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United States Department of Agriculture–Agricultural Research Service research on pest biology: weeds†‡

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Abstract: Over 125 permanent full-time scientists conduct research within the USDA Agricultural Research Service (ARS) on issues related to weeds. The research emphasis of most of these scientists involves ecology and management or biological control of weeds. Many scientists perform research on weed biology as components of their primary projects on weed control and integrated crop and soil management. Describing all ARS projects involved with weed biology is impossible, and consequently only research that falls within the following arbitrarily chosen topics is highlighted in this article: dormancy mechanisms; cell division; diversity of rangeland weeds; soil resources and rangeland weeds; poisonous rangeland plants; horticultural weeds; weed traits limiting chemical control; aquatic and semi-aquatic weeds; weed/transgenic wheat hybrids; seedbanks, seedling emergence and seedling populations; and weed seed production. Within these topics, and others not highlighted, the desire of ARS is that good information on weed biology currently translates or eventually will translate into practical advice for those who must manage weeds.
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1 INTRODUCTION

Successful weed control is never guaranteed. It requires at least two of the following items: good tools, good advice and good luck. The availability of good tools depends upon innovations by farmers, engineers, chemists and biotechnologists. These tools can be welded, crafted, synthesized and hybridized. Most can be purchased, but sometimes only at high prices. Not all tools are welcomed equally by society.

Fortunately, good luck is free, and it is always welcomed. Unfortunately, good luck vies with bad luck in terms of frequency and dependability. However, good advice, by definition, is both dependable and cost-effective, and usually it is welcomed. The main problem with good advice is its availability.

One of the primary functions of weed research is to increase access to good advice and information by farmers and other land managers. The types of useful information are quite varied, but one of the most critical for weed management is weed biology. Of course, not all aspects of weed biology are immediately useful to farmers and managers, but some facets are especially important. What features of weed biology are of practical significance? There are many. This paper attempts to highlight current USDA Agricultural Research Service (ARS) projects that emphasize important topics in weed biology, but no attempt is made to describe ARS research on weed management, which is a much larger topic that entails more researchers than just those who study weed biology.

Without doubt, some important projects on weed biology are not mentioned here, as ARS conducts a considerable amount of research on this topic. Weed biological research has not been tracked in the past as a specific topic within the agency and, therefore, complete reporting of the numerous projects on weed biology is difficult. ARS researchers who study weed biology often do so as projects that complement their primary research in mechanical control, chemical control, biological control, integrated management, cropping systems and so forth. Furthermore, many important aspects of biology studied by ARS weed researchers are included in other articles within this issue (allelopathy, application technology, aquatic weeds, biocontrol, herbicide resistance, invasive species and methyl bromide alternatives). Fortunately, the rigor that may be lacking in this article on weed biology is compensated by the high quality of information in the other articles.

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2 ARS ADMINISTRATION AND RESEARCHERS

Before describing some ARS research on weed biology, an understanding may be useful of how the agency recently began apportioning weed research and the number and frequency of researchers who work on weed-related topics within the agency. ARS administers much of its activities in weed related research through a 'National Program Area' known as Crop Protection and Quarantine, or NP304 (www.nps.ars.usda.gov/programs/programs.htm?NP-NUMBER = 304). NP304 includes ten research components, six of which deal entirely with insects and mites, and four relate to weeds. The weed-related components are biological control of weeds, chemical control of weeds, weed management systems, and weed biology and ecology. Within this latter component, six research problems were identified recently by ARS clients, but grouped and labeled by ARS researchers and administrators in 2001. These major problems are (a) invasive potential and ecological impact; (b) taxonomy and systematics; (c) early detection, rapid response and monitoring; (d) reproductive biology and seedbank dynamics; (e) growth, development and competition; and (f) population dynamics. Although the manner by which fiscal and human resources are allocated by ARS to address these high-priority problems continues to evolve, most research projects on weed biology within the agency should be aligned with one or more of these issues.

In most instances, ARS scientists who study weed biology do so within research units whose missions are not devoted primarily to weeds. The missions of these units range broadly, from soil conservation to irrigation efficiency to fruit production, but weeds stymie the success of the mission in each case. Because of this diversity of missions among research units, ARS scientists are involved in an amazingly wide array of issues related to weed biology. Consequently, research on weed biology is conducted not only under the auspices of NP304 but also other national programs, such as Crop Production (NP305) and Rangeland, Pasture and Forages (NP205), which are more fitting to the mission of the overall research unit. The apparent overlap of weed biology research among some national programs was foreseen and is expected to be complementary rather than supplementary.

