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Resilience in Quaking Aspen: recent advances and future needs

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Abstract

Quaking aspen (*Populus tremuloides*) sustainability is a topic of intense interest in forest ecology. Reports range from declines to persisting or increasing coverage in some areas. Moreover, there is little agreement on ultimate factors driving changes. Low aspen recruitment has been attributed to climate patterns, past management, herbivore increases, competitive interactions with conifers, predator and beaver extirpation, and livestock grazing. Several of these potential causes result from direct or indirect actions of human agency. On June 27-28, 2012 a group of leading aspen ecologists from diverse backgrounds convened at the High Lonesome Ranch in western Colorado to address the state of aspen science under the title, *Resilience in Quaking Aspen: restoring ecosystem processes through applied science*. The purposes of this meeting were to: a) present disciplinary updates on recent developments; b) focus our collective understanding on determining key research gaps; and, to the extent possible, c) develop a plan to communicate both advances and science gaps to wider audiences. Presentations and group discussions were framed mainly in the geographic context of the western U.S. The symposium addressed dual central themes—historical aspen cover change and ungulate herbivory—both of which have important ramifications for future aspen resilience. We also found emergent themes in disturbance, climate work, and genetic innovation. This paper presents a brief review of the state of aspen science and a synopsis of issues and needs identified at the symposium. Detailed treatments of topics mentioned here are found in accompanying articles of this volume. A key recommendation from researchers here is that there are many "aspen types" and novel, landscape- or aspen type-specific, approaches will be required to appropriately address this regional diversity. We further emphasize needed interdisciplinary work addressing changing climates, altered disturbance patterns, intensive herbivory, and human drivers of ecological change.

Keywords: cover change, *Populus tremuloides*, herbivory, climate, genetics, social science

1. Introduction

Quaking Aspen (*Populus tremuloides*) provides local diversity, regional links in conservation corridors, and is North America's most widespread forest type. Its successful establishment across diverse landscapes and environmental extremes demonstrates adaptability as a species. However, reports of aspen decline suggest that changing ecological conditions and current management strategies may impose constraints on aspen resilience in portions of its range. In contrast, other studies describe areas in which aspen is persisting or expanding its range. We define aspen r*esilience* as a condition wherein aspen can be sustained within its natural range of variation over time and space. Judicious intervention may be required to restore system resiliency where human actions have disrupted aspen functionality. Such efforts will involve intimate knowledge of forest dynamics, as the conditions that influence the sustainability and function of aspen ecosystems are complex. Additionally, humans have substantial influences on these processes, although little effort has been devoted to our society's aesthetic, cultural, and economic relationships with aspen and how they, indirectly, impact these systems. Ultimately, we need to know what value aspen ecosystems hold in our society and what the costs and benefits of sustaining them will be. The central goals of this Special Issue of *Forest Ecology and Management* are to identify aspen research advances for contemporary management applications and to highlight future avenues of study supporting system resilience.

Recent research is providing fresh perspectives on timeworn issues such as long-term cover change, as well as exploring novel conditions, such as the overlapping effects of increased browsing, drought, and landscape disturbance. Additionally, we have made great strides in the aspen sciences due to advances in technology and methodology (e.g., digital mapping, spatial analysis, computing capacity, and modeling approaches). We hope this Special Issue serves as a state-of-the-science compendium, but also catalyzes deeper exploration and innovation on several fronts surrounding contemporary aspen ecology and management.

On June 27-28, 2012 we assembled a group of aspen researchers in western Colorado to address resilience in aspen forests. Synthesis talks and group discussions were focused on the following topics: aspen functional types; long-term cover change; fire ecology; mountain pine beetle-aspen interactions; chemical defenses; ungulate herbivory; trophic cascades; facilitation and competition; mortality and climate effects; genetic advances; and human dimensions. All but the first and last of these topic areas are covered in more detail by individual papers of this volume. We present this Special Issue for the purpose of providing broader perspectives on research advances and to identify key knowledge gaps requiring investigation in the field of aspen ecology. The purpose of this overview is to update readers on recent developments within our focal themes of long-term cover change and herbivory in aspen, while also introducing the emergent topics of climate and genetic factors that affect these communities.

2. Themes in Applied Aspen Research

2.1 Long-term dynamics and cover change

Popular media often present us with sensational descriptions of change in aspen forests, likely due to the iconic nature of this species. However, scientists commonly offer more nuanced, empirical explanations for such phenomena.. Change in the status of any species is difficult to fully understand without historical context (e.g., past burning, grazing, management, climate). Aspen forests are no different, although our tools for determining historical conditions continue to expand and improve.

