A MULTIPLE-METHOD SYSTEMS APPROACH TO REVERSING REED CANARGYRASS INVASIONS

Craig A. Annen

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Integrated Restorations, LLC

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PART I: Background

As of January 2016, reed canarygrass (RCG) has been a topic of 913 published studies from 311 different peer-reviewed journals in ten languages, a compendium totaling more than 9,400 printed pages. Despite this large pool of information available to researchers and land managers, RCG is still considered one of the most problematic invasive species to tackle, and eradication is generally considered an unrealistic management goal, even at local scales. The gap in restoration ecology between experimental research and experiential management is partly to blame for this mindset. For instance, we know from management experience that reversing a RCG invasion is possible and has even become a matter of routine, but it requires 5 - 7 consecutive growing seasons worth of management effort. In contrast, the average length of time spent conducting an experimental eradication study is only two growing seasons, after which the researchers usually conclude control cannot be achieved or a tested method is completely ineffective. These hasty generalizations are usually based on the results of short-term, single-site experiments often conducted in artificial environments (such as greenhouses and campus gardens[1]) and have given rise to the widespread and misguided belief that current methods and restoration approaches are inadequate to address the RCG problem. Typically, such studies mention in their concluding paragraphs that "additional research is needed" before we can successfully confront RCG invasions. *Really???* How much more research is needed?

While gathering information for my thesis research, I recognized that there was considerable lack of metadata synthesis and cross-study comparison in the RCG literature. In other words, we have enough data to understand how and why RCG invasions occur and also to design and implement effective suppression and reversal strategies for RCG-dominated communities, but the information occurs in fragments scattered throughout the literature. These 913 studies need to be consolidated into a coherent framework. To address this need, in 2002 I began collecting and examining this extensive body of literature in detail. The objectives of this literature review are to summarize and combine existing information into a single source that can serve as a reference to guide restoration practice and future research, to identify gaps in our understanding of the biology and ecology of this species (gaps which will hopefully be filled by future studies), and to prevent excessive duplication of research efforts (for example, more than 40 studies document RCG's response to nitrogen, often under similar experimental conditions). To date, I have thoroughly reviewed almost 75% of the RCG literature, and it is already clear that while there are some areas of study that still need attention (for example, we don't know the lifespan of an individual RCG plant or the degree of clonal integration within a stand), we have a detailed profile of this species, including plenty of information to guide practitioners in reversing invasions.

In this essay I will elaborate on how a multiple-method systems approach to restoration is the key to making RCG eradication a matter of routine (and, more importantly, affordable) management. While I have made every effort to keep this discussion as non-technical as possible, plant communities are complex systems characterized by a myriad of interacting parameters and variable factor-level outcomes, and successfully reversing an invasion requires the practitioner to possess some familiarity with basic ecological concepts. In the interest of brevity, I have also endeavored to keep literature citations to a minimum unless a particular study is directly relevant to a point.

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[1] Artificial environments such as greenhouses, gardens, and mesocosms are popular because they allow the researcher to control much of the variability in natural systems, simplifying analysis, interpretation, and peer acceptance of measured results. However, if employed improperly they can also reduce a study's external validity because they provide idealized growing conditions (i.e., potting soil, nutrients added at constant rates) not typical of natural systems. In contrast, the Zedler lab at the University of Wisconsin-Madison purposely design their mesocosms to mimic actual site conditions based on parameters measured in the field. This practice greatly enhances the external validity and management applicability of their studies.

What is a Systems Approach?

A prevalent viewpoint in invasive species ecology is that effective long-term control of high-impact perennial invaders is simply a matter of finding the ideal herbicide formulation, application rate, and/or application timing window. This approach was developed for and has been widely applied to annual and biennial weed suppression in agricultural settings, yet has shown to be ineffective when applied to perennial weeds in natural areas settings. This quick-fix, 'treatment recipe' strategy is based on **community structure**, which represents a *snapshot of ecological condition and species composition at a given point in time*, and focuses on single-method corrective measures (usually herbicide application) without regard to rectifying the underlying problems that predispose sites to invasions in the first place.