As of 2001 there were 130 permanent full-time scientists within ARS who were identified as having at least some involvement in weed research. In the arbitrarily designated categories of (a) ecology and management, (b) biological control, (c) soil and water chemistry, (d) application technology and (e) other, there were 56, 51, 14, 6 and 3 scientists, respectively, who could be aligned with these topics. Clearly, ecology and management, and biological control, have been the main focal points for ARS research related to weeds and, fortunately, these foci conform closely to the newly mandated components of NP304.

The distribution by state of ARS researchers who work on weed-related issues also is of interest (Fig 1).

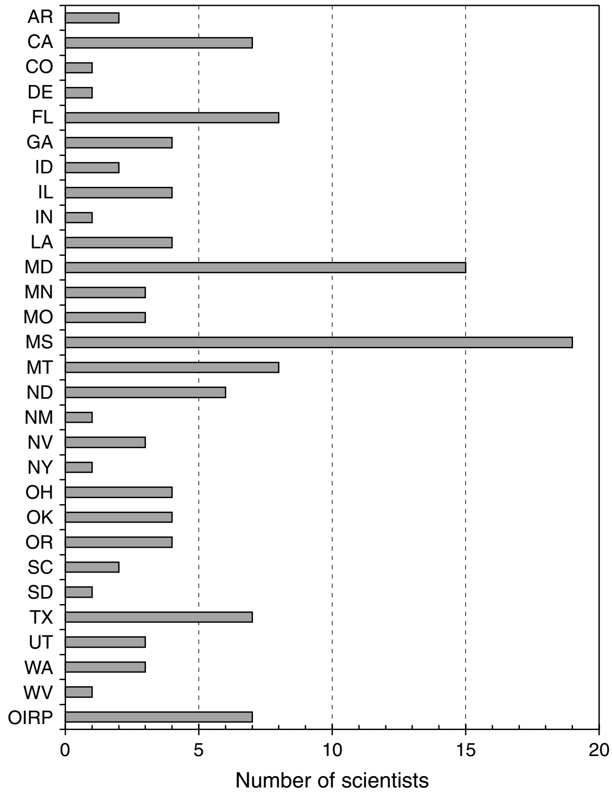

Figure 1. Number of permanent full-time ARS scientists as of 2001 who conduct research that pertains to weeds, and the state in which they are located. The bar labelled OIRP represents the Office of International Research Programs, with locations in Australia, Argentina and France officially employing ARS scientists.

Mississippi and Maryland lead all other states in hosting ARS weed researchers. ARS compartmentalizes the USA for administrative purposes into eight regions. The Beltsville (Maryland) Area is the location of ARS Headquarters. Because of its proximity to Washington, DC, it is a highly visible and well-deserving national symbol for agricultural research. The other areas are the North Atlantic, South Atlantic, Mid West, Mid South, Northern Plains, Southern Plains, and Pacific West. These areas can be used to illustrate the distribution of ARS weed researchers (Fig 2a). The Mid South Area ranks highest, and the Mid West Area ranks lowest, in terms of numbers of scientists who work on weed-related issues.

The USDA Economic Research Service lists gross agricultural sales by state at the following web site: www.ers.usda.gov/StateFacts/. The gross sales can be aggregated by ARS Areas and compared to the number of ARS weed researchers in each area (the Beltsville Area was combined with North Atlantic Area for this purpose). The result is a slightly downward trend in the relationship between gross agricultural sales and the number of resident ARS weed researchers (Fig 2b). The true impacts of weeds on society, of course, may not be associated with agricultural sales, and this may explain the agency's placement of weed-related researchers in regions not noted for high levels of agricultural production.

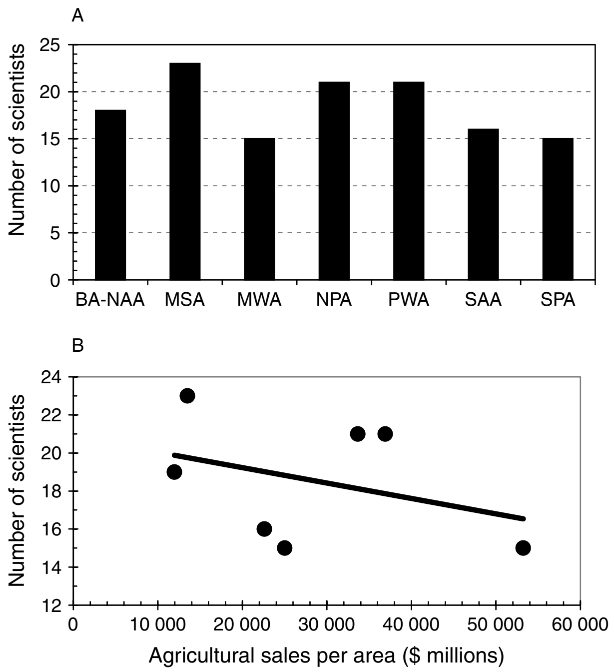

Figure 2. (A) Distribution of permanent full-time ARS scientists as of 2001 who conduct research that pertains to weeds, and the ARS-designated 'Area' in which they are located (see text). The Beltsville Area was combined with the North Atlantic Area, and OIRP scientists, whose work primarily involves biocontrol, were distributed according to the Area that best fits the work they perform. (B) Relationship between number of permanent full-time ARS scientists by Area (as in A) and the gross agricultural sales as calculated by the USDA Economic Research Service for 1999.

