A Global View of Aspen: Conservation Science for Widespread Keystone Systems

Paul C. Rogers
Utah State University

Bradley D. Pinno
University of Alberta

Jan Šebesta
Mendel University

Benedicte R. Albrectsen
Umea University

Guoqing Li
Northwest A&F University

See next page for additional authors

Follow this and additional works at: https://digitalcommons.usu.edu/eco_pubs

Part of the Ecology and Evolutionary Biology Commons

Recommended Citation

This Article is brought to you for free and open access by the Ecology Center at DigitalCommons@USU. It has been accepted for inclusion in Ecology Center Publications by an authorized administrator of DigitalCommons@USU. For more information, please contact rebecca.nelson@usu.edu.
Authors
Paul C. Rogers, Bradley D. Pinno, Jan Šebesta, Benedicte R. Albrechtsen, Guoqing Li, Natalya Ivanova, Dominik Kulakowski, Antonín Kusbach, Timo Kuuluvainen, Simon M. Landhäuser, Hongyan Liu, Tor Myking, Pertti Pulkkinen, and Zhongming Wen

This article is available at DigitalCommons@USU: https://digitalcommons.usu.edu/eco_pubs/95
Review paper submission to *Global Ecology and Conservation*:

**A global view of aspen:**
Conservation science for widespread keystone systems

Paul C. Rogers*\(^a\), Bradley D. Pinno\(^b\), Jan Šebesta\(^c\), Benedicte Albrechtsen\(^d\), Guoqing Li\(^e\), Natalya Ivanova\(^f\), Dominik Kulakowski\(^g\), Antonín Kusbach\(^h\), Timo Kuuluvainen\(^i\), Simon M. Landhäusser\(^b\), Hongyan Liu\(^j\), Tor Myking\(^j\), Pertti Pulkkinen\(^k\), Zhongming Wen\(^l\)

* Corresponding Author

\(^a\) Western Aspen Alliance, Wildland Resources Department, and Ecology Center, 5230 Old Main Hill, Utah State University, Logan, Utah, 84322, USA. p.rogers@usu.edu

\(^b\) Agricultural Life and Environmental Sciences, Renewable Resources, University of Alberta, Edmonton, Canada. bpinno@ualberta.ca, slandhae@ualberta.ca

\(^c\) Department of Forest Botany, Dendrology and Geobiocoenology, Faculty of Forestry and Wood Technology, Mendel University, Brno, Czech Republic. sebastian.cz@gmail.com, AKusbach@seznam.cz

\(^d\) Umeå Plant Science Centre, Department of Plant Physiology, Umeå University, Umeå, Sweden. benedicte.albrechtsen@umu.se

\(^e\) State Key Laboratory of Soil Erosion and Dryland Farming on the Loess Plateau, Northwest A&F University, Yangling, Shaanxi, China. liguoqing@nwsuaf.edu.cn

\(^f\) Botanical Garden of the Ural Branch of the Russian Academy of Sciences, Yekaterinburg, Russia. i.n.s@bk.ru

\(^g\) Graduate School of Geography, Clark University, Worcester, Massachusetts, USA. DKulakowski@clarku.edu

\(^h\) Department of Forest Sciences, University of Helsinki, Helsinki, Finland. timo.kuuluvainen@helsinki.fi

\(^i\) Department of Ecology, College of Urban and Environmental Sciences, Peking University, Beijing, China. lhy@urban.pku.edu.cn

\(^j\) Norwegian Institute of Bioeconomy Research (NIBIO), Thormølensgate 55, Bergen, Norway. Tor.Myking@nibio.no

\(^k\) Natural Resources Institute Finland (Luke), Production Systems, Helsinki, Finland. Pertti.Pulkkinen@luke.fi

\(^l\) Institute of Soil and Water Conservation, Chinese Academy of Sciences, Ministry of Water Resources, Shaanxi, China. zmwen@ms.iswc.ac.cn
ABSTRACT

Across the northern hemisphere, six species of aspen (*Populus* spp.) play a disproportionately important role in promoting biodiversity, sequestering carbon, limiting forest disturbances, and providing other ecosystem services. In many regions, aspen can maintain canopy dominance for decades to centuries as the sole major broadleaf trees in forested landscapes otherwise dominated by conifers. Aspen ecosystems are valued for many reasons, but here we highlight their potential as key contributors to regional and global biodiversity. We begin with an overview of the aspens’ ecological and economic roles. We then present a systematic literature analysis to assess topics of aspen study and how they differ by species and geographic region. We present global trends in research priorities, strengths, and weaknesses with the intention of bolstering a unified approach to aspen science and conservation. The body of this review consists of regional explorations of key aspen uses, threats, and research priorities with an eye toward developing strategies for research sharing and conservation practice. In that vein, we examine research gaps or areas in need of improved science resources by geographic location. Based on this global review of aspen research, we argue for the advancement of the “mega-conservation” strategy, centered on the idea of sustaining a set of common keystone communities (aspen) that support wide arrays of obligate species. This strategy contrasts with conventional preservation which focuses limited resources on individual species residing in narrow niches. Common threats to thriving aspen ecosystems include effects of herbivory, land clearing, logging practices favoring conifer species, and projected climate warming. Multi-scale research is needed that incorporates climatic variability with disturbance and how ecological, physiological, and genetic variability determine recruitment success in aspen. This review is intended to place aspen systems in a global conservation context by focusing on the many scientific advances taking place in these biologically diverse systems.

KEYWORDS: *Populus tremula*, *P. tremuloides*, *P. davidiana*, *P. adenopoda*, biodiversity, forests, world conservation, literature review

1.0 INTRODUCTION

Species in the genus *Populus* known as “aspen” are of global importance due to their high capacity for supporting biodiversity and providing many other important ecosystem services, including soil carbon sequestration, livestock forage, revegetation capacity, and novel wood products that have been documented extensively (DeByle and Winokur 1985, Peterson and Peterson 1992, Esseen et al. 1997, MacKenzie 2010, Boča and Van Miegroet 2017). Importantly, aspen are commonly designated “keystone species,” meaning their sustained existence supports an inordinate number of dependent plants and animals (Stohlgren et al. 1997, Kouki et al. 2004, Edenius et al. 2011, Berrill et al. 2017). Hundreds of obligate species are found in these systems, providing a unifying motivation for linking knowledge pools across international boundaries under a mega-conservation paradigm (Rogers and McAvoy 2018). This concept, in brief, prioritizes spending limited resources on preserving widespread keystone species that support many obligates, rather than conventional practices focused on narrow single-species habitats. The massive global extent of aspen makes it unlikely that individual researchers or even dedicated labs could adequately address worldwide aspen systems preservation. Moreover, linking science efforts comprises only a small portion of true conservation; transfer of knowledge to managers and policymakers is an essential component in implementing sound stewardship practices. Thus, this review initiates a multinational collaborative science that seeks to highlight aspen’s global importance as a first step toward more effective broad-scale conservation.
It is important to distinguish aspen within the greater array of *Populus* species. Here, we define aspen as being primarily upland *Populus* trees that commonly fulfill a pioneer role following forest disturbance. Aspens thrive in northern and high-elevation locations with cool summers. Poplars and cottonwoods, common designations for other *Populus* sub-groupings, are nearly exclusive to lowlands, riparian areas, and other seasonally watered zones. Aspens may grow in riparian corridors, sometimes alongside other *Populus*, though they are not confined to lowlands. Taxonomically, aspens are separated into the section *Populus* (syn. *Leuce*) of the genus *Populus* (Stettler and Bradshaw 1996). Within this group, further subdivision of white poplar (*P. alba*; subsection *Albidae*) form a distinction from the more widespread aspen subsection (*Trepidae*; OECD 2006). White poplars are functionally different from aspens and are distinguished by their highly varied leaf shape (coarsely toothed, deltoid, or even deeply lobed; Stettler and Bradshaw 1996, Dickman 2001).

