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The Potential for Herbicide Resistance in Non-Native Plants in Florida's Natural Areas

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ABSTRACT: There are several alternative herbicides with different modes of action for control of invasive plants in natural areas. Of the four classes of herbicides commonly used on invasive plants in natural areas of Florida, the acetolactate synthase (ALS) inhibitors, imazapyr, imazapic, and metsulfuron methyl, are the most likely to select for resistance. Invasive plants that have attributes such as numerous seed or spore production and log distance dispersal capabilities are most likely to develop resistance to herbicides following repeated application. In Florida, these species include Old World climbing fern (*Lygodium microphyllum*), cogongrass (*Imperata cylindrica*), torpedo grass (*Panicum repens*), and tropical soda apple (*Solanum viarum*). The best scenario for treatment of invasive plants in Florida's natural areas, to minimize potential for development of resistance, is to rotate herbicides with different modes of action or use tank mixtures of two or more herbicides with different modes of action.

Index Terms: herbicide resistance, natural areas, Florida

INTRODUCTION

Herbicides are chemicals used to control unwanted plants. They target specific plant processes such as amino acid production, growth regulator hormones, and photosynthesis. In some cases, herbicides can be used, through a variety of mechanisms such as deactivation or metabolism and dosage rates, to selectively control specific weed species without harming other vegetation. Herbicides have been extensively used for over 60 years in a variety of crop and non-crop areas (Anderson 1996). Repeated use of certain herbicides has resulted in the lack of control for certain species, which lead to the discovery of herbicide resistance.

In 2005, the Florida Department of Environmental Protection's Bureau of Upland Invasive Plant Management funded over $9.4 million for invasive plant treatment in upland habitat that consisted primarily of herbicide treatment (FLDEP 2006). The majority of the county, state, and federal agencies have invasive plant management units whose sole purpose is controlling invasive plants. With the large number of invasive plant species that occur in Florida's natural areas (Gordon 1998; Langeland and Burks 1998), it is likely that some invasive plants may develop resistance to one or more herbicides, creating greater problems for land managers.

Herbicide resistance is the inherited ability of a plant population to survive herbicide application that is normally lethal to the majority of the plants of that species (Powles et al. 1997). Plant resistance to herbicides was first reported by Ryan (1970) and has been increasing in frequency each year (Heap 2007). Currently, there are ca. 313 biotypes of plants that are resistant to herbicides (Heap 2007).

In agricultural systems where multiple weeds are targeted, the development of herbicide resistance by weedy plants has been associated with the repeated use of a single herbicide mode of action (Kudsk and Streibig 2003). The development of resistance to herbicides by plants is similar to resistance development of insecticides by insects (Georghiou 1986). Within the population of a particular weedy species, there exists a small fraction of the population that is less sensitive to the herbicide (Georghiou 1986). Broad-scale resistance to herbicides occurs only if the resistance trait is present in the population and subsequently selected for by herbicide use (Maxwell and Mortimer 1994). Additionally, the development of herbicide-tolerant crops amplifies the risk of increased selection pressure for resistance on weed species that are sprayed several times annually with the same herbicide type in herbicide-resistant crop systems (Kudsk and Streibig 2003).

Herbicide resistance can occur through target-site or non-target site based mechanisms (Heap and LeBaron 2001). Target-site resistance is the most common mechanism of resistance and occurs when enzymes needed for plant metabolism are modified (generally an altered amino acid sequence), which eliminates the ability of the herbicide to inactivate the enzyme (Heap and LeBaron 2001). Weeds resistant to target-site inhibiting herbicides are typically controlled by including an herbicide tank mix with a different type (i.e., targets a different enzyme or target site of action) or rotating with a different herbicide type. Non-target site resistance is less common and occurs when the plant metabolizes or sequesters the herbicide making it inactive or reducing the amount that is translocated through the plant. Populations of weeds that exhibit non-target site resistance may be of greater concern since resistance also develops to herbicides of different modes of action (Preston 2004).