In contrast, the systems approach is process-oriented and based on **community dynamics**, a branch of ecology concerned with *how and why community condition and species composition change over time*. Restoration within the context of a systems approach is a two-step process: The first step consists of assessing and modifying site-specific factors making a site vulnerable to invasion (e.g., fire suppression, hydrological disturbances and alterations, sedimentation) along with feedback cycles that reinforce the invasion (e.g., litter accumulation and nutrient inputs). The second step is to utilize multiple suppression and revegetation methods properly applied, timed, and sequenced to simultaneously exploit the invader's weaknesses (RCG has several) while drawing out native species' strengths. The systems approach is sometimes called integrated vegetation management.

Community Dynamics as a Framework for Restoration

There are two schools of thought regarding community dynamics in the context of restoration. The traditional **succession model** predicts that community degradation occurs in a linear stepwise manner, with the invasive species gradually replacing the existing vegetation community through a series of discrete and predictable transition stages. Restoration within the succession framework is the reverse of degradation; the invasive species is gradually forced out and replaced by native species until the system once again resembles its undisturbed remnant condition. Although this makes intuitive sense, several decades' worth of empirical research and restoration experience have revealed that restoration is seldom so direct and uncomplicated in practice. This is because the succession model doesn't account for the intrinsic complexity displayed by natural systems. Practitioners are in need of a restoration framework that recognizes complexity yet is tangible enough to be of practical use.

While examining relationships between species-abundance patterns of grassland birds along a gradient of RCG abundance, Annen et al. (2008) found evidence that RCG invasions conform more closely to the predictions of an **alternative states model** of community dynamics. The alternative states viewpoint predicts that degradation occurs gradually until a critical mass (the **degradation threshold)** is reached, after which system collapse progresses at an accelerated rate relative to an ecological time frame. Consider a degraded oak savanna invaded by buckthorn in the absence of fire. As buckthorn increases in density, there is a point beyond which simply returning fire to the system is inadequate to reverse the invasion and return the savanna to an undisturbed state; this point is the degradation threshold. Restoration of post-threshold communities becomes increasingly more difficult and expensive because new internal processes set in motion by the presence of the invasive species alter community dynamics in such a way to reinforce the invaded state (see Zedler 2009). Restoration within the context of the alternative states framework involves recognizing and manipulating system variables and feedback loops that contribute to and reinforce invasions in order to push the system over its **recovery**

threshold. Beyond the recovery threshold, the practitioner's job gets much easier (and less expensive) because dynamic processes within the system accelerate restoration gains and push the system toward recovery.

Elements of System Collapse

To illustrate how to use a systems approach to reverse a RCG invasion, we must first understand how a RCG invasion can transform a remnant sedge meadow into a degraded RCG-dominated alternative state, as summarized in Figure 1. Later in this essay we will see how understanding the dynamic processes and feedback cycles operating in RCG invasions is critical to designing effective reversal strategies. Although plant communities are complex systems and every invasion is unique, there are many commonalities in how a RCG invasion occurs and how a system responds to the invasion, and this illustration can be applied to an array of invasion scenarios with only minor adjustments.

We begin with a remnant-condition southern sedge meadow, similar to those described in Curtis (1959). Historically, southern sedge meadows experienced fire at a similar frequency as tallgrass prairie, probably every one to three years (Kost & Steven 2000; Richard Henderson, The Prairie Enthusiasts, *pers*. *comm*.), which maintained their open character by favoring herbaceous vegetation over shrubs and trees. More importantly, fires maintained species richness and diversity by removing accumulated litter and excess nutrients, preventing clonal matrix sedges from becoming dominant. Widespread fire suppression coincided with the arrival of European settlers, leading to encroachment of many southern sedge meadows by fire-intolerant shrub-carr species (initially native willows, box elder, and dogwood and later honeysuckle and buckthorn). Progression of the sedge meadow into a shrub-carr community had an indirect consequence: Shrub-carr species (especially willows) have high evapotranspiration (ET) rates and their presence lowered water tables, setting up a hydrological disturbance. At our case study site, this disturbance was intensified in the 1940's when a drainage ditch and tile system were installed in a portion of the sedge meadow and the wet-mesic prairie that buffered it to drain the site for agricultural production. Artificial draining augmented and intensified the existing hydrological disturbance and further predisposed the sedge meadow to invasion. The site experienced its first decrease in species richness as those herbaceous native species intolerant of lower water levels were extirpated, leaving small gaps in the herbaceous canopy and exposing empty niche space. Some of these canopy gaps were closed by the existing native species pool, some by expansion of shrub-carr species, and some by RCG. Other than initially delivering RCG germplasm to a site, seed rain is probably not an important factor in the expansion of RCG after initial establishment. RCG seeds have low viability and limited longevity in the seed bank. In well-established monotypic stands, only about 15% of culms develop a panicle in a given year (Evans and Ely 1941). Once established, a RCG clone spreads vegetatively through profuse rhizome growth. Clonal species expand by either a phalanx strategy, characterized by emergence of new tillers at a short distance from the parent clone, or by a guerilla strategy, where new tillers emerge in canopy gaps at longer distances from the parent clone. RCG is somewhat unique among clonal plants in that it can utilize both the phalanx and guerilla strategies for lateral spread.