Here we examine six aspen species worldwide, excluding hybrids used for commercial purposes. In North America *Populus tremuloides* and *P. grandidentata*; across Eurasia *P. tremula*; and in eastern Asia *P. davidiana*, *P. adenopoda*, and *P. sieboldii* (Figure 1, Table 1). We focus predominately on locales where aspen temporarily (seral) or permanently (stable) dominates the canopy cover. These ecosystems are most influenced by unique properties facilitated by long-term aspen cover, such as relatively rich soils and attendant diverse plant and animal assemblages. Aspen also occurs in a subdominant role in many stands, however, such forests are not our main consideration here even though small even minor aspen presence often carries some biodiversity benefits. To be clear, we focus on aspen *ecosystems* in this review; not merely a set of tree species. For this reason we emphasize systems that are most obviously aspen-dominant (or potentially so) forests. This approach allows us to directly address broad-scale biodiversity conservation when and where aspen are properly managed for long-term resilience.

Aspen commonly fulfill a role as a singular broadleaf among one-to-many regionally dominate conifers species. The element of even a single non-conifer species has been shown to contribute significantly to overall community diversity (Chong et al. 2001, Griffis-Kyle and Beier 2003, Rogers and Ryel 2008, Kuuluvainen et al. 2017). For example, addition of aspen species to otherwise exclusively conifer-dominated forests offers alternate bark texture and chemistry for epiphytes (Rogers et al. 2007), greater nutrient cycling (Boča and Van Miegroet 2017), higher snow/water retention (LaMalfa and Ryle 2008), and increased structural diversity facilitating avian diversity (Martin and Maron 2012). Aesthetically, aspen’s unique leaf structure (flattened petiole, perpendicular to leaf surface plain) lends visual and audial dimensions—the “quaking” or “trembling” namesake—to relatively calm needle-bearing forests. Finally, where aspen are isolated among vast conifer forests their autumn hues provide striking yellow, gold, and red colors to a contrasting dark green backdrop.

The aim of this review is to gain a comprehensive understanding of the ecological amplitude, biodiversity contributions, threats, and practices surrounding the aspens and their associated forests at the global scale. We highlight variability among partner nations in scientific prioritization of aspen research topics, resulting from the multidimensional nature of aspen ecology and management, which presents a biogeography that varies in opportunities, research interests, resources, and threats. In order to structure such a wide ranging inquiry, our objectives focus on: 1) Established research in order to better define aspens’ global ecological function; 2) Expert opinion poll on a country/region basis that identifies key aspen issues and prominent research avenues to date; 3) Threats and conservation needs for all aspen ecosystems; and 4) Regional- and global-scale aspen research gaps. By synthesizing the large body of aspen science currently available, we hope to establish a framework for advancing sustainable practices in these critical forest systems. Linking biological assets at very large scales—here, aspen forest systems around the northern hemisphere—provides a mechanism for moving beyond single-species conservation. Before proceeding, however, it is important to identify commonalities across the breadth of aspen species.
2.0 Common Characteristics of Global Aspens

There are a variety of traits, related to their ecosystem functions, growth patterns, and autecology, that are common to all aspen species. Aspen are characterized as early successional clonal species with rapid early growth rates, intolerance to shade, and a relatively short life span of individual ramets (Børset 1960, Lankia et al. 2012). Aspen respond rapidly and prolifically to disturbance through asexual root suckering (Frey et al 2003, Kobayashi et al. 2007, Gradel and Mühlenberg 2011, Caudullo and de Rigo 2016) with roots suckers arising up to 40 m from parent trees (Jobling 1990) and post-disturbance sucker densities as high as 250,000 stems ha\(^{-1}\) in boreal North America. Aspen are also capable of regenerating via annual seed production of many small seeds capable of wide distribution (over several kilometers), due to the tuft of hair attached to the seed (Landhäusser et al. 2019). Though less common than sucker regeneration—likely due to exacting germination requirements—seedling regeneration is more frequent than previously thought (e.g., Larva-Karjanmaa et al. 2003) and surely plays an important long-term ecological role (Landhäusser et al. 2019). Aspens grow in a variety of habitats, are tolerant of drought and frost, but favor fertile and well-drained soil with open light conditions, such as those created by disturbances (Worrell 1995a). Beyond responding to site conditions, aspens are known to increase soil productivity due to increased leaf litter and associated nutrient cycling (Ste-Marie and Pare 1999) and elevated snow and water retention (LaMalfa and Ryle 2008).

Aspens possess attributes of direct and indirect value to people. Commercial uses for aspen are similar around the world with aspen fiber being used in the production of pulp, strand board, solid wood, and specialty products (i.e., pencils, skis, sauna benches, coffins, furniture, matches, excelsior). People value biodiverse forests for products, animal forage, medicines, recreation, aesthetics, wildlife, and intrinsic properties. When aspen forests succeed or are converted to conifer forest types, biodiversity typically declines (McCulloguh et al. 2013, Rogers et al. 2008).

3.0 METHODS

We integrated known aspen research around the northern hemisphere (aspen is absent in the southern hemisphere) to gain broader understanding of the ecology, threats, values, and restoration practices to aspen forests on a global scale. As a work of review, we relied heavily on country expertise to synthesize information from their respective geographic zones. This review includes opinion poll participants (authors) from the following nations: Canada, China, Czech Republic, Finland, Norway, Russia, Sweden, and United States. Input consisted of four basic parts: 1) a systematic literature search using keywords to query two common research databases, 2) author completion of the opinion poll of activity level in 30 aspen research topic areas subdivided into three categories—basic science, applied science, and specific aspen threats, 3) summary of commonalities across all species/regions (Section 2.0), and 4) country syntheses capturing aspen ecology, prominent aspen science issues, restoration activities, and current research gaps. Literature search results for research databases are found in Appendix S1. Opinion poll responses, by region and specific topic areas, are found in tabular form in Appendix S2.

A systematic search of the technical literature since the year 2000 was queried based on location and region of studies within ISI Web of Science and SCOPUS. We searched titles, abstracts, and keywords using the basic term *aspen* or *Populus tremuloides* or *Populus tremula*. We further used term combinations including *forestry, diversity, management, water, and ecological function*. We screened out articles with similar author lists and similar topics in an effort to decrease duplication or multiple counts of closely related publications. Additionally, we searched reference lists of retrieved articles for other
relevant publications. In total, 200 articles representing 28 keywords in 9 regions were sampled. Analysis based on the linear responses were chosen because the number of keywords was low (28) and the data set was not highly heterogeneous. To better understand the data structure and heterogeneity, we projected the data set along two main axes using principal component analysis (PCA). Overlay ellipses were displayed with confidence limits of 0.70. The analysis were carried out in R v 3.0, for PCA analysis we used the “vegan” package (Oksanen et al. 2013).

In the process of retaining area experts to contribute to this aspen world review paper, we asked each national representative to rank the level of research investment and knowledge in key topic areas. We further suggested that survey participants provide seminal references to support their assessments of national research efforts. After receiving all author/expert poll responses, we grouped aspen science assessments by region in order to supplement our independent literature search and PCA analysis. By combining these two efforts—objective and subjective queries—our hope was to gain a broader understanding of contemporary aspen exploration, as well as shortcomings, in a geographic context.

