). In Australia, it is estimated that losses due to invasive weeds total more than 4 billion dollars annually (Cunningham et al 2004). Due to their remarkable ability to reproduce and spread, invasive terrestrial weeds are impacting our agricultural productivity, reducing the quality of our pastures and livestock, and also limiting our ability to preserve and protect the diversity of native species and landscapes (Levine 2000; Lonsdale 1999; Westbrooks 1998).

In Australia, many plant species initially introduced as food and fodder, medicinals, potherbs and ornamentals have become highly invasive. Some of these species have become invasive within years of being introduced, while others have exhibited long lag times after initial arrival before becoming widespread. It is not unusual for many weed species to have exhibited long lag times after initial arrival in Australia before becoming widespread. This has been well documented in Europe (Kowarik 1995) but is less well documented in Australia. Lag time to successful invasion may be influenced by environmental conditions experienced at the point of introduction, conditions experienced after introduction, and/or the frequency of unique introductions within a region.

There are likely many factors involved in a plant's ability to become a successful invader in a new non-native region. These included the following:

- 1) Ability to successfully reproduce by seed and disperse huge quantities of seed
- 2) Multiple means of reproduction; perennials can also reproduce vegetatively by underground plant parts
- 3) Ability to tolerate environmental stress and adapt to a changing environment
- 4) Exhibit diversity – genetic diversity versus phenotypic or morphological diversity
- 5) Ability to produce phytotoxins which limit the spread of neighboring plants and toxins which impact herbivores, pathogens and insects and serve as plant protectants

Although it is not currently understood what factors are implicated in a successful plant invader's ability to become highly invasive, it has become clear that rapid evolutionary change in invasive weeds, both annuals and perennials, is a common ecological phenomenon, particularly in ecosystems that are perturbed by human disturbance (Elton 1958; Levine 2000). Biological invasions that are fostered by rapid evolutionary change raise the question of the relative importance of phenotypic plasticity and potential for genetic change among weedy species.

In my research program at CSU, we are interested in the following related research ideas:

- 1) What are the factors that allow a non-native invasive to become most successful in an invasive site?
- 2) What is the time frame for invasion success? – how long after a species is introduced will it become widely invasive?
- 3) Which modes of reproduction and dissemination contribute to its ability to spread?

- 4) Does rapid genetic change in the species (since the time it was introduced) contribute to its ability to become invasive?
- 5) Does the plant exhibit allelopathic tendencies that contribute to invasion success? – does it produce toxins that impact other organisms?

Black and pale swallow-wort – examples of invasion success in the Northeastern U.S. and Canada

My research program in the U.S. recently focused on the study of non-native invasive weeds that impacted pasture, cropping sites and natural areas across New York State. One set of related weeds was of great interest to us, as they are closely related perennial vines that were introduced to New York and Canada, but at different times and places. They have since invaded and their ranges of infestation have recently converged across N.Y. State. Black and pale swallow-wort (*Vincetoxicum nigrum* and *V. rossicum*) are invasive plants that were introduced into the Northeastern U.S. over 100 years ago from the Ukraine and the Iberian peninsula, respectively (Di Tommaso et al. 2005). In their native range, these vines are relatively rare and non-invasive, but in invaded areas of North America they have spread aggressively and establish dense thickets. They have replaced native flora, threatened rare populations of endangered plants and whole ecosystems in western NY, and led to reductions in insect and bird species in old-field sites (DiTommaso et al. 2005, Douglass et al. 2009). They are now moving into pasture and cropland settings where they have become problematic in no-till settings, in orchards, nurseries and pastures as well as natural settings such as parks and reserves. Some have been forced to abandon their land as they are extremely difficult to control, either chemically or using cultural practices.

Vegetatively, the two species are nearly identical and are distinguishable mainly by their flower color and follicles. Both species produce large quantities of seed, many of which are polyembryonic, meaning that they have more than one embryo producing a viable plant per seed. While these species have a large root to shoot ratio, with a large underground portion of biomass, it appears that the rhizome-like roots formed by black swallow-wort do not contribute to the species ability to reproduce or spread (Averill, 2009). Spread appears to be associated mainly with seed dispersal. Grazing animals typically avoid this species in pastures, as it produces a number of secondary products that make it unpalatable. However, if left unchecked, it rapidly spreads throughout grazing lands where it had initially established.

