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Invasive Species Working Group

Invasive Species Science Update

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IN THIS ISSUE

From the Editor

This newsletter is designed to keep managers and other users up-to-date with recently completed and ongoing research by RMRS scientists, as well as to highlight breaking news related to invasive species issues. The newsletter is produced by the RMRS Invasive Species Working Group (ISWG), a core group of scientists who volunteer to disseminate RMRS invasive species science to managers and the public through this newsletter, the website, and periodic white papers. All of our products, including past issues of the newsletters and lists of publications, can be found online at: https://www.fs.fed.us/rmrs/groups/invasive-species-working-group.

In this issue, we cover new research on wide-ranging topics from the long-term effects of drought on competition between native and invasive plant species, to the effects of drought on pollinator visitation to invasive plants, to a novel use of insect pheromones to improve biocontrol of invasive saltcedar. There's also big news to report in weed biocontrol: two new biocontrol agents were recently approved and can soon be used to combat the invasive plants yellow toadflax and whitetop. As always, we welcome feedback on ways to improve the ISWG and this newsletter. If you have comments or questions, please contact the ISWG team leader, Justin Runyon, jrunyon@fs.fed.us.

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Figure 1. Collecting data in experimental plots in the first year after planting with the invader spotted knapweed and/or the native bluebunch wheatgrass. Shown are drought structures (in open position) used to manipulate precipitation levels in plots, see page 3 (photo by Yvette Ortega, RMRS).

Permit Issued to Release *Rhinusa pilosa*, a New Yellow Toadflax Biocontrol Agent

By: Sharlene Sing (ssing@fs.fed.us), RMRS Forestry Sciences Laboratory, Bozeman, Montana

The exotic toadflaxes *Linaria dalmatica* (Dalmatian toadflax) and *L. vulgaris* (yellow or common toadflax) tolerate a broad range of environmental conditions, which has facilitated their successful invasion throughout North America. Yellow toadflax is more difficult to manage using chemical or biological control than Dalmatian toadflax. Two closely related biocontrol agents, both stem mining weevils, are now established in North America: *Mecinus janthinus* on yellow toadflax and *M. janthiniformis* on Dalmatian toadflax. Survival of *Mecinus* adults is compromised by wide fluctuations in temperature, humidity, and snow cover. Dessication and destruction of their overwintering sites within host stems further constrain populations of these biocontrol agents. A suite of new toadflax agents that overwinter in the soil has therefore been proposed for release in North America. The application for a permit to release a yellow toadflax stem galling weevil *Rhinusa pilosa* was submitted to USDA APHIS in March 2012 and approved in January 2018.

*Figure 2. **Rhinusa pilosa**, the yellow toadflax stem galling weevil, was recently approved for release as a biocontrol agent (photo by Ivo Toševski, CABI).*

Rhinusa pilosa is a shoot-galling species that overwinters in the soil in the adult stage. Emergence of reproductive adults in the native range occurs from March to May, coinciding with new shoot growth from overwintering tap roots. Newly emerged adults briefly feed on *L. vulgaris* shoots and foliage before mating begins. Oviposition follows approximately 10 days later, stimulating gall development on *L. vulgaris* stems where eggs have been deposited. All three larval instars feed on host tissues within the developing galls. Pupation is also completed within the gall. Newly developed adults remain within the natal gall for 10-15 days, feeding on remnant gall tissues before escaping via holes chewed through the gall's outer surface. Emerged adults feed externally on host stems for about 10 days, reposing in litter or cracks in the soil during the heat of the day. An extended period of summer aestivation is interrupted by occasional feeding, mainly in the evening and at night. In late autumn, adults actively feed for a brief period before moving into the soil to overwinter. Results of initial field releases of this agent in Alberta and British Columbia indicate that establishment has occurred without significant overwintering mortality.