4.0 RESULTS

4.1 CUMMULATIVE ASSESSMENT

4.1.1 Aspen Research Priorities by Geographic Region (Literature)

PCA analysis of topics in the aspen literature by geographic region is shown in Figure 2. To better interpret the non-canonical axes the region, as an independent factor, was projected as ellipses overlays in the PCA ordination (standard deviation of point scores and correlations defines the main directional axis of the ellipse). Key aspen terms (i.e., subtopics of study) form the data space within the ordination, meaning regional aspen-related science endeavors group directionally towards the most explored topics for that area. While this graph shows more overlap than separation, we still gain some understanding of regional research priorities based on the recently published literature. General trends include a greater emphasis on landscape process/disturbance factors in the Western U.S., climate and growth related studies in Canada, and a focus on physiological and genetic topics in most of the remaining regions. Interestingly, as related to the present review, no regions appear to be placing greater energy toward the study of conservation and diversity as compared to other topics.

4.1.2 Aspen Research Priorities by Geographic Region (Expert Survey)

Our opinion poll of regional aspen experts was an independent and qualitative attempt to get at regional research priorities. Figure 3 displays the results of that opinion poll in terms of 30 aspen research (basic and applied) and ecosystem threat topic areas. The graphic is most valuable for comparing regions to the overall average (black bar), rather than comparing region to region given the subjectivity of the survey. In this sense, we see for example, that regions have devoted similar levels of attention to genetics/molecular and landscape assessment/mapping, but offer widely varying levels of investigation for topics such as defense chemistry or grazing practices. No regions have invested intensely in human uses and effects on aspen communities, such as social sciences, land use development, or mining/oil extraction. Overall, this modest survey of aspen research efforts, using two approaches, gives us an initial sense of strengths, weaknesses, and opportunities for technique and knowledge exchange.

4.2 REGIONAL STATUS OF SCIENCE AND ISSUES
4.2.1 North America, *P. tremuloides, P. grandidentata*

United States

In the Rocky Mountains, quaking aspen (*P. tremuloides*) forests exist in a wide variety of environmental settings, which necessitates a nuanced perspective in examining their ecological patterns and dynamics (Kashian et al. 2007, Kurzel et al. 2007, Rogers et al. 2014, Kulakowski et al. 2013a). Successional replacement of aspen by conifer species (seral-dominant; Figure 4a) is most pronounced in systems shaped by long fire intervals and can thus be seen as part of a normal, long-term fluctuation in forest composition (Kulakowski et al. 2004, 2006). Dominant aspen systems are quite common in the region, often across broad plateaus and in specialized niches (Figure 4b; Rogers et al. 2014). Aspen decline was initially reported primarily at the margins of aspen’s distribution, but may be becoming more ubiquitous due to the direct effects of climate (e.g., drought). In contrast, the indirect effects of recent climate (e.g., forest fires, bark beetle outbreaks, and compounded disturbances) may facilitate expansion of this forest type (Kulakowski et al. 2013b, Gill et al. 2017). Thus, future aspen trends are likely to depend on the net result of the direct and indirect effects of altered climate (Kulakowski et al. 2013a, Worrall et al. 2013, Yang et al. 2015).

Successive or compound disturbances have the potential to alter post-disturbance conifer regeneration by reducing seed sources or increasing the intensity of the secondary disturbance (Kulakowski and Veblen 2007), which in turn may influence soil and other micro-environmental conditions (Fonturbel et al., 2011). These two influences may be of minimal negative consequence for vegetative reproduction of aspen, but are more likely to inhibit regeneration of associated conifers (Gill et al. 2017). Although compounded disturbances may increase overall disturbance intensity (either additively and/or by increasing the intensity of secondary disturbances) to the point that below-ground aspen roots are killed and re-sprouting is impeded (e.g., Parker and Parker 1983), research to date suggests that compounded disturbances favor aspen over other species (Kulakowski et al. 2013b, Gill et al. 2017).

Fire suppression (including cessation of indigenous burning) in largely seral-dominant aspen systems has been among the major causes given for the decline of aspen (DeByle et al. 1987, Kay 1997, Bartos 2001, Kay 2001). However, fire suppression is not likely to have changed the structure and composition of most aspen stands in the western U.S. (Shinneman et al. 2013). Instead, long intervals between natural disturbances have commonly resulted in a range of variation of forest structures; from complex structures to single cohort types (Kulakowski et al. 2004, 2006). Fire suppression would have had little impact in fire-independent stable aspen systems (Shinneman et al. 2013).


Climatically-induced mortality of aspen could lead to long-term reduction of aspen cover in some areas. Rogers et al. (2010) reported that low mortality rates of aspen were rarely observed in drought-prone locations. Likewise, in southwestern Colorado, areas of high aspen dieback tend to be located on dry, south-facing slopes, implying that drought stress is an important mechanism driving aspen mortality (Huang and Anderegg 2012, 2014). In the southwestern U.S., Ganey and Vojta (2011) reported that aspen mortality in mixed-conifer forest was particularly pronounced (85%) and suggested that these early trends
may be indicative of future responses to climate change. This phenomenon appears to be widespread. At
the continental scale, Worrall et al. (2013) observed that aspen on marginal sites and near ecotones are
most likely to be susceptible to climatically-induced mortality. However, Hanna and Kulakowski (2012)
found that growth and climatically-induced mortality of quaking aspen in Colorado and Wyoming away
from transitional zones are also strongly associated with climatic variation. The interactive effects of
increased drought and chronic browsing by ungulates, particularly in the absence of fire (i.e., stable
aspen), is an increasing concern for western U.S. aspen systems (Shinneman et al. 2013, Rogers and
Mittanck 2014, Yang et al. 2015).

Other contributing factors leading to aspen decline include environmental variables or biotic
agents that can aggressively act on previously stressed trees. These factors include infestation from fungi
and wood boring insects (Frey et al. 2004, Kashian et al. 2007); and may be the final causes of tree
mortality (Worrall et al. 2008, Marchetti et al. 2011, Steed and Burton 2015), but are thought to be of
secondary importance rather than the key drivers of change.

Bigtooth aspen (P. grandidentata) is commonly a minor component of forests in northeast U.S.
and southeast Canada, although it may become temporarily dominant (< 40 yr.) following stand-replacing
disturbance. Bigtooth aspen may co-dominate alongside quaking aspen and balsam poplar (P.
balsamifera), though it is most commonly found as a subordinate constituent of a complex mix of some
20 species of hardwoods and softwoods (Laidly 1990, Peterson and Peterson 1992). Where quaking and
bigtooth aspen are found in the same stands, clonal boundaries seem to remain discreet (Perala 1981).
Bigtooth aspen is shorter in stature than quaking aspen and thought to be generally less adaptable to
different environments (Laidly 1990), perhaps reflecting its’ more limited range. These two species are
managed similarly and are used for the same forest products (small diameter lumber, veneer, and
pellitized for animal feed). Biodiversity attributes are also high among bigtooth aspen; they provide
habitat and winter food for moose, beaver, and grouse (Laidly 1990).