Similar to shrub-carr species, RCG also exhibits high ET rates (Schilling & Kiniry, 2007), and its contribution to existing hydrological disturbances increased as it increased in abundance. A feedback loop emerged as water table levels dropped, leading to additional losses of native species and further expansion of shrub-carr and RCG into the resulting canopy gaps, in turn promoting additional water loss from the system (Figure 1). Meanwhile, in the continued absence of wildfire, a dense mat of RCG litter began to accumulate, which had a mulching effect on native species near RCG clones, accelerating native species suppression and RCG expansion. As RCG expanded, it produced higher amounts of litter, furthering the mulching effect on native species and leading to further expansion. Thus, a **RCG-litter feedback loop** also developed in this system, leading to additional species loss (Zedler 2009). Curtis (1959:641) reported RCG was present in eleven different community types in

Wisconsin, with maximum frequency in shrub-carr (and shrub-carr develops when sedge meadows experience decreased fire frequency), highlighting the importance of fire dynamics in RCG invasions.

Crop production in the adjacent landscape also contributed to this invasion by increasing nutrient inputs. RCG is a strong competitor for light, but a weak competitor for nutrients; when excess nutrients entered this system, the balance of competition shifted toward RCG expansion. Nutrient additions also acted to amplify the RCG-litter feedback because luxury consumption by RCG increased its aboveground biomass production, accelerating litter accumulation and its mulching effect. At some point, RCG density reached a critical limit, after which litter accumulation began to rapidly displace not only the weaker competitors and rarefraction species, but also the common, subdominant, and eventually the dominant matrix species as the system sank further into collapse.

The central point in this scenario is that ***when RCG abundance reached a critical density, new feedback cycles that internally reinforced the invasion emerged in the system (litter and altered hydrology), favoring RCG expansion with concurrent loss of native species.*** The result was a degraded system dominated by shrub-carr with an understory of RCG. Note also that RCG does not need to be a genetically superior super-competitor to achieve dominance at a site.

PART II: Applying the Systems Approach to an Invasion

Once the underlying drivers of RCG invasions are understood, it becomes apparent that negative feedbacks that reinforce invasions need to be disrupted if attempts at reversal are to be successful.

Step 1: Determine if the invasion is reversible and the site is in recoverable condition.

Given unlimited resources, all sites can theoretically be recovered, but practical considerations restrict the number of sites where RCG invasions can be reversed. Put simply, recoverable sites are in a condition below the degradation threshold. Although researchers have yet to empirically pinpoint threshold values for RCG invasions, practical experience gives us some easy-to-follow guidelines for identifying recoverable sites (see Annen et al. 2008). These include sites where RCG is intermixed with well-established native species and sites where native propagule banks have managed to persist in the face of degradation. If you are uncertain if a site is in the latter condition, burn or hay the site (or at least the invaded areas) and then observe if native sedges and/or forbs re-emerge once accumulated litter has been removed. Many sites that appear dominated by RCG respond to litter removal with substantial increases in species richness, indicating that they are actually in recoverable condition despite their outward appearance (note that some sites require two burn cycles to achieve this effect). Restoring sites where well-established RCG dominates both the standing crop and propagule bank is possible, but cost-prohibitive and not always completely successful, at least in terms of regulatory and mitigation standards.

Step 2: Perform a site condition assessment and identify disturbances and feedback cycles that are triggering and reinforcing the invasion.