A 75 percent reduction in below-ground biomass was reported in plants galled by *R. pilosa* compared to control plants. This finding is particularly relevant because it indicates that galling might not only compromise the spread of *L. vulgaris* by limiting rhizomatous, clonal stem growth, but also probably reduces multi-year persistence and overwintering survival of the weed. In *Linaria* this depends on adequate storage of carbohydrates in the root. Galled plants were 55 percent shorter (37.2 cm ± 3.1 vs 58.4 ± 3.2 cm) and produced fewer shoots (3.5 ± 0.6 vs 13.6 ± 1.3) than control plants. Gall tissue represented 40 percent of above-ground biomass of treated plants, with non-gall mean dry above-ground biomass 4.6 ± 0.7 g versus 12.6 ± 1.4 g for control plants. Galling also significantly reduced the potential for sexual propagation of yellow toadflax, with the proportion of flowering stems much lower in treatment vs. control plants, and flowering either fully suppressed or delayed in galled plants.

For general information on toadflax biology and biological control, see:

Gassmann, A.; De Clerck-Floate, R.; Sing, S.; Toševski, I.; Mitrović, M.; Krstić, O. 2014. Biology and host specificity of *Rhinusa pilosa*, a

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recommended biological control agent of *Linaria vulgaris*. BioControl. 59(4): 473-483. https://www.fs.fed.us/rm/pubs_other/rmrs_2014_gassmann_a001.pdf.

Sing, S.E.; De Clerck-Floate, R.A.; Hansen, R.W.; Pearce, H.; Bell Randall, C.; Toševski, I.; Ward, S.M. 2016. Biology and biological control of Dalmatian and yellow toadflax. Third Edition. USDA Forest Service, Forest Health Technology Enterprise Team (FHTET). FHTET-2016-01. https://www.fs.fed.us/rm/pubs_journals/2016/rmrs_2016_sing_s001.pdf.

*Figure 3. Feeding by the stem galling weevil **Rhinusa pilosa** causes large swellings (galls) in yellow toadflax stems (photo by Ivo Toševski, CABI).*

The Tortoise and the Hare: Can Climate Change Reduce Invasion in Some Systems?

Dean Pearson (dpearson@fs.fed.us) and Yvette Ortega (yortega@fs.fed.us), RMRS Forestry Sciences Laboratory, Missoula, Montana

Climate change is expected to alter native plant communities and influence their susceptibility to exotic plant invasions, with important ramifications for the ecosystem services that these communities provide to humans. Yet how climate change will shift the balance between natives and exotics is largely speculative. Many predict that climate change will favor exotic over native plant species because exotics often exhibit stronger responses to disturbance, faster growth rates, and greater plasticity. Using a long-term experiment, we explored whether the outcomes of plant competition in response to simulated climate change could be predicted as a function of plant life-history strategies.

Plant life-history theory predicts that "fast" species (those using high-resource uptake strategies to achieve rapid population growth) should outperform "slow" species (those using low-resource uptake and slow population growth strategies) under high resource conditions, but that slow species should win under low resource conditions. We compared competition between the fast species, spotted knapweed, a highly invasive exotic forb in western Montana grasslands, with the slow species, bluebunch wheatgrass, a dominant native in these grasslands. After seven years of experimental application of drought versus normal precipitation conditions during the growing season, the winner of the plant competition battles was predicted based on the life history strategy of the players. The fast "hare" won when water was plentiful and the slow "tortoise" won when water was limited.

These patterns reflect field observations in western Montana wherein knapweed overtakes grassland habitats under normal precipitation

conditions, but declines under drought conditions when bluebunch still thrives. Our results suggest that climatic shifts toward hotter dryer conditions in semi-arid habitats may favor stress-tolerant natives over certain invaders. They also suggest that consideration of species' life history strategies may help to predict vegetation responses to climate change.

Pearson, D.E.; Ortega, Y.K.; Maron, J.L. 2017. The tortoise and the hare: Reducing resource availability shifts competitive balance between plant species. Journal of Ecology. 105: 999-1009.