Canada

Trembling aspen (P. tremuloides), as it is known in Canada, is a common upland species across
the boreal forest in western Canada often occurring in pure stands and in mixed stands composed of
differing amounts of white spruce (Picea glauca) and aspen, referred to as boreal mixedwoods (Padbury
et al. 1998; Beckingham and Archibald 1998). In this system, aspen is generally a seral-dominant species
that is replaced over time by the more shade tolerant spruce (Purdy et al. 2002; Solarik et al. 2010). In the
absence of a viable spruce seed source nearby or frequent disturbance, dominant aspen stands are
common across the landscape. Boreal mixedwoods of varying composition, however, are the prevailing
mesic forest type in this region.

Immediately south of the boreal forest is a transition to prairie grasslands is the region known as
the aspen parkland which is characterized by a mosaic of aspen dominant forests interspersed with
grasslands (Figure 5; Acton et al. 1998). In this region, aspen tends to be the only upland tree species
although other species, including other Populus species, form riparian corridor forests.

Aspen is a major timber species in the boreal forest and is a focus of forest management with
numerous pulp and strand board mills. In the province of Alberta alone, the annual allowable cut for
hardwoods (the vast majority of which is aspen) is currently set at over 12 M m³/year. High levels of
biodiversity, relative to the surrounding landscapes, have been recorded in both boreal seral (Macdonald
and Fenniak 2007; Berger and Puettmann 2000; Legare et al. 2001) and parkland stable aspen
communities (Grant and Berkey 1999). Within the context of forest management and timber harvesting,
aspen is generally regenerated through root suckers (Frey et al. 2003), but in the context of mine land
reclamation aspen is increasingly being planted or encouraged to regenerate via seeding as a beneficial early successional practice (Pinno & Errington 2015; Landhausser et al. 2012; Schott et al. 2014).

The most significant threat to aspen is generally considered to be prolonged severe droughts (Hogg et al. 2013) which can result in widespread aspen dieback and regeneration failures (Michaelian et al. 2011; Anderegg et al. 2013). This is particularly true further south in the aspen parkland with its dry climate which is not capable of supporting forests across the entire landscape. With anticipated increased future drought, this phenomenon may become more extreme and more common even in the boreal forest. In fact, projections indicate that the current area of boreal forest in western Canada is likely to have a climate in the future similar to the aspen parkland of today (Hogg and Hurdle 1995), calling into question the future of widespread aspen forests. Beyond drought and climate change, insects (in particular forest tent caterpillar [Malacosoma disstria] and aspen tortrix [Choristoneura conflictana]) are a significant pest of aspen. Although generally insect outbreaks do not result in widespread tree death, when they are followed by drought years, mortality may be significant (Hogg et al. 2002). Anthropogenic disturbances also have large effects on aspen, mostly due to agricultural expansion, heavy grazing, and resource extraction (i.e., mining & oil).

4.2.2 Europe, *P. tremula*

**Northern Europe**

Eurasian aspen (*P. tremula*) grows across Eurasia from Iceland to far eastern Russia, and from northern Scandinavia to outposts along the Mediterranean coast of Africa. In northern Europe it is the only native *Populus* species. Moreover, aspen is a pioneer and keystone species, but together with other broadleaved trees, it had been actively reduced during the mid-20th century to promote conifer growth (e.g., Esseen et al 1997, Axelsson et al 2002). In forestry, aspen was mainly thought to be harmful due to its role as a host species for *Melampsora pinitorqua* fungus which may threaten young Scots pine plantations. This lead to its systematic removal from many managed forests. Remnant aspen trees and small groves are scattered in old-growth forests regionally, and aspen populations are slowly rebounding from this earlier period (Figure 6). Similar conditions have historically been created by forest fires or land clearing. Today aspen often colonizes former disturbed habitats, such as abandoned arable land, slowly invading from the field edges by means of root suckers (Frivold, 1998). Overall, aspen occurs on the landscape as scattered subdominant individuals and small seral-dominant stands originating in a secondary succession process (Kouki et al., 2004).

European aspen is usually found growing in small groups or stands in spruce (*Picea abies*) forest types, and only rarely in pure stands. Aspen is highly sensitive to several type of biotic threats like insects (*Sarperda caricarias, Chrysomela populi*) and mammal herbivory by moose, deer, and hares. Even though local aspen populations are multiplying via suckering climate change may be threatening aspen because of a hardening and dormancy of aspen that is largely controlled by temperature and photoperiod (Pulkkinen pers. comm.). Likewise photoperiod, bud set, stomatal conductance, and chlorophyll content index (CCI) relate to photosynthetic rates and follow latitudinal clines in *Populus tremula* (Soolanayakanahally et al 2015).

In terms of cover, aspen-dominated forest constitutes a small percentage of overall forest area (e.g., 8% in Norway; Kucera and Næss 1999), though this limited presence caries great ecological value. Aspen’s fundamental importance in Scandinavia is in harbouring biodiversity. In fact, the number of red-listed (threatened status) host-tree dependent species is higher for aspen than for spruce (Jonsell et al. 2007). In Finland more than 200 species use dead or living aspen trees as a source of nutrition or as a habitat (Kouki et al. 2004, Vehmas et al., 2009). Ecological consequences of the forest praxis led to

Broad spatial impacts on aspen-associated species via forest fragmentation have been described (Harber et al. 2005). For instance, aspen is a highly preferred winter forage for large herbivores (Bergström and Hjeljord, 1987). Abundance of large trees, being very important for biodiversity, has increased in recent decades (Myking et al. 2011). These older trees possess specific structural properties important for species diversity, such as having hollow interiors for cavity nesting birds and rough bark of low acidity that facilitates prime lichen habitat. However, Norwegian forest inventory data indicate reduced recruitment rates of young aspen trees (60-79 mm diameter) during the last 25 years (Myking et al. 2011) leading to an imbalance in demographic structure; ample mature trees with little recruitment and intermediate aspen stems. This pattern is indicative of chronic sucker browsing by large ungulates (Edenius et al. 2011). Regeneration may also be hampered by lack of suitable stand initiating disturbance events (fire in particular).

Currently, however, previously discarded aspen is favored as a retention species because of its high biodiversity value. Accordingly, aspen volumes have increased, much of this being due to young trees in agricultural landscapes. Aspen in northern Europe does not carry high commercial value, however, some small-market uses prevail in the region. Aspen is rarely planted, with the exception of hybrid aspen, because of limited market values.

Although the commercial value of aspen is underappreciated in northern Europe, research interest has increased considerably after the genome of black poplar (Populus trichocarpa) was sequenced (Tuscan et al. 2007). This facilitated genetic and molecular studies of closely related aspen trees. For example, the Swedish Aspen (SwAsp) collection consists of a selection of 116 P. tremula genotypes that originated from 12 sites located east and west, at every second degree of latitude up through Sweden (from 56.818N, 12.854E to 66.812N, 22.812E) and thus represent a naturally varying population of aspen trees (Robinson et al. 2012, Bernhardsson et al. 2013). In 2004, four root-propagated replicates of each clone were planted into each of two common gardens: Ekebo (55.854N, 13.806E) and Sävar (63.854N, 20.836E). These gardens have since been surveyed for growth and damage and their genetics and physiology related to the reciprocal garden set-up and thus studies of genotype-environment (G-E) effects. A rich research output has resulted from SwAsp garden studies across Sweden. SwAsp genotypes are kept in tissue culture at Umeå University, which allows for propagation of genets of P. tremula with particular properties (Robinson et. al 2012).