A pre-treatment site assessment provides the practitioner with valuable information to help guide restoration planning, particularly in regard to identifying the presence of factors and processes that contribute to RCG invasions. Condition assessment also permits the experienced practitioner to predict how an invaded site will respond to management.

System and Forcing Variables

System variables are the factors and processes responsible for a system's condition. Hydrological cycles, nutrient status, and litter depth are examples of important system variables that influence the trajectory a vegetation community will follow through ecological time. Disturbance occurs when system variables are modified in a way that results in a transition from an undisturbed (remnant) condition to an alternative (invaded) condition. For example, nutrient enrichment alters competition outcomes, leading to changes in species composition. **Forcing variables** are parameters that, when altered, either reinforce a system condition or force the system into a new condition. Periodic burning is a familiar example of a forcing variable; fire forces a system to remain in an open condition characterized by a lack of fire-intolerant trees and shrubs; in the absence of fire, an open site dominated by herbaceous vegetation is forced into a trajectory toward a closed-canopy wooded community. Management can also be thought of as a forcing variable because its aim is to push a system toward a particular condition.

A condition assessment should answer the following questions: Are indicators of hydrological modification (ditches, drain tiles, culverts) present? Is it possible to correct or modify these disturbances without affecting adjacent properties? Is the wetland connected to a municipal stormwater system? What is the composition and relative abundance of vegetation present? Are silt deposits present on vegetation or have sedge tussocks been buried by soil deposits? How deep is the litter layer? Has the site experienced fire recently? What is the density and species composition of the shrub layer? Consider collecting soil samples and having them analyzed for NH_4-N, NO_3-N, and available PO_4, because nitrogen and phosphorus inputs from non-point sources are strongly correlated with RCG dominance.

RCG has a high degree of phenotypic plasticity (it can adjust its growth and development patterns in response to its environment) and readily adapts to growing conditions that drive off other species, such as flashy hydroperiods typical of stormwater-connected wetlands and artificial drainage, sedimentation, and nutrient inputs associated with agricultural production. The present ubiquity of RCG in the landscape results from the interaction of its life history traits with anthropogenic land-use patterns (particularly agriculture and urban expansion) and widespread fire suppression; these interactions impact system variables, and if they are strong enough can force the system into a RCG-dominated condition.

Whenever possible, primary and secondary hydrological disturbances, sedimentation, and nutrient inputs should be corrected (or at least modified) and feedbacks should be uncoupled prior to implementing treatments aimed at directly reducing RCG abundance. These actions are of critical importance, but are not always possible for a variety of monetary and legal reasons (e.g., removal of a culvert could risk flood damage to an adjacent property).

Step 3: Disrupt feedback cycles and reintroduce fire to the system.

As already discussed, litter accumulation is a primary feedback operating in systems dominated by RCG. Nutrient inputs into natural areas, common in agricultural landscapes, amplify this feedback by increasing aboveground biomass production and accelerating litter accumulation. We have also seen how conversion to shrub-carr creates a secondary hydrological disturbance that facilitates RCG expansion. These feedbacks can readily be uncoupled at relatively minimal cost with fire management.

Use of fire in RCG management is another example of how the gap between experimental ecology and management practice has misguided restoration efforts. Experiments show that burns are not directly lethal to RCG (even during peak growth), leading many researchers to conclude that burns are an ineffective suppression method. Quite the opposite, burning is an essential **accessory treatment** because RCG invasions are litter-driven. In addition to removing accumulated litter and preventing conversion of herbaceous wetlands into shrub-carr, burning removes nutrients from the system; 15 – 90% of N (depending on species and time of year) and up to 80% of available P is stored in senescent aboveground litter (Larcher 1995). Repeated spring burning facilitates invasion reversal by removing nutrients and altering competition trajectories, since sedges are stronger competitors for nutrients than RCG. Gradual nutrient removal by haying or burning is termed **nutrient**

mining, and Annen (2011) reported a 36% reduction of soil available P in a sedge meadow following three prescribed burn events. Initially, you will want to burn annually until RCG cover declines to ≈10%, after which you can burn at the historical frequency of 1 - 3 years.