3 ARS RESEARCH

The weed biology research conducted by ARS researchers can be divided into innumerable categories, with no system of division being entirely satisfactory. What follows are groupings of related research projects that fall under the arbitrarily chosen categories of dormancy mechanisms; cell division; diversity of rangeland weeds; soil interactions with rangeland weeds; poisonous rangeland plants; weeds in horticultural crops; weed characteristics that limit control by herbicides; aquatic and semi-aquatic weeds; jointed goatgrass and glyphosate-tolerant wheat; weed seedbanks, seedling emergence, and seedling populations; and weed seed production. Neither the order of discussion nor the length of discussion of these categories reflects their perceived importance. Although each of the categories can fit within one or more of the six high-priority problems for weed biology and ecology, listed above, these latter problems were defined so recently that they do not always align perfectly with current research. Finally, much of the information reported below was copied verbatim from reports written by the referenced scientists.

Upon mentioning ARS activities in the following pages, the relevant research unit will be cited by the city and state in which it is located. Because the locations of many units are rural and may not have the immediate recognition of large cities, the following web site will aid international readers in locating the ARS research units that are discussed herein: www.ars.usda.gov/research.html.

3.1 Dormancy mechanisms

The ability of a seed or vegetative propagule to remain viable but not grow under conditions that normally promote germination or sprouting is a key trait that allows many species of plants to persist in environments where high levels of seedling and shoot mortality are certain. In other words, by staggering emergence of seedlings or shoots, weed populations are able to maintain themselves despite management efforts that might achieve control rates of over 90%. Understanding, predicting and manipulating weed dormancy represents critical information for eventual long-term control.

ARS supports research on dormancy mechanisms relevant to weeds primarily at two locations. A well-integrated team of researchers at Fargo, North Dakota, specializes in studying the basic mechanisms of dormancy of wild oat (*Avena fatua* L) seeds and leafy spurge (*Euphorbia esula* (L)) underground adventitious buds. A second ARS team at Pullman, Washington, is focused on the biochemistry and genetics of seed dormancy in small-grain crops, where ABA-induced protein kinases appear to be important.[1] The connection between the two groups is that dormancy in wheat (*Triticum aestivum* L), rice (*Oriza sativa* L) and weedy grasses show genome colinearity, ie their genetic mechanisms may overlap considerably.[2] Moreover, weeds such as jointed goatgrass (*Aegilops cylindrica* (Ces) Host), which shares the D genome with wheat, have dormancy traits that may be useful if transferred into wheat to prevent pre-harvest sprouting.

Indeed, because of the generous global investments in genomic research for rice, for instance, the Fargo laboratory finds benefit in using this crop as a model for weedy grasses such as wild oat (*Avena fatua* L). Dormancy in wild oat and other weedy grasses may be governed by a wide variety of quantitative trait loci (QTL) coding for products that are produced by tissues within the seed, the pericarp/testa or by the hull surrounding the seed. Ten QTL have been linked to dormancy in wild oat.[3] Hull-imposed dormancy may be most important for wild oat and, as in rice, it seems to be controlled by three major genes. Wild oat genes at loci G1 and G2 enhance germination, whereas that at D delays germination.[4] Dormancy is recessive; any genotype other than $g_1g_1G_2g_2DD$ or $g_1g_1g_2g_2D\_$ will be non-dormant or intermediate.

Genome colinearity also may be found for a dicotelydonous perennial weed like leafy spurge and a crop such as cassava (*Manihot esculenta* Crantz), both of which are in the Euphorbiaceae. From 47% to 68% of DNA from leafy spurge hybridizes with that from *Arabidopsis*,[5] so even higher similarity between leafy spurge and cassava is expected. An expressed sequence tag database for microarray analysis is being developed for cassava by an international team with the involvement of the ARS team at Fargo.

Dormancy is an important part of this research because of its relationship with post-harvest storage losses and disease susceptibility of cassava. The biochemical–genetic resources developed for cassava may have direct bearing on understanding dormancy in leafy spurge, but the extraordinary expense of genomics research will not have to be borne by the leafy spurge team.