Central Europe

Eurasian aspen (P. tremula) co-exists with many other hardwood and softwood trees across central Europe to the Mediterranean where it mostly maintains a sub-dominant position. A few exceptions may include sites established for commercial (pulp, match industry) or research purposes, and on the waste heaps at former quarries and mines (revegetation). In southern Europe, subdominant aspen are found along the Mediterranean through Spain, Italy, Greece, Turkey and Algeria (Caudullo and de Rigo 2016). In central Europe, aspen is not commonly dominant in many stands but it typically fulfills a pioneering role. However, it is widespread as a sub-dominant in many forest habitats, displaying seral-dominance in recently disturbed forest stands, clearings, and agricultural landscapes. Its distribution rapidly increased in the Czech Republic as a result of introductions following acid rain die-off of conifer forests and planting for match production (A. Kusbach, pers. comm.). These large plantations are up to 40-50 years old and often remain unmanaged due to unclear ownership or because of unprofitability.
Occurrence in ecologically varied habitats demonstrates a broad ecological amplitude in central European aspen. For instance, we find aspen in extreme habitats, such as dry pine forests with shallow soils and in wet floodplains. Aspen is assumed to be mostly seral-dominant following disturbances (fire, wind-throw, pasturing). It reproduces mainly vegetatively from root suckers, establishing in predominately small stands (< 0.5 ha). Aspen has proved advantageous for improving site quality following acid rain and has even flourished under such conditions. Aspen is used to mechanically stabilize soils as dense the root networks expand and aid erosion control (Caudullo and de Rigo 2016). We expect that aspen contributes to forest biodiversity (as elsewhere), although region-specific corroboration has not yet been conducted. Aspen forests provide forage for ungulates, as well as aesthetic enjoyment for people as fall foliage adds forest hues of golden and purple among conifers and other hardwoods. To improve tolerance and quality of wood and increase productivity, a number of hybrids have been cultivated (Caudullo and de Rigo 2016). In fact, wood cultivation has been a primary research objective fueled by studies of genetic diversity as it relates to fiber quality.

In central Europe, aspen has been understudied due to relatively minor coverage and a subsequent low interest in ecology of the species. Two exceptions spurred some interest in the species: First, a former interest in aspen (e.g., Czech Republic) was instigated by an ecological disaster (air pollution a site degradation) leaving tens of thousands hectares of forest mortality. Cultivation of aspen in these severely damaged zones has shown wider promise in using aspen as a primary revegetation forest type. Second, demands of the match industry within a communist market oriented to the former Soviet Union, alongside a shortage of aspen fiber, promoted aspen silviculture. Future aspen interest may take advantage of these endeavors, by highlighting its use as a mechanism for reforestation and site quality improvement, a source of hybrid and wood fiber research, and as refugia for central European biodiversity under changing climates.

4.3.3 Trans-Siberian and Eastern Asia, *P. tremula, P. davidiana, P. adenopoda*

Russian Federation

Eurasian aspen (*P. tremula*) is a widespread tree species in Russia. In the Oligocene and Miocene all Kazakhstan and Western Siberia were covered with deciduous forests. Aspen was a common woody plant in these ancient forests (Khotinsky, 1977). Currently, this tree species occurs along forest-tundra ecotones and in forest and forest-steppe zones. The greatest distribution of aspen forests is observed between 53º N and 60º N (Vorobyev 1986). Small areas of Eurasian aspen can be found in the steppe zone. In sum, aspen forests cover 2.7% of all forests of the former Soviet Union (Smilga, 1986).

Aspen in Russia appears well adapted to different soils. It can form dominant stands or grow together (seral-dominant) with coniferous woody species (pine, larch, spruce) or birch, alder, oak in the Ural Mountains, for example (Figure 7). In these indigenous coniferous forests, aspen is present in a small amounts. It is an obligatory component of the dark coniferous taiga (boreal). Secondary aspen forests are formed after harvesting or on abandoned hayfields where aspen was part of the original forest (Smilga 1986, Danilin 1989, Ivanova 2014, Maiti et al. 2016). Otherwise, aspen stands are formed without conifers in subordinate tiers, even if individual spruce and fir are present in the stand (Ivanova and Andreev 2008). Aspen dominant forests are often found on abandoned hayfields with moist soils (Frivold 1998). Riparian aspen may be characterized as both dominant- and seral-dominant forests depending on specific locales (*sensu* Rogers et al. 2014). These are the most productive aspen forests and yield excellent quality wood (Smilga 1986).

Aspen timber is highly valued in Russia (Smilga 1986, Danilin 1989). In addition, the value of aspen for anti-inflammatory medicines has been recognized in Russia (Turetskova et al. 2011, Karomatov
and Rasulova 2017). However, large healthy trees occur infrequently, due to common stem pathogens and overtopping by conifers. Therefore, overall aspen is classified as a low-value species and production forestry is focused almost entirely on conifer species. A large number of studies are devoted to the polymorphism of this woody plant (e.g., Danilin 1989, Politov et al. 2016). An overview of this area of research was conducted by Smilga (1986). Extensive work has been conducted on the biomass and productivity of aspen in different habitats (Usoltsev 2001, 2003). This work incorporated biogeographic assessments of biomass limits and distribution for aspen of northern Eurasia based on the condition of stand self-thinning using a standardized biomass equations. Dependence of forest biomass limits upon the climate (continentiality) index and the sum of effective temperatures were first suggested by Usoltsev (2003). Additionally, photosynthesis studies helped determine the growth and productivity of these forests for different locales within the country (Obydenni, 1965), as well as optimizing growth potential for production forestry (Petrova, 2011, Vays, 2013). Numerous works have documented differences in aspen structure, biodiversity, and condition in different regions of the Russian Federation (Degteva et al. 2001, Lashchinskiy 2010, Popov 2017).

**Mongolia**

In Mongolian forests, Eurasian aspen (\textit{P. tremula}) is a ubiquitous, widespread species but it is absent in the Altai region (Altrell and Erdenejav 2016). Aspen occurs in small stands/clones (< 2 ha) or mixed with other tree species such as Scotch pine (\textit{Pinus sylvestris}) and white birch (\textit{Betula platyphylla}; Dulamsuren et al. 2005). Especially in native old-growth coniferous forests, aspen is present in minor amounts. Except extensively logged areas, it rarely appears as a total national volume of 3.5 M m\(^3\) (MET 2016). Aspen is a frequent component of the forest-steppe transitional zone (light taiga), complementing Siberian larch (\textit{Larix sibirica}) and white birch (Savin et al. 1988, Ermakov et al. 2002). Here, aspen stands form sub-taiga forests in the upper part of south-facing slopes of the lower montane belt (Tsedendash 1995, Dulamsuren et al. 2005). Analogous semi-arid montane aspen forests in North American \textit{P. tremuloides} are often cited as those most vulnerable to combined forces of herbivory and climate warming-induced drought (Worrall et al. 2008, Rogers and Mittanck 2014). Aspen is a minority component of the dark taiga in the upper montane belt (Müehlenberg et al. 2011, Kusbach et al. 2019). It also forms detached clones in lower areas (< 1000 m elev.) at the edge of the steppe zone in the forest-steppe/lower montane geo-vegetation zone (Kusbach et al. 2019). After extensive logging (legal and illegal) in 1960’s – 80’s, in which predominantly commercial conifer species were harvested, the percentage birch and aspen has increased (Tsogtbaatar 2007). Currently, residual broadleaves form large monospecific, often diseased, stands that often inhibit conifer regeneration.