Nonetheless, numerous studies addressing aspen cover change have not produced a single conclusion: differing results often reflect varying ecological conditions. However, methods and scales of study may play a role in these disparate findings. Taken individually these studies provide diverse perspectives on aspen community dynamics and resilience. Collectively they illuminate the complexity of aspen ecology and conservation status.

Despite a century of interest in measuring aspen forests, we cannot definitely say if aspen across any given region is expanding or contracting. While some authors have reported 20th century decline (DiOrio et al., 2004; Gallant et al., 2003; Bartos and Campbell, 1998), others have documented marked expansions (Kulakowski et al., 2004; Manier and Laven, 2002), and still others have shown both expansions and contractions in the same area (Brown et al., 2006; Sankey, 2009). Undoubtedly, variations in site conditions, as well as lack of standard terminology in defining change contribute to these different findings. For example, it is difficult to know where true change occurs when historical sources may have used vastly different methods to define dominant cover. Additionally, we acknowledge that aspen forests differ across their broad range. Accordingly, across their expanse, aspen may be affected in varying ways by disturbance mechanisms, plant-plant interactions, climate, water availability, soil resources, and other environmental factors. Rogers et al. (in review), provide further detail of this "functional type" approach to aspen classification. Indeed, an overarching theme that emerged from this symposium was the recognition of a multiple aspen type paradigm. This may be helpful in understanding aspen ecology and appropriate management actions, but further complicates measuring cover change: changing definitions and multiple aspen types make gross assessments difficult.

A diverse array of tools, explored more fully by Kulakowski et al. (*this volume*), may be used to investigate long-term cover change in aspen and associated vegetation types. Because aspen are relatively short-lived and prone to various heart rots, reliance on purely dendrochronological methods is limiting. In order to overcome methodological limits, and subsequent reduced inference, multiple lines of ecological and historical evidence are required to yield the best results in understanding aspen change. Even with the best of cross-indexed approaches, however, differing results may be found within adjacent stands or landscapes (Zier and Baker 2006, Sankey 2009); these results may often be explained by differing aspen types (i.e., functional processes) in close proximity. A takeaway lesson from these deliberations is that diverse patterns of aspen change are common and thus, despite media reports to the contrary, no single trajectory should be expected.

Further insight regarding aspen cover change depends on a deeper knowledge of widespread disturbances in the Intermountain West. In seral situations, aspen is an early successional species dependent on disturbance to regenerate existing stands or colonize new areas (e.g., Landhäusser et al., 2010). Common disturbances in aspen systems, such as fire, insect and disease outbreaks, wind storms, and avalanches, are widely thought to shape forests at large scales and over long periods. Specifically, we explored individual impacts of mountain pine beetle and wildfire on varying aspen forests. Recent outbreaks of beetles are thought to increase opportunity for aspen expansion, although mixed results have been described (Pelz & Smith, *this volume*). Aspen seedling establishment in beetle outbreak areas has apparently not been addressed by the scientific literature to date. While success of aspen's vegetative recruitment is highly dependent on pre-outbreak presence of mature ramets, other factors (e.g., competing species, soil conditions, resource availability) may enhance or inhibit success.

Aspen are paradoxically resistant to burning, yet dependent on fire. This situation, if properly understood, can inform appropriate use of prescribed and wildfire in aspen forests. We have long known that fire rarely begins in aspen (e.g., Fechner and Barrows 1976), although after a fire starts, further expansion will affect different aspen types to varying degrees. Wildfire occurrence in aspen depends on competing and surrounding vegetation, as well as interactive effects of other disturbance agents on aspen and cohort species. In general, wildfire affects stable aspen differently than seral stands. Introduction of a new scheme delineating "aspen fire types" is presented here to assist practitioners in appropriate understanding and use of fire in these forests (see Shinneman, *this volume*). We define "stable" aspen as stands remaining in single-species dominance for long periods (i.e., at least 150 years), while the more common seral aspen are subject to succession toward conifer dominance within a century. As a rule stable aspen are infrequently susceptible to stand-replacing events, including fire, whereas seral aspen are commonly vulnerable to catastrophic or mixed-severity fire.