The ARS team in Fargo has used expression of hormone and cell cycle-responsive genes as markers to follow the process of dormancy and subsequent regrowth of adventitious buds in leafy spurge.[5,6] Loss of mature leaves results in decreased sugar levels and increased gibberellin perception in underground adventitious buds. Gibberellin is sufficient for induction of S-phase-specific but not M-phase-specific gene expression during the cell cycle. Loss of both apical and axillary buds or inhibition of polar auxin transport does not result in induction of S-phase- or M-phase-specific gene expression. Loss of polar auxin transport is necessary for continuation of the cell cycle and further bud development if S-phase was previously initiated. As these studies progress and specific genes are identified that control dormancy induction, loss and bud regrowth, the next step is to understand the internal and external stimuli that regulate gene expression. This information provides the basis to predict the consequences of different weed-management alternatives and the responses of the plants to constantly changing microclimates.

Studying expression of genes governing dormancy can involve eliminating or silencing genes. The technical ability to lessen experimentally or remove the expression of a gene led to the concept of using virus-induced gene silencing (VIGS) for controlling weeds.[6,7] Normally, VIGS has been applied to analyze the function of unknown genes rapidly. For instance, a genetically modified virus was used to silence expression of a cellulose synthase gene. The team at Fargo is testing the lethality of a number of genes using a tomato stunt virus as the gene vector. The hypothesis is that a viral vector carrying host gene fragments may prevent expression of homologous chromosomal genes by the host. If the gene is vital to the plant growth of the plant will be inhibited. The inhibition occurs because when a virus carries a homologue of a plant gene into a plant, the plant's RNA-mediated defense mechanism targets both the viral RNA and the endogenous host RNA, which curtails expression of the host gene.[7] Although still at a very early experimental stage, VIGS is, perhaps, one of the more novel ideas for weed control in decades. Clearly, some safety issues regarding plant protection arise from this concept, but certainly the research should be encouraged.

3.2 Cell division

Many herbicides are grouped into a class known as mitotic disrupters. The commonly used dinitroaniline and carbamate herbicides are within this group. These herbicides affect plants by disrupting cell division. A much smaller group includes the cell wall or cellulose synthesis inhibitors, such as isoxaben and quinclorac. ARS researchers at Stoneville, Mississippi, lead in the study of cell division and cellulose biosynthesis. Experiments in which mitotic disrupters eliminated microtubules and then microtubules were allowed to reform have allowed identification of the subcellular sites responsible for microtubule nucleation and organization.[8] The cellulose synthesis inhibitors were shown to prevent formation of the cell plate, but they had no effect on microtubules.[9] Pectins almost completely substitute for cellulose in the presence of cellulose inhibitors.

Mitotic disrupters and cellulose inhibitors have been used to study not just herbicidal activities, but the basic biochemistry and genetics of cellulose synthesis, cell wall formation and cell division. Naturally, these features are important aspects of fiber growth in cotton, *Gossypium hirsutum* L.[10]

Interestingly, the battery of biochemical, cytological, immunochemical and microscopy techniques used in illuminating the effects of herbicides on the basic biology of cell division and cell wall formation can also be employed to decipher the manner in which parasitic weeds attach and establish themselves on host plants. For instance, the parasitic weed, dodder (*Cuscuta pentagona* (L) Engelm) forms trichomes as it approaches host shoots. The trichomes' soft cell walls conform to the surface of the host cells, whereupon the dodder cells secrete a pectin-like substance that cements them to the host. The dodder hyphae now induce the host to soften its cell wall and form new cell walls that coat the growing hyphae. The mixed hyphal/host cell walls have abnormally high levels of pectin, differentiating them from wall materials of either plant in isolation.[11] With greater understanding of the basic mechanisms of host/parasite interactions, especially at the time of initial attachment, new methods of control of parasitic weeds can be envisioned more easily.

3.3 Diversity of rangeland weeds

Genetic diversity has been recognized for some time as an important component of weed management, regardless of whether the management emphasis was on chemical control or biological control. The proliferation of modern techniques[7] has resulted in a corresponding increase in projects on weed genetics and diversity. For biological control, this is important for determining whether more than one population of the weed in the USA needs to be evaluated for suitability to the agent, and whether the weed in the USA is genetically similar to plants from which agents are collected in the country or continent of origin.

In this regard, ARS groups at Fort Detrick, Maryland, Albany, California, and Montpellier, France, are conducting studies on populations of yellow starthistle (*Centaurea solstitialis* L) collected from the Mediterranean basin, Eurasia and the western USA. They are using amplified fragment length polymorphism

(AFLP) to fingerprint and conduct similarity analyses on resultant banding patterns. Initial data from molecular fingerprinting indicate that the yellow starthistle from California best matches populations collected from Turkey and Spain,[12,13] which is consistent with the historical speculation on origins of this weed via alfalfa seed and hay. Considerably more research on this aspect of yellow starthistle is in progress, as is that for other species of *Centaurea*, the knapweeds.[12] Similarly, at Reno, Nevada, downy brome (*Bromus tectorum* L) variation is being examined via RAPD (randomly amplified polymorphic DNA) and RFLP (restriction fragment length polymorphisms) analytical techniques.