At this point, you might be thinking, "Won't burning just expose more of the RCG seed bank to light and make the problem worse?" The answer is yes, litter removal will initially increase RCG seedling density, but since seedlings are not fully established they are *particularly vulnerable to herbicide applications, allowing you to quickly purge the RCG seed bank.* RCG seeds remain viable for only a couple of years in saturated soils and you can expect few additional seedlings to emerge after the first couple of burn events. Importantly, since you will sometimes be burning wet sites, don't be overly concerned if you are not able to completely burn a site; incomplete burns are more effective at facilitating RCG reversals than not burning at all. Likewise, since the aim of using burning as an accessory treatment for RCG reversal is litter removal, a burn can be carried out at any time of year when conditions allow, though I wouldn't recommend burning in July through September since you could burn up sedge achenes before they can recharge the seed bank or interfere with wildlife nesting and breeding activities.

Step 4: Modify system and forcing variables.

Step 4a: Correct or modify primary hydrological disturbances. Cost share through government agencies (e.g., waterfowl stamp programs) and nonprofit organizations (e.g. Ducks Unlimited) is sometimes available for complete or partial hydrological restoration projects, such as removal of drain tiles, filling drainage ditches, or installing weir structures. If hydrological restoration is not possible or affordable, opt for installing water-level control devices to provide you with some control over site hydrology. It is still possible to reverse a RCG invasion without restoring hydrology, but doing so requires more effort because restoring historical conditions promotes native species recruitment and establishment.

Step 4b: Correct secondary hydrological disturbances. Beyond a threshold density, shrub encroachment can no longer be reversed by returning fire to the system; manual removal followed by cut-surface herbicide application is required. Following shrub removal, subsequent burning will deter additional shrub encroachment; shrubs might be present, yet inconspicuous and infrequent. Consider retaining randomly-distributed thickets of native shrubs and small trees as habitat structural elements for wildlife (unless you are managing for obligate grassland birds).

Step 4c: Address sedimentation. Sedimentation can be a difficult and expensive disturbance to correct, and often all the practitioner can do is prevent further sedimentation from occurring. If sedimentation is related to erosion from surrounding uplands, install silt fences or establish vegetation buffers to capture sediment before it enters the wetland.

Step 5: RCG suppression.

In the systems approach, RCG suppression does not begin until system variables and feedbacks that contribute to invasions have been addressed.

Choice of Herbicide

Selective herbicide formulations target narrow groups of related plant species. Non-selective herbicides target a wide range of unrelated species. The most commonly used herbicides for RCG suppression are (in order of popularity) glyphosate, clethodim, imazapyr, fluazifop, and imazapic. Clethodim and fluazifop are grass-selective, the others are broad-spectrum. Glyphosate elicits excellent dieback even at low concentrations, yet its long-term utility is limited because it prevents the ability to reestablish replacement species required to augment treatments. The persistent ALS herbicides imazapic and imazapyr share this problem, and they can sterilize soil for at least two growing seasons, sometimes indirectly leading to erosion problems. Additionally, often the first species to recolonize areas treated with broad-spectrum herbicides are undesired ruderal weeds, necessitating additional herbicide applications and suppression measures. Of the broad-spectrum herbicides, glyphosate has the most utility for reversal projects, especially during the initial treatment iterations at sites retaining a native propagule bank where RCG dominates standing crop. In mixed stands, grass-selective herbicides are a key element of the systems approach because they foster competition variance (discussed below) and augment the reversal effort by setting up a positive feedback involving native species abundance. A diverse herbaceous canopy of native species shades out RCG during its recovery period following herbicide applications, enhancing treatment effectiveness (see Lindig-Cisneros and Zedler 2002). Grass herbicides can be applied to RCG anytime up to flowering (mid-June in southern Wisconsin); after flowering they are less effective because cool-season grasses exhibit lower growth and productivity during warm summer months. Refer to the label of the product you are using for herbicide application rates.