Additionally, some plants develop cross resistance to several types of herbicides with the same mode of action or multiple-resistance to two or more types of herbicides with different modes of action (Moss 1990; Christopher et al. 1991; Walsh et al. 2004). Some weeds in agricultural systems have become resistant to low dose, high potency herbicides, such as acetolactate synthase (ALS) inhibitors, after only several years of exposure, indicating that this class of herbicides exerts a strong selective pressure on plants (Lovell et al. 1996; Heap 1997). It also suggests that the frequency for resistance may be higher with this chemistry class. The increase of resistance in weeds to ALS inhibitor herbicides may have led to the development of herbicide resistant crops because it was believed that better weed control may be obtained in a glyphosate, an EPSP Synthase inhibitor-based cropping system (Owen and Zelaya 2005). ALS inhibitor herbicides are effective against broadleaf plants and some grasses, while glyphosate is a non-selective herbicide effective against all plants.

There have been at least 35 herbicide resistant weed biotypes reported from roadsides, railroads, and industrial sites (Heap and LeBaron 2001) that are typically treated with herbicides at a frequency much less than production agriculture sites. Thus, the potential for development of resistance in natural area weeds is high. One advantage to treating natural area weeds versus agricultural weeds is that there are often several alternative herbicides with different modes of action for control of invasive plants in natural areas. It is therefore believed that weeds in non-crop sites that develop resistance to one herbicide may easily be treated with an herbicide with a different mode of action or tank mixture of two herbicides (Heap and LeBaron 2001).

HERBICIDES USED IN NATURAL AREAS OF FLORIDA

The primary herbicides used to control invasive plants in Florida natural areas are listed in Table 1 (Langeland and Stocker 1997). These include acetolactate synthase (ALS) inhibitors (imazapyr, metsulfuron methyl, and imazapic), EPSP synthase inhibitors (glyphosate), synthetic auxin (triclopyr and 2,4-D), and photosystem II inhibitors (hexazinone). The EPSP synthase and synthetic auxin herbicides have resulted in less resistance in agricultural weeds than the ALS inhibitors and photosystem II inhibitors. The ALS and photosystem II inhibitors now account for the majority of the agriculture weeds that have developed resistance (Heap 2007).

The ALS inhibiting herbicide class was introduced commercially in 1982. The major advantage of ALS herbicides is their high specific activity and low dosage rate, which is often 100 times lower than conventional herbicides such as glyphosate, triclopyr, and 2,4-D (Fairbrother and Kapustka 2001). However, since 1982, there are now more weed species (n = 95) resistant to this class of herbicides than any other class (Tranel and Wright 2002; Heap 2007). Weed biotypes that have developed resistance to ALS herbicides seldom exhibit cross-resistance to herbicides with other modes of action (Boutsalis and Powles 1995); thus, alternative herbicides are available to treat resistant biotypes. In Europe, where ALS herbicides have been used in rotation with herbicides that act through a different mode of action, there have been few weeds that have developed resistance to ALS herbicides (Heap 1997).

Glyphosate was introduced commercially in 1974 and is one of the most widely used herbicides in the world (Baird et al. 1971). Until recently, this compound was primarily used in natural areas and industrial sites; with the advent of herbicide resistant crops, its use has magnified greatly. Yet, with widespread use over ca. 31 years, only eight weed biotypes have developed resistance to glyphosate (Heap 2007). However, glyphosate-resistant crops have only been available for a relatively short period, and this increased pressure is thought to greatly increase the likelihood of resistance development in weeds (Owen and Zelaya 2005). Horseweed (*Conyza canadensis*)

Table 1. The most commonly used herbicides in natural areas of Florida (Langeland and Stocker 1997).

Herbicides used in Natural Areas	Product Name	Mode of Action	Number of Resistant Plants (Heap 2007)	Chemical Family
Glyphosate	Roundup, Rodeo, etc.	EPSP Synthase	8	Glycines
2,4-D	2,4-D	Synthetic Auxin	24	Phenoxy
Triclopyr	Garlon 3A and 4	Synthetic Auxin		Carboxylic acid
Imazapyr	Arsenal	ALS Inhibitor	93	Imidazolinones
Metsulfuron methyl	Escort XP	ALS Inhibitor		Sulfonylureas
Imazapic	Plateau	ALS Inhibitor		Imidazolinones
Hexazinone	Velpar	Photosystem II Inhibitor	65	Triazinone

developed resistance to glyphosate within three years of use in glyphosate-resistant soybeans (VanGessel 2001).