ARS units at Albany and Fresno, California, and Montpellier also work on Russian thistle (*Salsola tragus* = *Salsola kali* L), in which three distinct genetic types, based on isozymes, DNA markers and chromosome numbers, have been found.[14] Insects attack one of these (type A with 36 chromosomes) more than another (type B with 18 chromosomes).[15] So far, no matches have been found in Eurasia to the types B and C that occur in the USA. Consequently, the origins of the forms in the USA remain unknown.

New introductions of the same alien species occur repeatedly. The separately introduced populations may have differing origins and varying genetic structures. Invasive populations are expected to overlap and hybridize with time. Hybrid vigor, or heterosis, may occur with hybridization, and this may explain some aspects of range expansion and environmental acclimation in certain invasive species. Recently established populations of downy brome were targeted for repeated sampling over time by the ARS unit at Reno to look for evidence of invasiveness facilitated through heterosis (Longland W, 2002, pers comm). Common garden designs in the field, and replacement series and reciprocal planting experiments in the greenhouse, are being used to test for ecological correlates of local adaptation in weeds.

3.4 Soil interactions with rangeland weeds

ARS researchers at Reno, Nevada, are studying the biology and ecology of a number of rangeland weed species. An exciting and very promising direction for this research involves the interactions of soil, soil nutrients and plants.

Perennial pepperweed (*Lepidium latifolium* L) is an exotic crucifer and is invading wetland and riparian habitats in the western USA.[16] It is a major concern to ranchers, alfalfa growers and wildlife refuge managers. The Reno team studied the impact of perennial pepperweed on soil properties. In areas where soils have detrimental physical properties due to high sodium content, this weed is capable of ameliorating the site. It does so by increasing the content of soluble calcium that counteracts the negative effects of sodium.[17] This weed also increases soil enzyme activities relative to those beneath vegetation it is replacing. The elevated enzyme activity is responsible for the increased available soil nitrogen necessary for pepperweed's remarkable growth rate. Soil treatments that can reduce activities of nitrogen-cleaving enzymes are a potential control strategy for this plant.[18] The most common weed in the Great Basin of the USA is downy brome, and the much larger pepperweed often must compete with it to survive. Although pepperweed grows best in soil rich in phosphorus, over time it compartmentalizes much phosphorus at the soil surface so that fibrous-rooted plants like downy brome invade and replace pepperweed.[19]

In a similar fashion, grass weeds like downy brome and medusahead (*Taeniatherum asperum* Nevski = *Elymus caput-medusae* [L] Boiss) clearly use soil nitrogen more effectively than native range plants.[20–22] Limiting nitrogen availability at the time of rangeland revegetation are goals for research and management of ARS units at Logan, Utah; Reno, Nevada; and Dubois, Idaho. One simple and cheap method of limiting nitrogen is through immobilization with added carbon. For example, application of sucrose suppressed growth of herbaceous annuals like downy brome, and allowed species that are preferred in rangelands to grow more vigorously.[21] Problems involving resource availability and use by invasive species also are being addressed by the ARS unit in Burns, Oregon. Throughout the arid western USA disturbances such as fire, logging and road construction create temporary pools of available resources, eg soil water and nutrients. Weeds typically pre-empt these resources. Sowing disturbed sites with diverse assemblages of preferred plant species appears to help restore vegetation more reliably than where only monocultures are sown, presumably because niche occupation and resource use by desirable plants increases with the number of desirable species sown.[23] This useful and logical conclusion must be conditioned by the fact that active weed management, as with herbicides, must be implemented during the establishment year if the benefit from the diversity-resource use relationship is to be realized.[24] In a reciprocal fashion as to how diversity of preferred vegetation affects weed establishment, presence of invasive weeds is being examined by ARS (Reno, Nevada) for effects on native plant and animal diversity, especially in the Great Basin[25] where so many alien species have invaded.

Because fire is such an enormously important component of rangelands in the western USA, the research programs at ARS units in Burns, Oregon; Logan, Utah; Reno, Nevada; and Dubois, Idaho include the effects of rangeland fires on weed invasion. To a large extent this work involves resource capture, as mentioned above. However, livestock grazing adds another dimension to this complex system. In this regard, the Dubois unit plays a leading role, investigating the effects of reseeding plants and restocking animals (sheep) at different times after a rangeland conflagration (Seefeldt S, 2002, pers comm).