Black and pale swallow-wort were traditionally used as medicinals in their native ranges, containing numerous secondary products of interest. The roots of related swallow-wort species are known to contain the poisonous glycoside vincetoxin (Weston et al. 2005). Others have reported numerous alkaloids in the stems, fruit, roots and leaves of the plant which likely contribute to its anti-fungal, anti-bacterial and anti-feedant properties. We do know that the plants, when consumed in small quantities, can be extremely toxic to grazing animals, in studies performed with goats who ingested these materials. Alkaloids are known to be potent inhibitors of DNA and protein synthesis and may play a function in interrupting neurotransmissions in mammalian systems (Douglass et al. 2009; Wink et al. 1999).

I will present some of our work evaluating both black and pale swallow-wort infestation across New York State. This work can be used as a model, in fact, for some of the studies we wish to conduct on many non-native invasive weeds in Australia. In our studies in New York State, we wished to obtain more basic information about the biology and ecology of these two little-studied weed pests, so we could better understand how to manage this species and consider the potential for the development of biocontrol strategies. In particular, we wished to study the invasive range of these two species across N.Y. State, their ability to spread across this invasive range in time, their ability to suppress other neighboring plants by production of plant toxins, or allelopathy, as well as their inherent genetic variability or genotypic diversity. We had observed that various populations exhibited great physical diversity and we wondered if this diversity also had a genetic basis versus an environmental basis. Our findings will be summarized in my presentation and are the subject of

several papers by Cameron Douglass, a former student who worked on this research project for his M.S. degree, that are currently submitted for publication.

Most recently, my program in Australia has been developing, with an emphasis on root physiology as well as ecology of weeds of pasture, crop and rangelands of Southern Australia. We are particularly interested in one weed which has become widely invasive across millions of acres of pasturelands and yet has been little studied in the literature.

Paterson's curse – a noxious non-native invasive.

Paterson's curse (*Echium plantagineum*), also known as Salvation Jane or Riverina Bluebell, is a plant that has become widespread in inland Australia, from south-east Queensland, to New South Wales, to southwest Western Australia (Adams, 2000; Piggin 1982). Paterson's curse was thought to be introduced to Australia in the 1880's from Europe as an accidental contaminant of pasture seed and as an ornamental plant. Its name is thought to derive from the experience of the Paterson family, early settlers around Albury NSW, which brought the seed from Europe to beautify their garden, but instead observed infestation of pastures and grasslands for miles around (Carter, 2009; Land Care Notes, VDPI). Originally a native of the Mediterranean, Paterson's curse has now become naturalized over 30 million hectares of grazing land. In 2002, it was estimated to cost the Australian wool and meat industries over A\$125 million per year (Carter, 2009; Piggin, 1982).

Paterson's curse can completely dominate a mixed community of grasses and forbs as it is highly dominant and suppresses growth of neighboring species over time. A prolific reproducer, it has been estimated to produce up to 30,000 seed per square meter (Burdon et al., 1988; Carter, 2009; Piggin 1982). It is thought that seed remains dormant for up to 6 years in the soil seed bank, but most appears to germinate within 2 years. Seed germination is encouraged by high levels of moisture encountered in the fall and moderate soil temperatures. It is also highly resistant to drought, and dominates grasslands in exceptionally droughty conditions, germinating rapidly after drought is broken. Paterson's curse is also a serious threat to natural areas and has potential to spread to woodlands, native prairies, and dry upland slopes. Recently, it has become a noxious weed in Oregon in the USA, after first detection in 2003 (Butler, 2004).

Seed is also readily dispersed on animal fur, by bird or animal ingestion, via water and also as a hay or grain contaminant, with spread potentially associated with movement of grain and hay along the rail lines through Southern Australia. Its invasion may also have been assisted by habitat degradation as well. Livestock overgrazing and the introduction of the rabbit has caused degradation of bush and grasslands, and appears to be associated with rapid infestation by Paterson's curse (Bird, 2007; Piggin, 1982). Despite the information available in recent on-line bulletins and the few publications available, much of which appears to be anecdotal, little has been published in refereed publications on its biology and ecology or its ability to interfere with native plant growth.

Toxicity and chemistry of Paterson's curse.