Proper Use of Herbicides

Additive systems inexpensively (only 10¢ - 50¢ per mixed gallon) enhance herbicide performance. Additives are critical for herbicides to work effectively against RCG. Grass herbicides are strictly foliar-absorbed; stem-bundle and wicking methods are ineffective. RCG leaves are covered by a waxy epidermis that must be penetrated before foliar-applied herbicides can enter the plant body and elicit phytotoxic effects. **Nonionic surfactants (NIS)** help spread applied herbicide over the leaf surface. **Methylated seed oils (MSOs)** dissolve the epidermis to promote herbicide penetration. A variety of **MSO-NIS blends** are commercially available, and should be added to tank mixtures at a rate of 1 - 3% by volume. When applying grass herbicides to RCG, adequate coverage is essential; > 90% of leaf surface area should be covered when spot spraying and >70% when broadcast spraying. Clethodim formulations are sensitive to degradation from UV light (fluazifop is resistant), and another advantage of MSOs is they act as a temporary UV protectant. Higher-quality MSOs (organosilicone-based formulations) also lubricate and extend the functional life of sprayer components, and are more resistant to pump-shear degradation than less-expensive alternatives. When applying grass herbicides near sensitive species, **sticking additives** are very useful because they cause applied herbicide to physically stick to treated surfaces, reducing drift and runoff from leaves (the rate for this purpose is 2 - 4% by volume). When mixing herbicides formulated as IPA salts (glyphosate and imazapyr) you should add a **water conditioning agent** to mix water at a rate of 0.5% by volume, because calcium ions in hard water will react with the herbicide and prevent its translocation throughout the plant body. Lastly, you should **always clean and neutralize spray tanks before mixing herbicides!** Most practitioners, even many professional contractors, leave out this important step. Use of 'dirty' tanks has led to widespread anecdotal reports erroneously claiming grass-selective herbicides are not actually selective[2]. The herbicide label will have details on how to neutralize herbicide residues in spray tanks.

Step 6: Actively promote native species recruitment.

Competition Variance: The Achilles' Heel of RCG

Competition-invariant species (e.g., garlic mustard and crown vetch) can invade a site regardless of canopy structure and diversity. In contrast, RCG is a **competition-variant species** that cannot invade a remnant

[2] Grass-selective herbicides are noncompetitive inhibitors of acetyl coenzyme A carboxylase (ACCase), an allosteric enzyme that catalyzes the initial irreversible chemical reactions in fatty acid biosynthesis. In the majority of vascular plants, ACCase consists of three separate subunits, each catalyzing a sequential step of a three-part chemical reaction that converts acetyl CoA into malonyl CoA. In the Poaceae, ACCase consists of a single multienzyme complex, and only the multimeric ACCase assembly possesses a binding site for the inhibitor, rendering ACCase inhibitors truly grass-selective.

community unless a disturbance removes a portion of the existing canopy (Maurer et al. 2003). It is well-documented in the literature that RCG establishment is low in situations where it has to compete with other species. This means that the presence and abundance of native species will supplement and augment suppression efforts, and gives hope that once an invasion is reversed, a diverse vegetation assemblage that utilizes all available niche space and captures surplus resources will prevent (or at least minimize) subsequent invasions and our restoration efforts can have cumulative effects across the landscape. Therefore, it is advisable to plant sedges and forbs (seeds and/or live plants) to provide competition, even in instances when natural revegetation of relic species is occurring. The Wisconsin Reed Canarygrass Working Group developed detailed recommendations and species lists for revegetation of RCG restoration sites (which can be downloaded at no cost from www.ir-wi.com/research-papers).

Step 7: Repeat steps 3, 5, and 6. Multiple-year suppression efforts are required to reverse a RCG invasion because apical dominance in its rhizomes leads to non-uniform distribution of applied herbicide within the plant body. For details on this mechanism, see Annen (2010). Essentially, RCG (along with many other rhizomatous perennial plants) possess dormant renewal buds at all but the most distal nodes of their rhizomes. Systemic herbicides translocate along with sugars only to actively growing tissues; thus, a single systemic herbicide application is only effective at killing actively-growing distal portions of the rhizome and the target plant is able to reestablish itself from dormant buds. Multiple-year applications are required to exhaust this dormant bud renewal bank. At most sites where the initial condition is characterized by RCG intermixed with native sedges and forbs, expect noticeable improvement after completing two or three cycles of burning and herbicide applications. Complete reversal requires 5 - 7 years of management effort, after which periodic baseline scouting and spot spraying are advisable to wipe out any remaining clones and derail subsequent invasions.

Step 8: Reestablish the original feedbacks that characterized the remnant condition.

Just as negative feedback cycles in a disturbed condition internally reinforce RCG invasions, positive feedback cycles reinforce the remnant condition. The positive feedback set in motion by combining accessory treatments such as burning and active revegetation with selective RCG suppression involves native species recruitment. Figure 2 illustrates the positive feedbacks that force system on a trajectory of recovery.