A key research need in addressing the effects of disturbance on long-term cover change, including aspen fire ecology, is to determine historical range of variability (Landres et al. 1999) for various aspen conditions and sites. Site-specific historical range investigations will incorporate not only interactive effects of disturbances in aspen, but also use of modeling techniques to predict future impacts under altered climate scenarios. Until now, climate modeling efforts have taken a deterministic approach (Rehfeldt et al., 2010). To be effective, climate models addressing aspen cover change must incorporate elements driving both declines and expansions in a range of aspen types. For example, warming climates at many locations may limit aspen habitat, however where warming also includes frequent drought, there are many places where the resulting wildfires may contribute to aspen rejuvenation and even expansion (Zier and Baker, 2006).

2.2 Ungulate herbivory

Since the 1920s, impacts of wild and domestic herbivores on aspen have been a major concern in western North America. However, it is only within the last decade that ecologists have begun to achieve a more global understanding of how herbivory interacts with landscape-scale issues, such as aspen persistence, fire suppression, and climate disruption. Additionally, within the last decade scientists and managers are beginning to gain an understanding of how managing ungulates for "sustained yield" creates changes in aspen communities beyond the historical range of variability in these communities. In general, relatively short-lived aspen ramets depend on some level of continuous or episodic recruitment to persist. Where regenerating sprouts, or in some instances seedlings, are subjected to continuous browsing whole stands or landscapes may be threatened by a lack of "next generation" aspen to replace dying cohorts. In seral stands, aspen's facilitative role in conifer establishment and development (Calder and St.Clair 2012) could lead to modified forest structure or even loss of forest communities (St. Clair, *this volume*). There is also recognition that we need better knowledge of seasonal use and nutritional needs of ungulates (Beck et al. 1996, Jones et al. 2009), and of the ecological impacts of wildlife management strategies that include maintaining elevated ungulate populations in the absence of predation. This type of knowledge may help ecologists not only address ungulate numbers, but perhaps influence seasonal movements to minimize excessive damage to regenerating aspen. Before we make recommendations, however, we must gain better understanding of environmental influences (e.g., predation risk, climate, nutrition, chemical defense) controlling ungulate-aspen interactions.

Aspen, like many plants, employs a variety of strategies to deter excessive herbivory. Chemical defense systems are used by plants to dissuade both insect and ungulate herbivory. While these effects have long been known, new work on how aspen chemical defenses interact with environmental conditions has advanced this science in the past decade. Of specific interest is the ability of aspen's chemical defense mechanisms to repel or tolerate browsing by elk (*Cervus edaphus*) in the Rocky Mountain region (Wooley et al. 2008). Work presented by Lindroth and St. Clair (*this volume*) explores not only tradeoffs between growth and defense, but the precise role of phenolic glycosides in deterring browsers. Phenolic glycoside concentrations found in aspen foliage are highly variable across landscapes depending on genotype, tree age, light availability, and previous browse history. Chemical variability may explain anecdotal observations of low, medium, and high levels of browse in adjacent aspen stands that may easily be accessed by the same animals. Future investigations of spatial inconsistency of sucker survival due to chemical ecology may provide further tools for land and wildlife managers in curtailing overbrowsing, as well as educating the public.

Both wild and domestic browsers at high density, or in lower numbers for extended periods, can disrupt ecosystem function. In addition to reducing or eliminating aspen recruitment, there are cascading effects on aspen-dependent species (Martin & Maron, 2012; Rogers et al. 2007). Seager and Eisenberg (*this volume*) focus our attention more specifically on wild ungulates and the effects recent population trends are having on aspen, but also how they are indirectly affecting aspen-dependent plants and animals. Additionally, all ungulate populations at high density can compact soil, trample plants, and increase erosion; though moderate levels of browsing may actually increase plant diversity (Hobbs and Huenneke 1992). Historical context provides a critical piece of information in evaluating aspen resilience and its relationship to herbivory. For example, livestock were absent until the late 19th century from most aspen communities in western North America, and large herbivore numbers were kept lower due to predation. Thus, in exploring future management approaches, we are directed back toward enhancing our knowledge of historical use and natural processes, which may be used proactively to regulate ungulate numbers and movement for the benefit of aspen resilience.