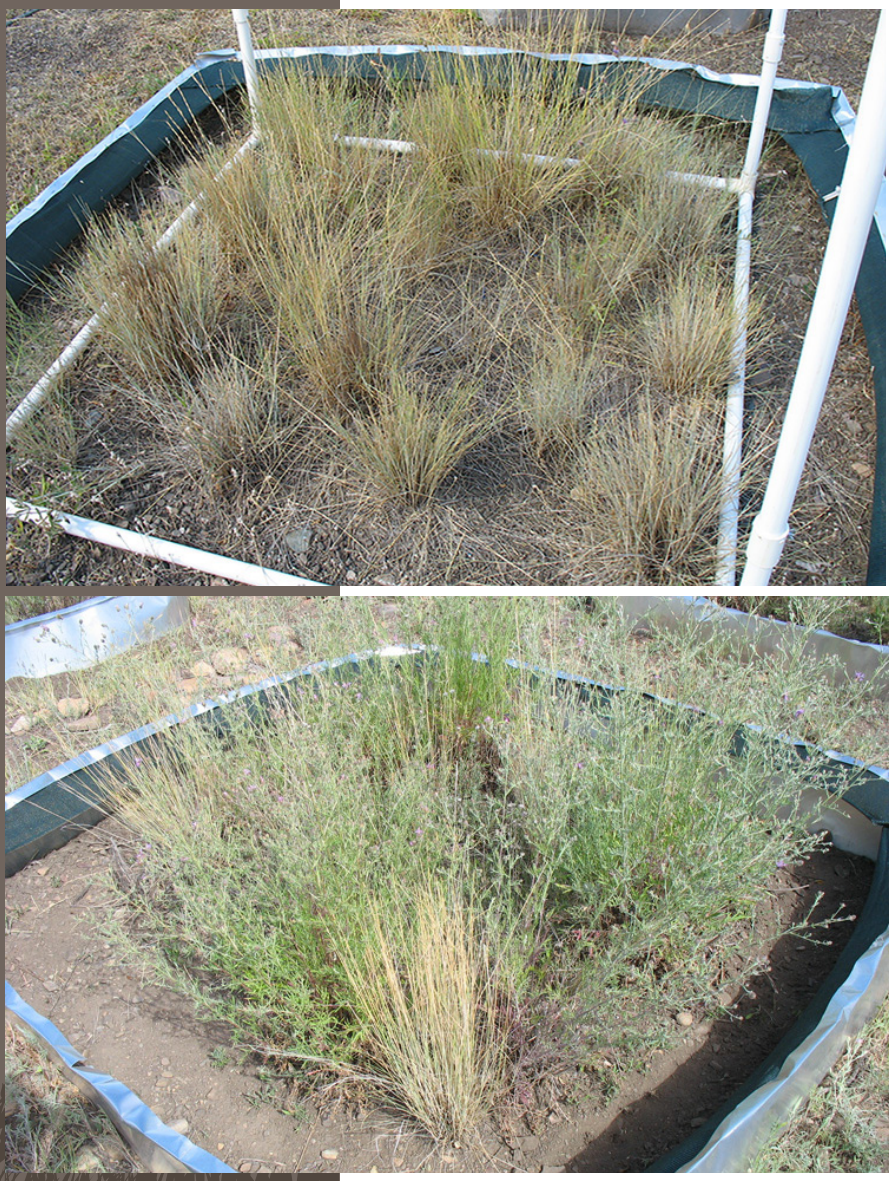

Figure 4. Experimental plots initiated with equal mixes of exotic spotted knapweed and native bluebunch wheatgrass, as seen after 7 years of receiving either a drought treatment (top photo) or normal precipitation levels matching the 50-year average (bottom photo). The exotic plant "won" under normal precipitation conditions but "lost" under drought (photos by Yvette Ortega, RMRS).