Further Reading

Annen (2011) presents a case-study of how this systems-based approach was used to successfully reverse a RCG invasion in a 26-acre sedge meadow remnant in southcentral Wisconsin. Today, this once degraded site is now a high-quality remnant supporting over 200 native species across multiple trophic levels, several of which possess at-risk conservation status.

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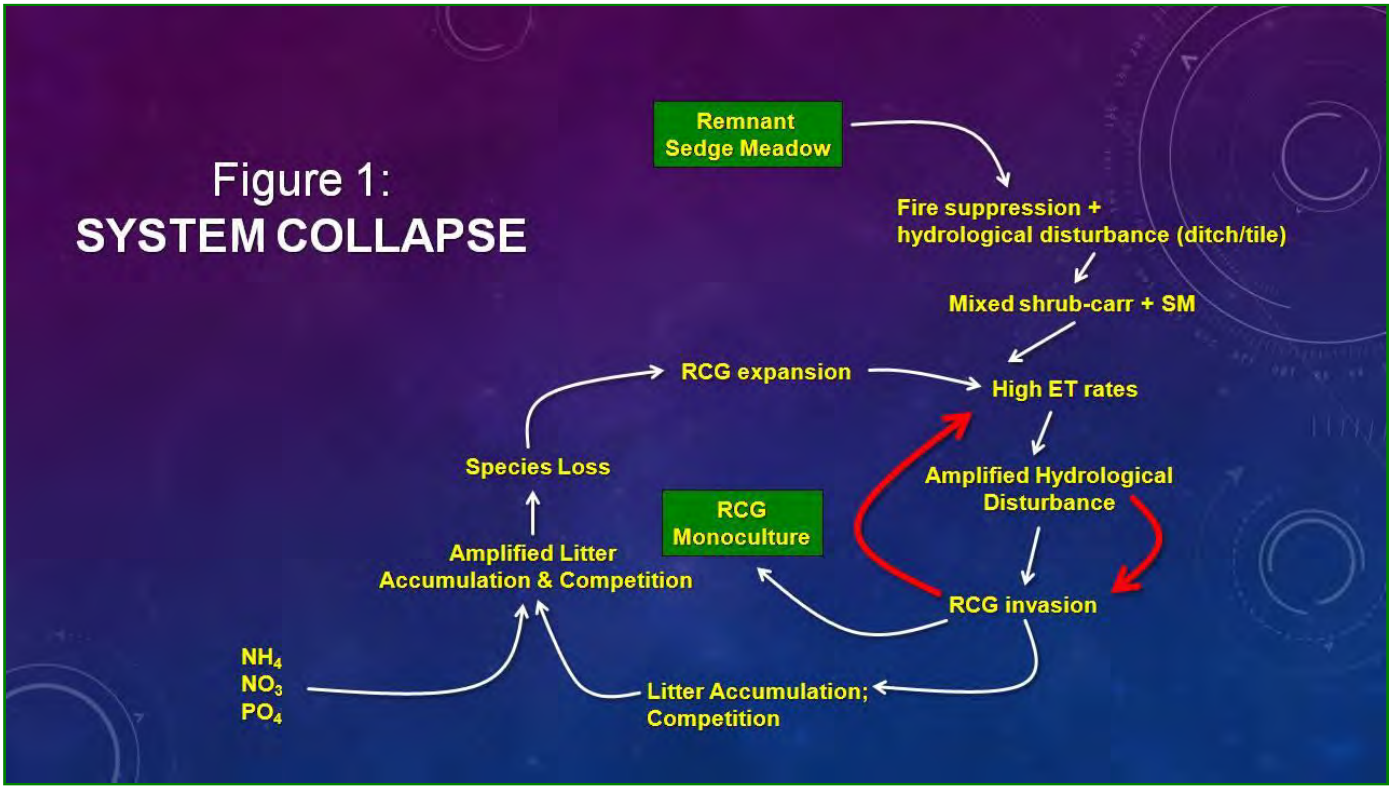
Figures 1 & 2: Concept maps of system variables and feedback cycles involved in system collapse and recovery.