3.5 Poisonous rangeland weeds

The ARS Poisonous Plant Laboratory in Logan, Utah, is one of the few such research units in the world. Its importance for agriculture is that the arid western USA has a large number of native and introduced poisonous weeds.

Researchers from Logan have studied population dynamics of many species of poisonous plants.[26] Typically, plants germinate and establish in seasons of high precipitation, and die during drought. Management decisions to graze infested areas are based on the risk of poisoning, which is dependent on the density and availability of the poisonous plant. Ranchers need to anticipate outbreaks of poisonous plants in wet years and move cattle if outbreaks materialize.

Concentrations of the toxic alkaloids in larkspurs (*Delphinium* spp) remain stable despite most types of environmental stress (shade, drought, herbicides, etc). However, mowing in one year appears to reduce the pool of alkaloids in the following year in these perennial plants.[27] Most alkaloids are produced early in the spring and are concentrated in young shoots. Alkaloid concentrations decrease quickly after anthesis. The characteristic decline in alkaloid concentration in tall larkspur (*Delphinium barbeyi* [L] Huth) allowed the team at Logan to develop a model that predicts alkaloid concentration throughout the growing season. Various parameters for plants (height and weight) and weather (days since snow melt, precipitation, temperature and growing degree days) are used in the model. This model has been coupled with information on grazing behavior of livestock to develop poisoning risk models. The model allows graziers to integrate this diverse information easily and better define grazing periods with lowered risks of poisoning.

3.6 Weeds in horticultural crops

The rapid acceptance of genetically modified and herbicide-tolerant field crops has been a tremendous boon for weed management. Despite this technological advance, however, weed management in many other crops remains problematic. This is especially true in minor crops, where there were few herbicides available in the first place but, even so, many of those are being withdrawn from the marketplace. Furthermore, costs of manual labor for weed control is increasing steadily. Consequently, understanding weed behavior and using this knowledge to manage weeds is more important now than ever before.

ARS research teams in Tifton, Georgia, and Charleston, South Carolina, are studying weed biology to help devise control methods for problem weeds in minor crops. Two infamous weeds worldwide are purple nutsedge (*Cyperus rotundus* L) and yellow nutsedge (*Cyperus esculentus* L). Methyl bromide often was used in high-value minor crops to control pests, including the nutsedges. However, use of methyl bromide will be discontinued in the near future. Plastic mulches can be used to control many weeds, but the sharp-tips of emerging shoots of nutsedge pierce plastic mulches rendering them useless for nutsedge control.[28] Because the spatial dynamics differ between yellow nutsedge (sedentary) and purple nutsedge (gregarious), they may pose different problems for mulched horticultural systems.[29]

Many horticultural crops have tremendous morphological diversity, and some morphotypes may help suppress weed growth. Some sweetpotato (*Ipomoea batatas* (L) Poir) varieties were found to require shorter weed-free periods for maximum yield than others.[30] Consequently, the effect of sweetpotato growth habit on weed interference is being studied by the ARS unit at Charleston.

Plastic mulches are used for horticultural crops more commonly than biological mulches. However, plastic mulches have some detrimental features, such as the need for disposal. Biological mulches typically do not control weeds as well as plastic mulches, but they have more fringe benefits: they recycle naturally, and they can increase soil quality parameters; leguminous mulches also increase soil nitrogen. The Sustainable Agricultural Systems Research unit at Beltsville, Maryland, is the world's leader in research on living mulches in horticultural and field crops.[31–33] An important contribution of this unit was defining the boundaries under which biological mulches can be expected to control weeds. For instance, not all weed species are controlled equally well by mulches, and for annual species the order of sensitivity to mulches seems inversely related to seed size.[34]

Although most biological mulches are composed on plant materials, animal by-products can also be used. The ARS unit in Morris, Minnesota, has used low-quality sheep's wool to construct landscaping fabric for weed control during the establishment year of transplanted strawberry.[35] Weeds were not able to emerge through this type of mulch, but the roots of strawberry daughter plants (runners) were able to penetrate and establish themselves better than in all other treatments investigated.

3.7 Weed characteristics that limit control by herbicides

The ARS unit at Beltsville, Maryland, tested whether the efficacy of chemical weed control might change as atmospheric carbon dioxide concentration increases by determining whether tolerance to a widely used, phloem-mobile, post-emergence herbicide, glyphosate, was altered by a doubling of carbon dioxide. Tolerance of redroot pigweed (*Amaranthus retroflexus* L) was not affected, but that of common lambsquarters (*Chenopodium album* L) and quackgrass (*Agropyron repens* (L) Beauv) was increased.[36,37] Changes in herbicide tolerance at elevated carbon dioxide levels could limit chemical control of some weeds, especially those with C-3 photosystems, and increase weed–crop competition.

Plant morphology and anatomy affect herbicide efficacy, but in many, disparate and complex ways.