Double Whammy: Drought and the Presence of Native Forbs Reduce Pollinator Visitation to Invasive Sulfur Cinquefoil

By: Will Glenny (willglenny@gmail.com) and Laura Burkle (laura.burkle@montana.edu), Montana State University, Bozeman, Montana; Justin Runyon (jrunyon@fs.fed.us), RMRS Forestry Sciences Laboratory, Bozeman, Montana

Climate change is anticipated to decrease water availability across much of the western United States resulting in drought for plants. How drought will affect the spread of nonnative plants is unknown, but one route by which drought could influence invasive plants is by altering pollinator attraction. We recently showed that experimental drought decreases pollinator visitation to some plants by altering the number, size, and scent of flowers (Burkle and Runyon, 2016). In that study, drought reduced pollinator visits to invasive sulfur cinquefoil (*Potentilla recta*) much more so than to several native plant species, suggesting that some native species might have a leg up over sulfur cinquefoil during droughts.

In a new study, we tested how neighboring plants affected these drought-induced responses by comparing pollinator visitation to groups of sulfur cinquefoil alone versus sulfur cinquefoil grouped with three native forbs (*Campanula rotundifolia*, harebell; *Heterotheca villosa*, hairy false goldenaster; and *Phacelia hastata*, silverleaf phacelia). When exposed to drought in the presence of native forb species, pollinator visitation to sulfur cinquefoil flowers was further reduced by 18 percent compared to when drought-treated sulfur cinquefoil was grouped alone.

These results suggest that the effects of drought on pollinator visitation depend on what other plant species are growing nearby: drought reduced the ability of sulfur cinquefoil

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to compete for pollinators, especially when sulfur cinquefoil co-occurred with other native forb species. These results emphasize the importance of maintaining and restoring healthy native plant communities as part of invasive plant control methods.

Burkle, L.A.; Runyon, J.B. 2016. Drought and leaf herbivory influence floral volatiles and pollinator attraction. Global Change Biology. 22: 1644-1654.

Glenny, W.R.; Runyon, J.B.; Burkle, L.A. 2018. Drought and increased CO_2 alter floral visual and olfactory traits with different effects on pollinator visitation in single- and multi-species plant assemblages. New Phytologist. https://doi.org/10.1111/nph.15081

Figure 5. Drought effects on pollinator visitation was measured for groups of invasive sulfur cinquefoil alone (top) versus sulfur cinquefoil co-occurring with other native forb species (bottom). Drought reduced pollinator visitation to sulfur cinquefoil greatest when native forb species were nearby (photos by Will Glenny, Montana State University).

A Kermes Scale Insect (*Allokermes galliformis*) and Bacterial Pathogen (*Lonsdalea quercina* subsp. *quercina*) Are Causing an Emergent Disease of Red Oaks Called Drippy Blight

By: Rachael Sitz (rachael.sitz@colostate.edu), RMRS Forestry Sciences Laboratory, Moscow, Idaho and Colorado State University Department of Bioagricultural Sciences and Pest Management, Fort Collins, Colorado; Jane E. Stewart, Colorado State University Department of Bioagricultural Sciences and Pest Management, Fort Collins, Colorado

In urban forests of eastern Colorado, several species of red oak (e.g. *Quercus rubra*, *Q. palustris*, and *Q. schumardii*) were exhibiting symptoms from an unknown disease. The symptoms included branch dieback, leaf drop, branch abscission, and witches' brooms. Unfortunately, damage is typically severe enough to result in tree removal several years after the symptoms first appear. A kermes scale insect (*Allokermes galliformis*) and a phytopathogenic bacterium (*Lonsdalea quercina* subsp. *quercina*) were present on all symptomatic trees. The combined damage of these agents is referred to as "drippy blight" because bacterial exudates drip from small branches at kermes scale feeding sites and other tree wounds.

Our research studies have identified the causal agents of drippy blight disease in Colorado and provided insight into the disease cycle through studies that document the life history of the kermes scale insect and look at the role social insects may play in bacterial dissemination. Although this bacterium has caused a related disease, "drippy nut", in California since the mid-1990s, it is thought to be invasive in Colorado, and the native range is unknown. Notably, diseases caused by other subspecies of *Lonsdalea quercina* have been described in Europe and

Figure 6. Two drippy blight diseased red oaks on the University of Colorado main campus showing branch dieback and flagging, as well as abscised branches littering the ground underneath their canopies (photo by R. A. Sitz, Colorado State University).