Mongolia’s strongly continental climate is thought to be largely responsible for great genotypic and phenotypic heterogeneity across aspen’s broad ecological amplitude (Hamrick 2004). Fire, snow, and ice are important disturbance factors which often drive regeneration and cover change in Mongolian forests (Altrell and Erdenejav 2016). Recent research suggests that aspen dominance may persist for centuries (perhaps millennia?) based on a pedoanthracology (aging and identifying plants in ancient charcoal) study in the Khaan Khentii Mountains, central Mongolia (Novák et al., in preparation). Thus, it is yet undetermined if viable dominant aspen stands will persist alongside the more common seral-dominant type in this region.

**China**

David’s aspen (\textit{P. davidiana}) is found throughout eastern Asia (i.e., northeast China, Korean peninsula). Here we discuss the species mostly in the context of China. David’s aspen is a tree species
with wide ecological amplitude from warm to cold temperate zones (Zhang and Dai, 1984). David’s aspen are generally seral-dominant, transitioning over decades to conifer forests via succession (Figure 8). This aspen community is generally a mixed tree system that initiates when the original forest is altered by human activity or fire. With succession, the community will eventually be replaced by other species such as oak, pine, spruce, or fir species (Zhu and Huang, 1991).

In the past, due to deforestation and overconsumption, much of the aspen forest was converted into cropland or grassland. Since the Natural Forest Protection Program in China (1998), tree harvesting in these forests has been prohibited. According to the Chinese vegetation map (ECVAC 2001), David’s aspen forest covers about 21,600 km² in China which is substantially less than the potential/historical extent as shown in Figure 1, Table 1. Past land clearing, agriculture, and grazing/browsing practices may impede the sustainability of aspen in China. However, recent research suggests that high-intensity fire is beneficial to the species’ regeneration (Tian et al. 2014) and moderate thinning is better for maintenance of plant diversity than clearfelling. New work also indicates advantages from a warming climate; moderate drought may favor aspen’s quick regeneration response over competing species (Zhao et al. 2018) but aspen in poor condition may react adversely to prolonged drought, thus threatening community stability.

David’s aspen has a high economic and ecological value in China. Forest harvest rotations are generally short and the fast growth facilitates commercial forestry for a range of products. Concurrently, aspen has been listed as a candidate afforestation and restoration tree species in China due to its fast growth, self-renewal capacity, and adaptability to diverse environments (Hou et al. 2004). As such, it has been widely planted in northern China through encouragement of government programs targeting conversion of crop lands to forest cover.

At present, most research on David’s aspen focus on molecular phylogeny, water consumption characteristics, response of tree growth to soil moisture, community biodiversity (Hou et al. 2018, Zheng et al. 2017) and successional trends, carbon sequestration, soil erosion, and forest cutting strategies (Zhu and Huang 1991, Zhao et al. 1994, Shen et al. 2016). Research to date has greatly improved our understanding of the properties of David’s aspen communities (Zhu and Huang 1991, Wang et al. 2000, Guo and Li 2012).

Chinese aspen (P. adenopoda) is a less widespread species in China and it is distributed in the subtropical Yangtze and Huaihe River basin (Tang et al. 2011). This species possesses a robust sprouting ability, similar to David’s aspen. Chinese aspen regenerates readily in clearfell-coppice areas. In natural settings, this species coexists with Pinus massoniana, Betula luminifera, Rhus chinensis, and a variety of Quercus spp. Chinese aspen is used to make pulp and has important economic value. Due to cold tolerance, P. adenopoda has also been widely planted in the low hills region of southern China with altitude range from 800-1800 m. Mechanical reductions of the mid- and lower- storey associate tree species increases growth and thus economic value in Chinese aspen stands (Jiang and Tan 2009). Current research on Chinese aspen is focused on inheritance and breeding, reproduction, and growth characteristics (Tang et al. 2011, Jiang and Tan 2009).

Japan

Pure stands of Japanese aspen (P. sieboldii) are rare. This species, as most aspen, is a colonizer of recently disturbed sites; however, its endemism in Japan finds it revegetating volcanically impacted locations effectively, a somewhat unique mechanism for stand rejuvenation in aspen. P. sieboldii is commercially important, especially when hybridized with P. grandidentata (Dickmann and Kuzovkina 2014). Overall, this species does not appear to play a major role in Japan’s forests, though we expect that there is still an important biodiversity function where it is found.
5.0 DISCUSSION

5.1 A global aspen perspective: biodiversity and threats

Aspen communities are widespread around the northern hemisphere and characterized by similar dynamics, as well as ecosystem services: clonal replication, enhanced species diversity, water retention and conservation, deterrents to fire spread, and aesthetic attributes. In some regions, however, aspen are still viewed as marginal wood resources and may be actively suppressed or eradicated to facilitate commercial species. We suggest that sharing science resources across international boundaries may elucidate previously unrealized benefits of aspen species, promote sustainable management, and enable broad-scale conservation of aspen and obligate species.

In many, though not all, locales aspen systems are biodiversity hotspots where they are often a minority species among vast conifer forests. This highlights the fact that even small stands of aspen add disproportionately to overall landscape diversity (Kouki et al. 2004, Macdonald and Fennia 2007, Rogers and Ryel 2008). For example, where aspen stands in the southwest U.S. are in decline, avian diversity has been shown to decrease (Griffis-Kyle and Beier 2003, Martin and Maron 2012). In Sweden, small groves of aspen contributed significantly more than the matrix of conifers to total epiphytic lichen varieties (Hedenås and Ericson 2003). In terms of conservation, an important implication is that the viability of some obligate species—including epiphytes, understory plants, birds, mammals, or invertebrates—can follow the trajectory, either plus or minus, of the vitality supporting aspen communities (Chong et al. 2001, Oaten et al. 2008, Rogers and Ryel 2008, Bailey and Whitham 2002). Thus, though aspen are widespread, their degradation holds outsized capacity for influencing broad-scale regional and continental biodiversity.

There are numerous threats to aspen ecosystems, however, given the functional diversity within these forests, we should expect variation in the response of aspen to common stimuli (Rogers et al. 2014). Even so, some common threats are evident. Persistent drought is already occurring in some regions and is expected to increase under climate change (Gray et al. 2011, Hogg et al. 2013, Worrall et al. 2013). Intense herbivory, whether in combination with wildfire or prolonged drought, often presents acute barriers to aspen resilience (Edenius et al. 2011, Rogers and Mittanck 2014). While land reclamation using aspen to re-colonize developed or mined land has many benefits, neglect or conversion of these lands will likely still lead to overall aspen decline (Pinno and Errington 2015). In some regions, silvicultural selection for conifers has historically, sometimes actively, degraded aspen forests. Modern realization of aspen’s ecological, aesthetic, and commercial values has often reversed such trends, but legacy effects persist. Similarly, long-term fire suppression in seral-dominant aspen may allow advanced succession to overtop aspen, though this process is not thought to be widespread (Hessl 2002, Kashian et al. 2007, Lankia et al. 2012, Kulakowski et al. 2013a). Recognition of varying aspen fire types (Shinneman et al. 2013) provides an initial step toward acknowledging benefits of fire, as well as curtailing inappropriate use of prescribed fire or silvicultural surrogates to “restore” aspen (Rogers et al. 2014). In some cases, invasive species (e.g., exotic grasses, insects, or mammalian herbivores) may suppress aspen vitality and sustainability (Chong et al. 2001, Bailey et al. 2007, Logan et al. 2007). Any combination of these threats, such as climate-herbivory or invasive species-land clearing, may exacerbate the extent and speed of aspen type conversions. Multiple combinations of impacts, therefore, should be viewed as opportunities to employ cross-disciplinary investigation as a proactive tactic for aspen conservation.
5.2 Research gaps in aspen sciences