The ARS unit at Stoneville, Mississippi, is examining leaf biology, in particular, to determine factors important in herbicide efficacy.[38,39] This research is especially important at the moment for the herbicide, glyphosate, because of the dramatic increase in land area in the southern USA sown to glyphosate-tolerant soybean and cotton.

3.8 Aquatic and semi-aquatic weeds

Weed research by ARS scientists at Stuttgart, Arkansas, and Davis, California, is focused on aquatic weeds. The primary weed of rice in the southern USA is red rice (*Oryza sativa* L), which is simply a weedy form of domestic rice, and the two forms hybridize easily but can be distinguished with DNA markers[40] even though the red rice populations are diverse.[41] Ironically, although the close genetic relationship complicates many control tactics, which are primarily regimes of herbicide use, genetic solutions are being employed to help control red rice in domestic rice. The most significant is transgenic development of herbicide-tolerant rice, which allows selective control of red rice with glufosinate. However, there is concern over the transfer of herbicide tolerance to red rice. Other genetic methods are aimed at suppressing red rice and other weeds, and these methods include development of varieties with high-tillering capacity, rooting volume and secretion of allelochemicals.[42]

The ARS satellite unit in Davis, California, has had a long and distinguished history of work on weed problems in reservoirs and waterways, including irrigation canals. Recent biological studies involved phenological prediction and invasive potential[43,44] and responsiveness to growth regulators.[45] The newly discovered and invasive marine alga, *Caulerpa taxifolia* (Vahl) C Agardh, has been the focus of much recent interest.[46]

3.9 Jointed goatgrass and glyphosate-tolerant wheat

Transgenic wheat tolerant to the herbicide, glyphosate, likely will be grown extensively in the same manner as glyphosate-tolerant soybean, corn and cotton. These latter summer-growing crops, however, typically compete with weed species in the USA to which they have little genetic similarity. This will not be the case for wheat in the western USA. In recent years the winter annual weed, jointed goatgrass (*A cylindrica*) has invaded the entire region and become a major concern in winter wheat.[47] Jointed goatgrass is very difficult to control selectively in wheat,[48] with which it hybridizes[49] and shares the D genome.

ARS units in Pullman, Washington, and Akron, Colorado, have worked extensively with jointed goatgrass in wheat. Biological research at these locations has contributed much to help devise strategies for jointed goatgrass management.[50] Sowing spring wheat instead of winter wheat is only a partial solution because, even though jointed goatgrass' life cycle is not adapted to spring wheat culture, it still can emerge and reproduce if spring wheat is sown very early, which is a goal of most farmers who plant spring wheat.[50] Evenly spaced wheat rows allowed jointed goatgrass to produce abundant seed, but paired wheat rows lowered seed production by this weed.[51] Considerable basic research on the biology of jointed goatgrass and other weeds, and responses to many forms of non-chemical management have been studied by ARS scientists at Akron and Fort Collins, Colorado, and Mandan, North Dakota.[47,52]

3.10 Weed seedbanks, seedling emergence and seedling populations

Understanding weed population dynamics from seedbanks to seedlings to adults to seeds remains an important component of ARS weed research. This type of research in one form or another is conducted within many ARS units. The following brief outline will consider only those locations performing such research on weeds in arable crops.

Seeds remaining viable in soil provide a means of resiliency for weed populations, and study of this feature of weeds has had considerable support in the weed research community.[53] However, sampling weed seedbanks and seedling populations has tremendous labor requirements. ARS researchers at Fort Collins, Colorado, have pioneered the study of sampling strategies, efficiencies and costs.[54,55] Much of the work at Fort Collins and at Morris, Minnesota, was in the context of spatially variable weed populations.[56,57]

Timing of emergence of seedlings is a critical life cycle stage for a weed population, and it is an equally critical component of information for crop managers. A number of ARS units have worked on this issue, often in a collaborative manner (Akron, Colorado; Ames, Iowa; Columbia, Missouri; Morris and St Paul, Minnesota; Urbana, Illinois; etc). Data from studies on the timing of weed seedling emergence have been pooled for these sites, and other sites, to develop predictive, microclimate-based software, which predicts weed emergence and growth in real time and that is 'friendly' toward the intended user groups, namely crop consultants, agri-chemical industry personnel, extension services and farmers.[58,59] The software has been particularly popular with organic farmers, as the mechanical control operations can be timed better if they are based upon levels of weed emergence rather than more traditional criteria.[60]