Asia in recent years including drippy bud and bark canker as well as one type of oak decline. This bacterium may be problematic to many species of oak throughout the world due to its apparently wide host range.

Sitz, R.A.; Zerillo, M.M.; Snelling, J.; Caballero, J.I.; Alexandar, K.; Nash, K.; Tisserat, N.A.; Cranshaw, W.S.; Stewart, J.E. 2018. Drippy blight, a disease of red oaks in Colorado produced from the combined effect of the scale insect *Allokermes galliformis* and the bacterium *Lonsdalea quercina* subsp. *quercina*. Journal of Arboriculture and Urban Forestry. In press.

*Figure 7. A red oak branch with an adult kermes scale insect (indicated by the arrow) and a mass of dried exudates of the bacterial pathogen **Lonsdalea quercina** subsp. quercina (photo by R. A. Sitz, Colorado State University).*

New Biocontrol Agent for Control of the Invasive Plant Whitetop Approved for Release

By: Jeff Littlefield (jeffreyl@montana.edu), Department of Land Resources and Environmental Sciences, Montana State University and Justin Runyon (jrunyon@fs.fed.us), RMRS Forestry Sciences Laboratory, Bozeman, Montana

Whitetop (or the hoary cress "complex": *Lepidium draba* L. and *L. chalapense* L.) is a weed in the cabbage family (Brassicaceae) that was introduced from Eurasia to the United States in the late 1800s and has since spread to much of North America. Whitetop has dramatically increased its distribution in the Intermountain West (Washington, Oregon, Idaho, Montana, and Wyoming) in the past 20 years, and has become particularly problematic in cropland, pastures, rangelands, and riparian habitats. As a result, whitetop negatively affects crop production, grazing, recreational opportunities, and degrades wildlife habitat and native plant communities. Available options for management of whitetop are often costly, temporary, and not always effective, and can have unwanted impacts on nontarget plants. For example, herbicides or cultural control practices are often not effective against whitetop, but can have negative effects on native plants.

Fortunately, land managers will soon have another tool to help manage whitetop. The gall mite, *Aceria drabae* (Acari: Eriophyidae), was recently approved for biological control of whitetop in the United States. Feeding by *A. drabae*, a natural enemy of whitetop found in the native range, causes abnormal growth and deformities of plant tissues (galls); this stunts plant growth and reduces or completely eliminates seed production. Based on laboratory and field studies (in its native range), *A. drabae* is expected to help reduce hoary cress populations by impacting seed production and possibly whitetop biomass; thereby reducing spread of this weed into new areas.

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*Figure 8. Abnormal growth and deformities (galls) on the weed whitetop caused by the gall mite, **Aceria drabae**. These galls stunt plant growth and reduces or completely eliminates seed production (photo by Jeff Littlefield, Montana State University).*

Plant rearing and host specificity studies on *Aceria drabae* were completed at the biological control containment facility located at Montana State University, Bozeman. The permit for release of this biocontrol agent is expected soon and the first field releases should occur this summer. This will represent the first release of a classical biocontrol agent for a Brassicaeae weed worldwide.