Forest scientists often look to restoration of ecological function to guide successful management. To the degree possible—frequently involving difficult social and political choices—managers should allow multiple species interaction (i.e., contrast with select-species management) to influence stewardship decisions. Where that is not possible, emulation of natural disturbance, climate impacts, predator-prey relations, and other large- and small-scale processes may provide guidance for active and passive restoration. In relation to native browsers, the cascading effects of top-down predators on ungulates are thought to be a driving influence on aspen recruitment (Ripple et al. 2001). Eisenberg et al. (*this volume*) review previous work placing it in the context of their ongoing studies of wolf (*Canis lupus*), elk, aspen linkages in the Northern Rockies. Eisenberg et al. reveal varying levels of predator (i.e., process) influence on ungulate-aspen systems. As with other aspects of aspen ecology, context plays a key role in trophic cascades involving wolves, elk, and aspen, with effects such as fire, hunting of ungulates and carnivores by humans, and climate moderating these relationships. The current body of trophic cascades research indicates that recruitment of aspen ramets into the forest canopy is driven by multi-causal factors. Once again, we arrive at the conclusion that we cannot neatly assign all aspen systems, or even what are thought to be predominant influences, to one-size-fits-all paradigms. Future trophic cascades research will involve examining how to functionally measure trophic interaction strength and direction in an aspen system, thereby enabling manipulation of key elements (i.e., herbivore and apex predator populations, disturbance regimes) to effectively restore impaired aspen communities.

2.3 Climate impacts

Climatic patterns play a large role in forest changes through time. Aspen forests have shown some sensitivity to climate extremes, particularly drought (Hogg et al., 2008). Today we have a far more advanced awareness of the current and potential global impacts of climate change than we did even one decade ago, but much work remains to be done. There is strong concern that expected climate warming, and in some regions accompanying drought, will have deleterious effects on aspen persistence (Rehfeldt et al. 2009). However, little work has been done to explore potential aspen range expansions, either via vegetative or sexual regeneration, where new habitat for this species may arise. Some examples of past expansions were noted where seedling habitat was created (Landh□usser et al., 2010) and where elevated nitrogen emissions spurred forest expansion (Kochy and Wilson 2001). In contrast, Worrall et al. (*this volume*) take a North American range-wide look at the role of drought and modeled the effect of climate futures on aspen decline and mortality. This promising new work, in which they identify areas of both weak and strong climatic effects on aspen and potential upslope migrations or expansions of suitable aspen habitat in some mountainous regions, has the potential of helping us understand the impacts of climate change on this species' range.

New areas for future work include climate modeling devoted to understanding resilience in aspen (and many other species). This science is still in its infancy, with iterative improvements in this field likely to follow. Other climate-atmospheric concerns, for instance direct impacts of carbon, nitrogen, and ozone inputs, coupled with inclusion of disturbances and environmental variance within aspen communities, may further complicate future modeling work. However, these elements are essential to improving predictive ability in a resilience context.

A final consideration that may inform our understanding of aspen resilience is use of knowledge and modeling of past climates to predict aspen responses to future climate scenarios. For example, can long periods of historical drought (e.g., Medieval Warm Period) be used as analogues for future climate conditions? If so, perhaps disturbance ecology dating methods, such as dendrochronology, charcoal dating, and pollen cores, can be used to estimate past conditions in order to provide model inputs for future climate scenarios. While reliance on historical ecology may only provide partial solutions, complementary efforts to restore key processes appear to hold the greatest promise for “managing for resilience” in the face of climate uncertainty (Millar, et al., 2007)

2.4 Aspen genetics

Aspen's ecology and management is governed by its clonal nature. Rapid advances in genetic research are shedding new light on old assumptions about clone sizes, number of clones within stands, clonal boundaries, and frequency of sexual reproduction. The ability to precisely define current clonal boundaries both above and below ground is helping managers to understand how clones become established and spread in a landscape. Mutation accumulation can even be used in some circumstances to estimate clonal ages (Ally et al., 2010). Scientists are using genetic tools to determine ploidy levels (numbers of chromosome copies) in aspen. These levels may be linked to physiological and phytochemical differences (See Lindroth and St. Clair, *this volume*), and used to describe patterns of range-wide genetic diversity and historical range expansions and contractions. Rapidly emerging technological advances in genetic analysis also offer exciting possibilities for understanding adaptive variation, responses to climate change, and ecological tradeoffs in aspen. In order to connect the potential of these genetic tools to aspen management issues, increased communication will be needed between geneticists and forest practitioners. Mock et al, (*this volume*) present a review for non-geneticists of current and emerging genetic tools, with applications for aspen ecology and management.