Several factors may contribute to the lack of resistance from glyphosate use. These include lack of soil residual activity and the absence of metabolic degradation or deactivation of glyphosate by plants (Baylis 2000). Rigid ryegrass (*Lolium rigidum*) developed resistance to glyphosate after 10 treatments over a 15-year period, providing a forewarning that other weeds may eventually become glyphosate resistant following multiple treatments (Heap 1997). Italian ryegrass (*Lolium multiflorum*) developed resistance to glyphosate after being treated three times annually for 8-10 years (Perez and Kogan 2003). Recent evidence also indicates that a weedy morning glory (*Ipomoea purpurea*) of agricultural sites in the southeastern United States has developed resistance to glyphosate (Baucom and Mauricio 2004). Some concern has been voiced that weeds associated with glyphosate-resistant crops may spread into natural areas (Marshall 1998), but most weeds of agroecosystems are poor competitors outside the agricultural environment (Hancock and Hokanson 2001).

Synthetic auxin inhibiting herbicides, such as triclopyr and 2,4-D, were first discovered in the 1940s but only 24 weeds to date have developed resistance to this class of herbicides (Heap 2007). The first reported case of an auxin resistance weed was from New Zealand in 1981 (Heap 2007). Auxin inhibiting herbicides are selective towards broadleaf plants and have little effect on most grasses. Yellow starthistle (*Centaurea solstitialis*) is a broadleaf weed of rangelands in the western United States and has developed cross-resistance to four auxin inhibitors, including triclopyr and 2,4-D (Miller et al. 2001). However, considering the heavy use of this class of herbicides over the past eight decades, relatively few weeds have developed resistance when compared to ALS herbicides. For example, 2-4,D has been used for almost 60 years in Florida to control water hyacinth (*Eichhornia crassipes*) without the development of resistance (FLDEP 2005).

Photosystem II inhibitors were introduced in the early 1950s and have 65 weeds or biotypes with resistance (Kudsk and Streibig 2003; Heap 2007). The first reported case of herbicide resistance for any weed (*Senecio vulgaris*) was reported for photosystem II inhibitors by Ryan (1970). In 1997, it was estimated that more than three million ha were infested with photosystem II inhibitor resistant weeds, but these weeds can be controlled with herbicides of different modes of action (Heap 1997). Photosystem II inhibitor herbicides, such as hexazinone, are only occasionally used in natural areas in Florida. They are used in forestry, pastures, rangelands, and right-of-way areas.

PROSPECTS OF NATURAL AREA WEEDS DEVELOPING HERBICIDE RESISTANCE

Based on statistics compiled by Heap (2007), there is a greater chance of invasive plants in natural areas developing resistance to ALS inhibitor and photosytem II inhibitor herbicides than synthetic auxin and EPSP synthase inhibitor herbicides. Factors that contribute to resistance in plants may include the repeated use of a single herbicide over large areas, little or no use of other herbicides with alternative modes of action, high efficacy of herbicides on the plant at the rate used, and long soil residual activity of the herbicide (Tranel and Wright 2002). High seed production combined with a high germination rate may accelerate herbicide resistance, because susceptible plants are removed and individuals that retain resistant genes remain in the population (Prather et al. 2000).

The first occurrence of herbicide resistance to fluridone in an aquatic weed was hydrilla (*Hydrilla verticillata*) in Florida in 1999. The mechanism of this resistance was recently reported (Michel et al. 2004), and now several populations are currently resistant to fluridone. Fluridone is the only approved systemic herbicide approved to treat hydrilla (Michel et al. 2004). Fluridone was approved for aquatic use in 1986, so Florida populations of hydrilla have developed resistance to this herbicide in less than 20 years. Hydrilla biotypes resistant to fluridone were found in Florida lakes that were treated several times (Michel et al., 2004). Dotted duckweed (*Landoltia punctata*), a non-native floating aquatic plant, has developed a 50-fold resistance to diquat and cross-resistance to paraquat (Tyler Koschnick, University of Florida, pers. comm.). These aquatic examples from Florida appear to follow a trend observed in California where herbicide resistance is most widespread for aquatic weeds in commercial rice fields (Prather et al. 2000).