In our opinion poll of researchers around northern hemisphere countries with aspen forests (Figure 3), we discovered a number of underexplored topical areas. A few of these research gaps were common among all or many geographic zones. For example, there has been little systematic exploration of social or cultural uses of aspen forests. A general need for international cross-border research is to improve understanding of broad-scale, long-term aspen dynamics across geographic and biophysical gradients to complement and connect research already conducted at finer spatial and shorter temporal scales. Such endeavors may permit a meta-analysis of aspen cover change based on numerous regional studies. A prime research need is to articulate how aspen ecology differs across the range of a species (e.g., Rogers et al. 2014), as well as among ecosystems dominated by different aspen species. Moreover, multi-scale research is needed to understand how climatic variability interacts with other predisposing factors to contribute to aspen mortality; and how ecological, physiological, and genetic variability determine successful vegetative and sexual reproduction of aspen. It is also important to understand how the cumulative effects of a changing climate and altered disturbance regimes will affect overall aspen dynamics and extent. Each of these large-scale research questions should consider comparing multiple, or single widespread, aspen species across ownership, political, and ecoregion boundaries to fully understand commonalities between aspen functional types and species. Other common themes include effects of herbivory, land clearing, past logging practices, and commercial uses and production. Each of these factors may have practical outcomes for large-scale biodiversity conservation given aspen’s known value in this regard (Esseen et al. 1997, Chong et al. 2001, Kouki et al. 2004).

Areas of research are not equally developed across regions and countries (Figure 2, 3). Thus, the following represents an overview of research needs by geographic domain:

**United States:** Detailed knowledge is lacking in how aspen cover would be affected by current fire and climate trends; increasing extent, severity, and frequency of fires under projected widespread drought scenarios. Increasing the network of paleoecology sites may inform both historical and ancient responses of aspen to past climatic shifts (e.g., Carter et al. 2017). Furthermore, given the likelihood that forest ecosystems will be increasingly affected by multiple disturbance types over short time periods, future research should explore geographic variability in how such compounded perturbations affect aspen regeneration and potential dominance (e.g., Kulakowski et al. 2013b, Gill et al. 2017). Other fertile areas for research may include opportunistic studies of aspen response to recent fire or bark beetle outbreaks, experimental fire and mock beetle outbreak studies to identify mechanisms underlying aspen response to disturbance, differential aspen response to climate variability on sites of varying functional types and disturbance regimes, spatially-explicit modeling of aspen population dynamics, and high-resolution remote sensing of aspen distribution and condition. An important knowledge gap is an integrated synthesis of regional or ecoregional trends in aspen dynamics that will better explain forest landscape patterns. Finally, exploration of social mechanisms related to aspen value, use, and change over time is a highly underexplored realm of study.

**Canada:** Over the past few decades there has been considerable research focused on aspen in western Canada, however there remains a number of critical gaps in the biology and management of this species. One of the major gaps is related to response and adaptations of aspen to drought, including physiological and morphological adaptations. For example, it has been noted that aspen root-leaf area ratios vary with climate, but it is not known if this is genetically controlled. Thus, this is one example of how the future adaptability of the species for a warmer climate is not well understood. Another area of potential research relates to aspen regeneration. Most aspen regeneration work has focused on suckering responses to
disturbance, though this response only allows aspen to remain at an established site and will not allow long-distance movement across the landscape. Understanding the relationships between seed production, seedling establishment, and climatic and microsite requirements will be crucial to evaluate the response of aspen and aspen forests to future climates and its ability to be maintained on the landscape (Landhausser et al. 2010) either naturally or through assisted migration programs (Gray et al. 2011).

**Northern Europe:** In Scandinavia, there is need for more knowledge about how various ungulate densities affect the recruitment rates of aspen, as well as relations between differences in predation, disturbance, and national policies on herbivores and aspen regeneration success rates (Anglestam et al. 2017). This can be surveyed at a large scale by means of forest inventory data including the sapling stage (<5 cm DBH) together with monitoring of ungulate densities, but also experimentally at a smaller scales with fenced exclosures. There is also a need for thorough population dynamic studies to infer the effect of the declining recruitment on older age classes. Moreover, for the purpose of knowing the efficiency of seed dispersal, and thus the capability of migration and escaping from browsers, small-scale spatial genetic studies should be undertaken in various habitats from the center to the periphery of the distribution of aspen. These understudied research questions are both relevant for the future conservation of aspen (Myking et al. 2011). Active research throughout the region has been focused on biodiversity and in the breeding of hybrid stocks. The most probable knowledge gaps may be connected with aspen regeneration ecology and recruitment success, as well as cataloguing and understanding linkages of the numerous aspen obligate species reliant on mature natural stands.

**Central Europe:** Aspen may be a promising forest species in the uncertain future of climate change. However, little is known about how this species will fare under increasing drought and, potentially, the onset of multiple forest disturbances. Elsewhere, we have seen increases in drying and disturbance-related forest replacement that favor aspen over other species (Kulakowski et al. 2013b). Besides, aspen as a pioneer tree with broad ecological amplitude is promising tree species for disturbed and extreme sites. However, further research on this topic in the context of Central Europe is required. Additionally, aspen and other fast-growing poplar hybrids may prove to be promising forest species for capturing carbon. Due to rapid colonization, aspen possesses the ability to sequester large amounts of carbon within just a few years of stand-replacing events. While there are common government incentives with the European Union that support afforestation of former agricultural lands, we need further research to bolster suggested advantages of utilizing aspen as carbon stocks. Another burgeoning research field is paleoecology. There are several methodological approaches in paleoecology that may be used to better understand the role of past aspen clones in central Europe (and elsewhere). Pedoanthuracology holds great promise for examining aspen’s long-term role in forest development in Europe (Novák et al. 2018). As climates and disturbance patterns change over time it is expected that greater understanding of past developments will inform future roles of aspen in central Europe. For instance, will aspen increase in prominence as European climates warm and become drier, potentially facilitating shorter and more intense disturbance regimes?

**Russian Federation:** Further investigation is needed in ecosystem-centered studies, such as biodiversity enumeration and system change associated with human- and natural-caused impacts to aspen. These areas are a priority in Russia and more attention will be paid to it in the future (Bases of State Policy 2018). An example of such studies will be to fully understand changing climate, disturbance, and successional regimes in forests devoted to wood productions, as well as those which will remain mostly unmanaged.
Mongolia: As in Europe, aspen carries important ecological values that may be threatened by uncertain climate futures (Hessl et al. 2018). Due to their large genotypic and phenotypic variability, as well as positive feedback loops associated with shortened disturbance cycles (Kulakowski et al.), this species has the potential for great adaptability to future climatic changes (Hamrick 2004). However, little is known about how P. tremula in a strongly continental environment will respond to climate change. Still, in plantation forestry, aspen is becoming more important for wood production, therefore hybridization research would be desired to explore broad tolerance for anticipated stresses related to rapid climate change (Hajek et al. 2013). Understanding how central Asian aspen fits into a global and regional context (e.g., functional and species variations) may assist in narrowing current research gaps. Further use of paleoecology techniques to understand ancient climate-disturbance adaptations could prove fruitful in developing future management strategies for resilient aspen systems.

China: In David’s aspen, root development and ecology of the species, as well as additional restoration methods for these forest is still lacking. Further exploration of how aspen forests provide for wildlife habitat has received little attention in China so far. The research on the ecological value and function of Chinese aspen is relatively scarce and will require systematic exploration. No studies have addressed threats to this species broadly, to our knowledge. We suspect that threats faced are similar to David’s aspen, mainly from past land clearing and agriculture practices, however this is largely conjecture without the support of dedicated investigations. Preliminary research has been reported on pests and diseases which may attack the species, but further work is needed in this arena (Meng et al. 1986, Li et al. 2006).