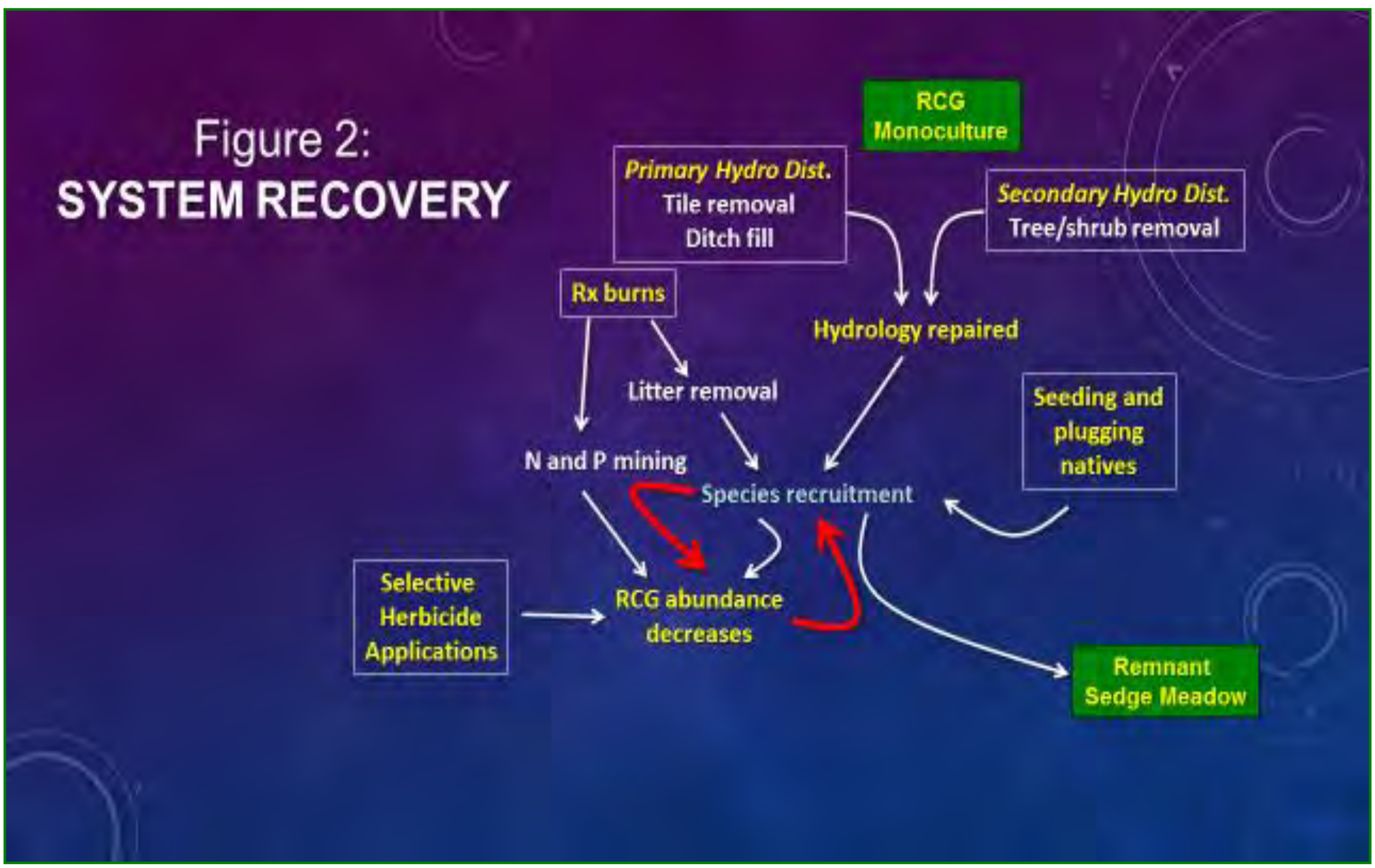


Figure 3: (2008; BEFORE REVERSAL) Sedge meadow in degraded condition, dominated by RCG and other aggressive species (tree and shrub removal was completed the previous winter).

Figure 4: (2014; AFTER REVERSAL) The sedge meadow has been returned to its remnant condition, co-dominated by *Carex* sedges and *Calamagrostis canadensis*. Note how restoration also changed the physical structure of the vegetation, with implications for wildlife habitat. Prominent white flowers are *Cacalia tuberosa* (WI-SC).