Perennial plants, including those with vegetative reproductive structures, are less likely to develop resistance than weeds with annual life cycles, which produce abundant seeds and have greater genetic diversity (Prather et al. 2000). High seed production and germination rates increase the likelihood that a resistant biotype will occur within a population of plants as susceptible plants are eliminated by follow-up treatments. The majority of the invasive plants of Florida's natural areas are perennial or woody plants; thus, it would be expected that resistance for most invasive plants in natural areas of Florida is less probable than in agricultural systems where the majority of the weeds are annuals.

No shrubs or trees are known to have developed resistance to herbicides (Heap 2007). Melaleuca (*Melaleuca quinquenervia*) and Brazilian pepper (*Schinus terebinthifolius*) exhibit some of the characteristics of plants that have developed herbicide resistance. These characteristics include: (1) invasion over large areas in central and south Florida, (2) abundant seed production, and (3) repeated herbicide treatments on many populations. It could be theorized that multiple treatments on these two invasive plants over large areas in Florida would have been selected for resistant biotypes; but, at present, this has not been observed. In addition, several herbicides with different modes of action (e.g., glyphosate, triclopyr, and imazapyr) are approved for treatment of these plants, and biocontrols have been released for both species. Moreover, most large scale aerial treatments of melaleuca stands use tank mixes of imazapyr and glyphosate. Thus, if a highly invasive shrub or tree in Florida's natural areas develops resistance to an herbicide, there are alternative herbicides with different modes of action that can be used to control these species.

Invasive plants in natural areas of Florida that appear to be the most susceptible to developing herbicide resistance are grasses. Many invasive grasses in Florida reproduce both sexually and vegetatively, produce numerous amounts of seeds, are difficult to eradicate, and require multiple herbicide treatments for control. In agricultural systems, the grass family has 27 species that have developed resistance, cross-resistance, or multiple-resistance to the four classes of herbicides typically used in natural areas (Heap 2007). In natural areas, there are several invasive grasses, including West Indian marsh grass (*Hymenachne amplexicaulis*), cogongrass (*Imperata cylindrica*), silk reed (*Neyraudia reynaudiana*), torpedo grass (*Panicum repens*), Napier grass (*Pennisetum purpureum*), natal grass (*Rhynchelytrum repens*), and paragrass (*Urochloa mutica*) (Langeland and Burks 1998; FLEPPC 2005). Control of these grasses is difficult and requires multiple applications of herbicide, possibly creating the selection pressure needed to develop herbicide resistant biotypes.

Other families that have developed herbicide resistance in agricultural systems and that have related invasive species in Florida's natural areas include morning glory (Convolvulaceae), dayflower (Commelinaceae), spurge (Euphorbiaceae), and nightshade (Solanaceae) (Heap 2007). In natural areas, members of these families include water-spinach (*Ipomoea aquatica*), green wandering Jew (*Tradescantia fluminensis*), Chinese tallow (*Sapium sebiferum*), wetland nightshade (*Solanum tampicense*), turkey berry (*Solanum torvum*), and tropical soda apple (*Solanum viarum*) (Langeland and Burks 1998). Of these, tropical soda apple has been the most problematic, invading both agricultural and natural areas of Florida. A close relative of tropical soda apple, black nightshade (*Solanum americanum*) is the most prevalent herbicide-resistant weed in Florida (Heap 2007) exhibiting resistance to paraquat.