Paterson's curse is known to be extremely toxic to livestock, particularly horses and pigs (Adams, 2009; Peterson and Jago, 1984). It produces a series of pyrolizidine alkaloids in its shoots which when metabolized in mammalian organs cause cell death in the liver, kidneys and lungs (Peterson and Jago, 1984). Although horses are most sensitive to these alkaloids, grazing sheep can tolerate their presence, but often show serious impacts upon wool quality and weight, up to a year after ingestion. Under normal conditions the plant is often avoided by grazing animals, likely due to its coarse leaf hairs and bitter taste. However, in droughty conditions or when Paterson's curse becomes the dominant species, it is less avoidable by livestock. It is almost impossible for most livestock not to have some intake of this weed in its rosette form when pastures are green and well-established in spring. Over time, it causes gradual and accumulative liver damage in livestock (Adams, 2009).

We have recently observed that Paterson's curse exhibits unique morphological and ecological traits which would lead one to suspect that it is highly allelopathic to neighboring plants

as well as toxic to mammalian systems. In particular, it exhibits two types of root hairs, long and short, both of which appear to be involved in active exudation processes in the plant (Tsai et al 2003). We have discovered that the epidermis of both its younger lateral roots and older taproots produce extremely unusual, bright red- colored chemical constituents which are localized in the outer epidermal layers of its roots. Upon microscopic investigation, the compounds appear to be contained within vesicles or vacuoles which are produced intracellularly in the epidermis of roots (McCully and Weston, personal observation 2009). Most production occurs in younger root tissue, as older sloughed off epidermal cells likely contain oxidized or polymerized by products or metabolites of these components. This oxidative process apparently turns the older roots a remarkable black or dark red color, whereas younger roots exhibit a bright red epidermal layer. Although production of unique secondary products in roots is not unknown and is reported in plants which are known producers of phytotoxins, antimicrobials and antifungal constituents (Bertin et al. 2007; Duke 2007; Weston and Duke, 2003), the production of red pigmented derivatives in higher plants is very unusual. Brigham et al 1999 reported the existence of pigmented naphthoquinone derivatives of shikonin in *Lithospermum erithrorhizon* roots. In this case, pigment production could be induced by abiotic and biotic elicitors in cell culture. In the developed root itself, the pigment was observed in root tips, root hairs and outer layers of epidermal cells of lateral roots, all of which were red with the presence of the pigment. The pigment consisted of a mixture of naphthoquinones, several of which were biologically active. These compounds proved to be potent inhibitors of certain soil microbes. Hyphal presence of various pathogenic fungi caused an increase in production of these constituents in cell suspension cultures.

Other plants in the borage family. Interestingly, the *Lithospermum* spp. along with Paterson's curse are members of the borage family. Borage family members are distributed worldwide and naphthoquinones from these plants have been used as colorants for food, cosmetics and fabrics (Jain and Mathur, 1965; Tabata and Fujita, 1985). They also have medicinal applications and demonstrate antitumor, anti-inflammatory and antimicrobial activity (Tabata and Fujita, 1985). Shikonin and its derivatives are recognized as valuable pharmaceutical agents because of their antimicrobial properties (Brigham et al., 1999). However, it seems likely that these compounds also play an important role in plant defense in the rhizosphere (Uren, 2000). After evaluating the preliminary chemical composition of the extracts of both younger lateral and older tap roots of Paterson's curse, we have evidence that naphthoquinones are also present (Weston, unpublished results 2009). Naphthoquinones such as juglone are active as allelochemicals (Bertin et al., 2003; Binder et al., 1989; Weston and Duke 2003) and also in plant –insect interactions. They are known inhibitors of electron transport (Brigham et al, 1989; Hauska, 1988). Many of these compounds appear to be produced in response to multiple stresses in the environment and lead to the further production of antimicrobial compounds by plants (Bertin et al. 2003; Chappell, 1995; Dixon and Paiva, 1995; Weston and Duke, 2003). Therefore, it is of considerable importance ecologically to study the role of these unknown and recently discovered constituents produced by Paterson's curse.

Future research plans to focus on 1) identification and localization of these interesting root constituents produced by Paterson's curse, along with localization of production of the toxic alkaloids produced by the weed. 2) study of the role of these constituents in allelopathy and anti-herbivory mechanisms used by members of the Borage family 3) the basis for plant and population variation in morphology – are the differences associated with genotype or phenotype? 4) can we develop a predictive tool to using diagnostic metabolomics in grazing mammals to predict or test for toxicity after ingestion?

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