U.S. Department of Agriculture, Animal and Plant Health Inspection Service. 2018. Field release of the gall mite, *Aceria drabae* (Acari: Eriophyidae), for classical biological control of hoary cress (*Lepidium draba* L., *Lepidium chalapense* L., and *Lepidium appelianum* Al- Shehbaz) (Brassicaceae), in the contiguous United States. Environmental Assessment, January 2018. 36 p. Riverdale, MD: U.S. Department of Agriculture. https://www.aphis.usda.gov/aphis/ourfocus/planthealth/plant-pest-and-disease-programs/sa_environmental_assessments/hoary_cress

Using Pheromones to Increase Aggregations and Herbivory by Biocontrol Agent of Saltcedar

By: Sharlene Sing (ssing@fs.fed.us), RMRS Forestry Sciences Laboratory, Bozeman, Montana and Alex Gaffke, Montana State University, Bozeman, Montana

Semiochemicals for monitoring, attracting, or repelling pest and beneficial organisms are increasingly deployed in agricultural and forest systems for pest management. However, the use of aggregation pheromones and host-plant attractants for the express purpose of increasing the efficacy of classical biological control agents of weeds has not been widely reported. Field-based assays confirmed that a specialized wax-based matrix (SPLAT) impregnated with an aggregation pheromone of the northern tamarisk beetle *Diorhabda carinulata* or host-plant volatiles increased the efficacy of this agent. Reported release rates suggest that this matrix is a viable formulation for enhancing *D. carinulata* aggregations under field conditions. Pheromone-treated saltcedar plants (*Tamarix* spp.) not only had higher

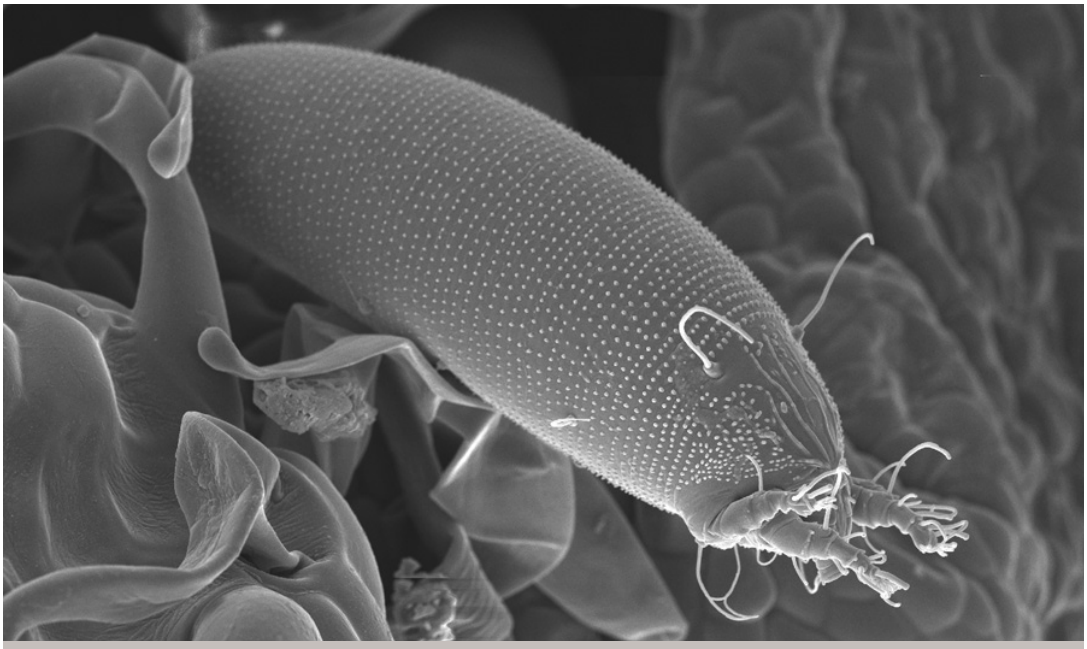

*Figure 9. A scanning electron microscope image of the whitetop gall mite, **Aceria drabae**, which was recently approved for release as a biocontrol agent (photo by Annie de Meij, Montana State University).*

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Figure 10. Application of a wax-based matrix containing an aggregation pheromone of the tamarisk beetle to saltcedar (onto white tag). These pheromones concentrated feeding by the beetle and increased damage to the plant (photo by Sharlene Sing, RMRS).

densities of adult and larval *D. carinulata*, but also sustained greater levels of foliar damage than control plants. Increased damage from the focused feeding of *D. carinulata* caused an increase in foliar dieback and decrease in live canopy volume of semiochemical-treated plants.