Of the four classes of herbicides commonly used on invasive plants in natural areas of Florida, the ALS inhibitors (imazapyr, imazapic, and metsulfuron methyl) are most likely to select for resistance. Within the past few years, imazapyr and metsulfuron methyl have been approved for use over wetlands, and are used to treat infestations of melaleuca and Old World climbing fern (*Lygodium microphyllum*), respectively. Imazapic is also being tested on a number of invasive plants, including air potato (*Dioscorea bulbifera*), Old World climbing fern, and Japanese climbing fern (*Lygodium japonicum*). Due to recent use of ALS inhibitor herbicides on certain invasive plants, populations of these plants being treated should be closely monitored for development of resistance.

Herbicide resistance in many weeds is nuclear inherited, controlled by dominant alleles, and expressed in gametophytes and sporophytes (Richter and Powles 1993; Darmency 1994). Old World climbing fern may be analogous in some ways to *Conyza canadensis*, a problematic weed of agricultural sites. Horseweed has developed cross- and multiple-resistance to herbicides, is primarily self pollinated, and produces many seeds that are wind dispersed (Owen and Zelaya 2005). Old World climbing fern has the potential to cross-fertilize (Lott et al. 2003) and is primarily dispersed by wind blown spores. In some natural areas, greater than eight applications of glyphosate have been applied to Old World climbing fern to maintain control – a situation that may exert strong selection pressure for resistance. With the ability for self-fertilization, wind dispersed spores from a single resistant plant could rapidly spread the resistant biotype of the fern across large areas. Being a relatively recent invader to natural areas in south Florida, Old World climbing fern has been exposed to repeated herbicide treatments for less than 10 years, a threshold well below the time frame at which some weedy plants have developed herbicide resistance in agricultural systems (Primiani et al. 1990; LeBaron 1991). However, the tremendous number of spores increases the frequency of resistance when compared with most angiosperms.

CONCLUSION

Continuous use of herbicides with the same mode of action on a specific invasive plant will inevitably lead to resistance (Kudsk and Streibig 2003). The rate of herbicide use in natural areas is much less intense than in agriculture systems where some crop-systems may be treated 2-3 times annually. To effectively eliminate reproduction potential, management of invasive plants in natural areas is dependent on eliminating or reducing seed and spore production. Extended use of herbicides below the recommended label rate may select for resistance and replenish the seed bank with resistant seeds (Doyle and Stypa 2004) that in time will dominant a population and potentially spread the resistant biotype into other areas.

Although there are no known upland invasive plants in natural areas of Florida that have developed herbicide resistance, there are some herbicides (e.g., ALS inhibitors) in use that have caused rapid development of resistance in agricultural weeds throughout the world. Only five years after the introduction of the ALS inhibitors, two species of agriculture weeds developed resistance (Tranel and Wright 2002). Application of dose rates below the recommended label rate using an ACCase inhibiting herbicide have been shown to select for resistance in rigid ryegrass in less than three generations (Neve and Powles 2005). Studies modeling herbicide resistance in weeds indicate that smaller populations over a large area are less likely to develop resistance because rare resistance genes are less likely to be present (Diggle et al. 2003). These models would likely predict that invasives that are widespread in Florida (such as Old World climbing fern, cogongrass, torpedo grass, and tropical soda apple) produce numerous spores or seeds and have long distance dispersal mechanisms; these invasives have the greatest potential to develop resistance.

In most natural areas of Florida, the use of herbicide and biocontrol are the only practical methods to control invasive plants. Many invasive plants occur in highly isolated areas that can only be reached by foot, airboat, or helicopter, making treatment time consuming, difficult, and costly. Prescribed fire, mechanical treatments, and hand removal are options, but are limited in use due to cost, limited personnel, and other problems (e.g., smoke management).

The best scenario for treatment of invasive plants in natural areas is to rotate herbicides with different modes of action or use tank mixtures of two or more herbicides with different modes of action, since in most cases only one invasive plant is being targeted. Regardless, if a single herbicide is being utilized to control an invasive plant, strict monitoring of the treated population is advised in order to detect potential resistant populations. An integrated approach utilizing two or more herbicides with different modes of actions, combined with the introduction of biocontrols, and prescribed fire and mechanical treatments (when appropriate), offers the best approach to control invasive plants in natural areas and reduce the potential of these plants developing resistance to herbicides.

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