3.11 Weed seed production

Fecundity of weeds always has been recognized as being a critical stage of a weed's life cycle, but seldom has fecundity been investigated as a topic in its own right. It is crucial information for developing weed population models. Fortunately, many ARS investigators have included fecundity measurements as components of larger studies. For example, after harvesting winter wheat in the Pacific Northwest, isolated Russian thistle (*S kali*) plants that were not controlled in the crop continue to grow unabated, persist in using valuable soil water in this arid region, and eventually produce more than 25 000 seeds per plant.[61] This level of fecundity is more than enough to replenish the seedbank. Identical processes occur after spring wheat harvest in the Corn Belt with foxtails (*Setaria* spp),[62] and almost certainly they occur in all other cropped fields as well. In many instances lush maturing crops will hide smaller seed-bearing weeds and, thereby, lull managers into a false sense of accomplishment. Greater emphasis must be placed upon weed fecundity by researchers to ensure that seed-bearing weeds are eliminated not only in the gaps of crop canopies, where they are most visible, but also under canopies, and especially amongst crop residues after crop harvest.

Ramifications of weed seed production extend well beyond that of mere weed interference with crops in following years. In Europe, for instance, genetically modified herbicide-tolerant crops are restricted, in part, because of the fear that weed seed production will be reduced too much, possibly even eliminated.[63] However foreign this prospect may sound to American ears, it is a seriously debated issue overseas. The argument for maintenance of weed seed production and, therefore, weed diversity in crops is that other members of the agro-ecosystem depend upon weeds for sustenance or cover. Current studies at the ARS unit in Morris, Minnesota, are examining these problems in glyphosate-tolerant soybean sites along a north–south gradient from Minnesota to Iowa to Missouri to Arkansas to Louisiana. Preliminary results are somewhat surprising, but consistent at every site. A single application of glyphosate at the prescribed time and rate for that region increases weed biodiversity in comparison not only to two glyphosate applications, standard herbicide treatments, or standard treatments plus glyphosate, but also in comparison to the weedy check treatments.[64] Thus, genetically modified herbicide-tolerant crops may actually help maintain biological diversity rather than diminish it.

Another fascinating extension of the topic of seed production, which is ripe for scientific harvest, is the dynamics of granivores and their differential effects on preferred and weedy range plants. This research by the Reno, Nevada, unit permits inferences regarding the mechanistic basis for specific patterns of vegetation change, thereby increasing our ability to predict future post-disturbance responses of vegetation based on the species composition of the local granivore community. ‘Ecological titrations’ test for desirable results of restoration efforts by systematically varying such factors as seedbed preparation, seeding density, and the local density and species identity of granivores.[65]

Lastly, a novel and special case of tentative research on weed seed production involves the Seed Arrest System (SAS) proposed by the ARS unit in Lubbock, Texas.[66] These researchers propose to develop transgenic yellow starthistle (*C solstitialis*) plants that contain a controllable gene system which, when activated by a chemical seed treatment, will grow to normal size and appearance. However, the plants will not produce seeds but will produce pollen that carries a gene that inhibits pollen development. Flowers fertilized with transgenic pollen produce no seeds but continue to compete for resources, including pollinating insects, with fertile plants. Thus, fertile plants would be expected to produce fewer seeds because of competition, and infertile plants would produce few if any seeds.

Like the transgenic ‘terminator gene’ technology conceived by the same research group, SAS technology may be equally controversial. Nevertheless, the idea has considerable intellectual appeal. Indeed, not only can the SAS concept be adapted to non-transgenic technology, it may be better adapted to non-transgenic systems, especially for insect-pollinated weeds in areas where herbicides cannot be applied easily or willingly. For instance, one can speculate that artificial ‘pollen’ can be formulated with herbicides non-toxic to insects (eg glufosinate) and dusted onto bees when they exit specially constructed hives, which can be positioned near populations of invasive weeds that are pollinated by bees. Tiny amounts of such pollen would be transferred to flowers of the target weed with each visitation by dusted bees. Minute amounts of glufosinate-enriched artificial pollen eliminated seed production when applied to flowers of geranium (*Pelargonium* × *hortorum*) in greenhouse tests in Morris, Minnesota. Because bees develop strong search images for pollen- and nectar-bearing flowers of specific species during specific seasons, they might be expected to achieve high levels of efficacy for ovule abortion if used as ‘messengers of death’ in areas highly infested with some species of invasive weeds.

4 CONCLUSION

The Agricultural Research Service within the US Department of Agriculture directs much of its activities in weed-related research through a National Program Area known as Crop Protection and Quarantine, and to a lesser extent through other national programs. In most instances, ARS scientists who study weed biology do so within research units whose missions are not devoted primarily to weeds. Despite the absence of a central focus on weed research within the agency, ARS scientists are involved in a very wide array of projects in weed biology. Regardless of this diversity, the unifying desire of ARS is that good information on weed biology currently translates, or eventually will translate, into good advice for controlling weeds. Indeed, good advice coupled with useful tools should be more dependable than good luck for weed management.

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