Gaffke, A.M.; Sing, S.E.; Dudley, T.L.; Bean, D.W.; Russak, J.A.; Mafra-Neto, A.; Grieco, P.A.; Peterson, R.K.; Weaver, D.K. 2018. Semiochemicals to enhance herbivory by *Diorhabda carinulata* aggregations in saltcedar (*Tamarix* spp.) infestations. Pest Management Science. http://onlinelibrary.wiley.com/doi/10.1002/ps.4848/epdf.

Figure 11. Extensive damage to saltcedar caused by feeding of the tamarisk beetle that was enhanced by using pheromones (photo by Sharlene Sing, RMRS).

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Other News

Schoettle Gives Talks on Saving/Restoring Tree Species Threatened by White Pine Blister Rust

Anna Schoettle (RMRS, Fort Collins) delivered the invited presentation "Genetic Resistance to Insects and Disease: Applications and Options to Inform Regeneration Decisions" at the Reforestation "Matters" Workshop in Portland, OR on April 12-13, 2017. She also presented "Disturbance Mitigation and Recovery: Natural and Artificial Regeneration to Increase Resilience of Limber Pine and Bristlecone Pine Forests" at the 2018 Regions 1, 2, 3, 4, 5, 6, & 10 Reforestation Workshop in Missoula, MT on February 21, 2018. These talks presented a decision framework to set priorities for regeneration decisions for species whose populations are under threat of extirpation by white pine blister rust.

Anna is also participating in the development of the (1) National Whitebark Pine Restoration Strategy lead by the Whitebark Pine Ecosystem Foundation, American Forests, and USFS-WO and (2) Crown of the Continent Restoration Strategy lead by a Canada-USA partnership to restore and conserve whitebark pine and limber pine.

Invasive Species National Assessment Nearing Completion

The U.S. Forest Service is completing a national assessment of the state of science on invasive species. The WO General Technical Report is edited by Forest Service scientists (including members of the ISWG) with university partners and contains chapters covering topics including early intervention strategies, management and restoration, inventory and monitoring, tools and technologies, impacts of invasive species, climate change effects, social and societal aspects, and others. Summaries detailing regional invasive species issues are also part of this extensive review. This report will help the Forest Service protect forests and grasslands from invasion and better manage those public lands impacted by invasive species. Be on the lookout for this important publication.

International Symposium on Biological Control of Weeds, August 2018

The XV International Symposium on Biological Control of Weeds is taking place August 26-31, 2018 in Engelberg, Switzerland. The aim of this meeting is to bring together practitioners, scientists, and regulators working in the field of weed biological control to share their experiences, network, foster collaborations, and discuss emerging issues that affect invasive plant management. More information can be found at: https://isbcw-2018.com.

Montana Invasive Species Council, Invasive Species Summit, November 2018

Please join the Montana Invasive Species Council (MISC) for its 2nd Invasive Species Summit November 15-16, 2018 in Helena, Montana. Montana has a multitude of invasive species laws, regulations, and administrative rules in place to prevent, manage, and mitigate invasive species. The MISC has partnered with the University of Montana Law School's Land Use & Natural Resources clinic to compile current federal, tribal, and state statutes and rules related to invasive species in Montana.

The results of the law review will be the focus of the 2018 summit where participants will identify and discuss potential solutions to gaps in management, authority, and funding. This two-day event will also feature national and State leaders and technical experts who provide on-the-ground applied science and actions to prevent and manage invasive species. Please join us for this important and timely collaboration to learn and plan together for effective, local invasive species prevention

in Montana. For more information about MISC and the 2018 Montana Invasive Species Summit go to: http://dnrc.mt.gov/divisions/cardd/montana-invasive-species-program/misc.