3. Future Directions

A key outcome of this symposium and the papers found within this Special Issue is a growing realization of unique aspen "types." The papers herein comprise an attempt to communicate this vital message via a number of disciplinary experts. Ongoing investigations into cover change, disturbance and chemical ecology, ungulate herbivory and wildlife uses, genetics, and changing climates contain a common thread emphasizing this diversity. We believe consideration of these advancements will better inform managers toward more appropriate aspen prescriptions.

Beyond this broad conclusion, several other themes emerged that build and expand on the findings of previous aspen symposia (e.g., Shepperd et al., 2001) to help guide future aspen work: 1) consideration of multiple disturbances and their interactive effects; 2) the need for further clarity among scientists on exactly what constitutes aspen "decline" (e.g., are there specific spatial, temporal, physiological requirements?); 3) herbivory can reduce community resilience and significantly alter future aspen cover; 4) unraveling and managing herbivore impacts demands interdisciplinary approaches using plant physiology (i.e., defense and growth), wildlife biology and behavior, aspen ecology, and the social sciences; and 5) there is greater genotypic complexity than previously thought in these landscapes and we are only beginning to understand the ecological ramifications of this diversity. For instance, where management often takes place at the "stand" level—a term admittedly fraught with ambiguity—western aspen stands should not automatically be thought of as individual clones. High genetic variation in aspen underlies a wide-ranging phenotypic diversity (St.Clair et al., 2010) that influences plant community characteristics and ecosystem processes.

Beyond key messages, we found numerous instances of research questions that would benefit from multi-disciplinary analyses. For example, participants at the symposium felt that the combination of changing climates, altered disturbance patterns, and intensive herbivory is placing aspen in a potentially non-resilient situation. From this starting point alone, a number of exploratory avenues arise:

a) How effective are chemical defenses in aspen at deterring browsing elk? How does this vary at stand, landscape, and regional scales, and with increasing animal populations?

b) Can historical range of variability, determined via written accounts and anthropological methods, be a useful means of establishing wild ungulate targets today?

c) Is "carrying capacity" a useful precept for browsing ungulates? Can aspen recruitment be used as an indicator of success (or failure) of carrying capacity?

d) Can large disturbances producing large-scale regeneration overwhelm ungulate herbivory?

e) Do apex predators, such as wolves, have the same cascading impacts on all aspen environments (i.e., with varying prey numbers, disturbance intensities, aspen densities)? If not, what factors are most important in explaining variation?

Interdisciplinary work—via hypothesis generation, field, and laboratory research—using wildlife, forest, physiological, geographic, and molecular ecologists will increasingly be required. Effective investigation of these questions, and like inquiries on other aspen topics, will increasingly require collaboration across institutions and disciplines.

We acknowledge that some topics were excluded from the "Resilience in aspen..." symposium, due to space and time limitations. Topics such as linking aspen conditions (and change) to species diversity, exploration of niche theory as related to future climates, water use and storage in altered communities, soil properties and carbon accumulation, and various socio-economic issues all deserve greater attention. We believe these topics are not only important in their own right, but may be useful as interdisciplinary links with subject areas discussed here. Thus, we encourage continued inclusion of multidisciplinary approaches via these and other (unmentioned) aspen-related topics in future forums.

Finally, this gathering of aspen investigators felt that we should engage the social sciences to a greater degree in aspen problem-solving. Social, cultural, and economic decision-making underlies many ecological issues surrounding aspen science and management, yet we have little sound information regarding how and why people act in this arena. For instance, in many western states and provinces wild game management is driven by hunter license fees. Increased hunting (and fees) often leads to greater herbivore numbers, which in turn directly impacts aspen survivorship. How can science improve these socio-economic mechanisms so they mesh with positive ecological outcomes? It became clear to attendees at the "Resilience in aspen . . ." symposium, as it should be to most readers, that human activities ultimately drive many of the ecological issues we face. Applied research in this area is clearly lacking. There are probably many reasons for this, but we would be remiss if we didn't point out the vital need for better collaboration in bridging ecological and social research endeavors related to aspen sustainability. One glaring avenue in need of strong social context is effective communication of findings to a variety of audiences. In the end, clear messages from the science community, in both academic and public spheres, provide the most promise for aspen's long-term resilience. Toward that end, articles in this Special Issue of *Forest Ecology and Management* invite readers to reconsider existing paradigms in aspen ecology, inspire collaborative work in the areas in which we have identified knowledge gaps, and facilitate clearer and more effective communication of aspen conservation science to a wider audience.

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