50 Worst Invasive Species Identified by Western Governors

The Western Governors' Association (WGA) has developed a list of the top 50 invasive species affecting their States. The list was created by surveying invasive species coordinators in the 15 WGA member States and territories and includes both terrestrial and aquatic species. The terrestrial list was dominated by invasive plants (e.g., cheatgrass), but also included pathogens (e.g., white nose syndrome), mammals (e.g., feral hogs), and insects (e.g., the little fire ant). The aquatic list featured fewer plants (e.g., Eurasian watermilfoil) but also amphibians (American bullfrog), fish (e.g., silver carp), mussels (Quagga and Zebra mussels), insects (mosquitofish), and other taxa. The list can be found here: http://westgov.org/images/editor/WGA_Top_50_Invasive_Species.pdf.

Other Recent Publications

Arnesen, S.; Coleman, C.E.; Meyer, S.E. 2017. Population genetic structure of *Bromus tectorum* in the mountains of western North America. American Journal of Botany. 104(6): 1-12.

Boswell, A.; Sing, S.E.; Ward, S.M. 2016. Plastid DNA analysis reveals cryptic hybridization in invasive Dalmation toadflax populations. Invasive Plant Science and Management. 9: 112–120.

Briggs, J.S.; Fornwalt, P.J.; Feinstein, J.A. 2017. Short-term ecological consequences of collaborative restoration treatments in ponderosa pine forests of Colorado. Forest Ecology and Management. 395: 69-80.

Burkle, L.A.; Runyon, J.B. 2017. The smell of environmental change: Using floral scent to explain shifts in pollinator attraction. Applications in Plant Sciences 5(6): 1600123.

Chambers, J.C.; Board, D.I.; Roundy, B.A.; Weisberg, P.J. 2017. Removal of perennial herbaceous species affects response of cold desert scrublands to fire. Journal of Vegetation Science. doi: 10.1111/jvs.12548.

Chambers, J.C.; Maestas, J.D.; Pyke, D.A.; Boyd, C.S.; Pellant, M.; Wuenschel, A. 2017. Using resilience and resistance concepts to manage persistent threats to sagebrush ecosystems and greater sage-grouse. Rangeland Ecology and Management. 70: 149-164.

Chambers, J.C.; Beck, J.L.; Bradford, J.B.; Bybee, J.; Campbell, S.; [et al.]. 2017. Science framework for conservation and restoration of the sagebrush biome: Linking the Department of the Interior's Integrated Rangeland Fire Management Strategy to long-term strategic conservation actions. Part 1: Science basis and applications. Gen. Tech. Rep. RMRS-GTR-360. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 213 p.

Fonseca, N.R.; Guimarães, L.M.S.; Pires, R.P.; Klopfenstein, N.B.; Alfenas, A.C. 2017. Eucalypt powdery mildew caused by *Podosphaera pannosa* in Brazil. Topical Plant Pathology. 42: 261-271. doi:10.1007/s40858-017-0143-7. https://www.fs.fed.us/rm/pubs_journals/2017/rmrs_2017_fonseca_n001.pdf.

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Kim, M.-S.; Fonseca, N.R.; Hauff, R.D.; Cannon, P.G.; Hanna, J.W.; Klopfenstein, N.B. 2017. First report of the root-rot pathogen, Armillaria gallica, on koa (*Acacia koa*) and ʻōhiʻa lehua (*Metrosideros polymorpha*) on the island of Kaua'i, Hawai'i. Plant Disease. 101: 255. https://www.fs.fed.us/rm/pubs_journals/2017/rmrs_2017_kim_m001.pdf.

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Ott, J.P.; Butler, J.L.; Rong, Y.; Xu, L. 2016. Greater bud outgrowth of *Bromus inermis* than *Pascopyrum smithii* under multiple environmental conditions. Journal of Plant Ecology. 10(3): 518-527.

Pearson, D.E.; Ortega, Y.K.; Runyon, J.B.; Butler, J.L. Secondary invasion re-redefined: the distinction between invader-facilitated and invader-contingent invasions as subclasses of secondary invasion. Ecology and Evolution. In press.

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