6.0 PLOTTING AN INTEGRATED CONSERVATION COURSE

The immensity of integrating world aspen sciences for conservation purposes calls for a cooperative research framework. Here we have included expertise from nine nations, plus literature review including several other regions. A key initiative moving forward will be to expand our burgeoning Aspen Conservation Consortium to include more national experts. As we have seen here, disciplinary strengths and weaknesses abound (as would be expected) across international boundaries. However, awareness of “what is possible” through the current work, as well as an active expertise exchange program, could reduce effort spent with experimentation on initial steps that have already been addressed elsewhere. More to the point of biogeographic conservation, coordinated efforts to standardize diversity assessment methods will simplify future world syntheses and tracking of progress (or decline) in species retention. Such coordinated practices will also facilitate adaptation as likely biogeographic shifts taking place in aspen ranges accompanying warming climates, changing precipitation patterns, and land development or resource extraction (Gray et al. 2011).

Integrated practices should not be interpreted as uniform prescriptions. An overarching lesson gleaned from our review is that species and functional types (within species) perform differently under varying biophysical conditions (Kurzel et al. 2007, Shinneman et al. 2013, Rogers et al. 2014, Özel et al. 2018, Usoltsev et al. 2018). A more nuanced understanding of these differences will alleviate one-size-fits-all practices that are often counterproductive. For instance, aspen dominant and seral-dominant forests should not be expected to react identically to cutting, fire, herbivory, or extended drought. Their reproductive mechanisms and intensities are divergent. In order to create resilient systems, an intelligent strategy encompasses working within the bounds of ecological function as opposed to battling against evolutionary adaptations. At the community-level, this assumes some basic understanding of aspen autecology and Natural Range of Variability (Keane et al. 2009). While some have criticized this approach as we enter new climate realms (Millar 2014), understanding aspen’s response to earlier climate variation (Carter et al. 2017) retains value for informing adaptive responses to future extended droughts, for example.
Bringing these broad concepts together—shared aspen knowledge and intimate functional understanding—will greatly empower a mega-conservation strategy predicated on the idea that conserving widespread keystone aspen ecosystems that support high biodiversity has merit as a viable approach to global species retention (Rogers and McAvoy 2018). We contrast this strategy with conventional species preservation which focuses vast resources on select high-profile species with (sometimes) narrow habitat requirements. We do not advocate for replacing one tactic with another, so much as acknowledging the great potential value of mega-conservation for preserving larger overall numbers of aspen obligate species. To step forward with shared knowledge and coordinated global strategy for aspen conservation and management holds great promise for species retention across a broad swath of our planet.

ACKNOWLEDGEMENTS

Authors wish to acknowledge all of our respective institutions in supporting this international collaboration. PCR highlights the contribution of Western Aspen Alliance donations, EJF Philanthropies, Fulbright Specialist Program, and the USDI Bureau of Land Management (Grant # L16AC00175). We appreciate editor and reviewer comments to earlier drafts of this work that lead to a final, much improved, publication. This ambitious project was originally inspired by PCR’s partnership with Pando Populus, an organization working to address large-scale social and environmental using ecological principles.

REFERENCES


Bases of the State Policy in the field of use, protection, protection and reproduction of the woods in the Russian
Federation for the period till 2030. APPROVED by the order of the Government of the Russian Federation

Forest Service, Northern Forestry Centre, Edmonton, AB.


Bergström, R., Hjeljord, O. 1987. Moose and vegetation interactions in northwestern Europe and Poland. Swedish
Wildlife Research. Supplement 1, 213-228.

structure in metabolome and herbivore community co-occurs with genetic structure in plant defence genes.

understory light and growth of young aspen in mixed stands around Lake Tahoe, California and Nevada,


Carter, V.A., Brunelle, A., Minckley, T.A., Shaw, J.D., DeRose, R.J., Brewer, S. 2017. Climate variability and fire
effects on quaking aspen in the central Rocky Mountains, USA. Journal of Biogeography 44:1280-1293.
https://doi.org/10.1111/jbi.12932.

Caudullo, G., de Rigo, D. 2016. Populus tremula in Europe: distribution, habitat, usage and threats. In: San-Miguel-
Ayanz, J., de Rigo, D., Caudullo, G., Houston Durrant, T., Mauri, A. (Eds.), European Atlas of Forest Tree

Chong, G.W., Simonson, S.E., Stohlgren, T.J., Kalkhan, M.A. 2001. Biodiversity: aspen stands have the lead, but
will nonnative species take over? In: Sustaining aspen in western landscapes. U.S. Department of


Western Journal of Applied Forestry 2:73-76. https://doi.org/10.1093/wjaf/2.3.73.

Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO. RM-119.

Degtava S.V., Zheleznova, G.V., Pystina, T.N., Shubin, T.P. 2001. Phytoocoenotic and floristic structure of
deciduous forests of the European North. St. Petersburg. 269 p. [In Russian]

Dickmann, D.I., Kuzovkina, J. 2014. Poplars and willows of the world, with emphasis on silviculturally important
species. FAO, Forestry Dept., Rome, Italy. 22(8):60.


https://doi.org/10.1016/j.foreco.2009.05.035.


http://elar.usfeu.ru/handle/123456789/3303.


http://dx.doi.org/10.12911%2F22998993%2F79403.


Figure Captions

Figure 1: Major world aspen species and ranges. Colored polygons represent range extent and should not be construed as tree species coverage densities (i.e., species may be very dense or extremely sparse within colored polygons).

Figure 2: Principal Component Analysis (PCA) of aspen literature for *Populus tremula* and *P. tremuloides* only. An initial search of all aspen species yielded approximately 95% of literature was centered on these two species; the remaining 5% addressed hybrid *Populus* spp. and the remaining species designated in Figure 1.

Figure 3: Results of a qualitative opinion poll of authors of the current work gauging research energy expended on aspen sub-topics. This bar graph gives a broad indication of topics of interest and their respective regional prioritization. Numbers along the y-axis are poll rankings, as estimated by respective area experts (see author list) from low to high of regional research efforts: 1= no investigations, 2= poor understanding, 5= moderate understanding, 8= high level, 10= complete knowledge.

Figure 4: Seral-dominant (a) *P. tremuloides* in Idaho. Dominant (b) *P. tremuloides* in Utah. These types occur throughout the western United States (Rogers et al. 2014).

Figure 5: The aspen dominant forest in west-central Canada is known as the “parkland.” These forests are bordered by prairie to the south and boreal (aspen seral-dominant) mixedwoods to the north.

Figure 6: A boreal seral-dominant *P. tremula* forest in northern Sweden. A lone mature aspen exists in a forest where this species at one time was more dominant, but due to historical logging practices has been nearly eliminated.

Figure 7: A recent forest treatment that was intended to favor *P. tremula* in the Ural Mountain region, Russian Federation. Competing conifers quickly recolonize the site and will overtop aspen without repeated disturbance.

Figure 8: In northern China *P. davidiana* dominates the current forest cover though this species is predominantly seral-dominant throughout its range.
Figure 1
Figure 2
Figure 3: Regional Expert Poll of Aspen Research Priorities by Sub-Topic
Figure 4

(a)

(b)
Table 1: World aspens attributes. Aspen species within the genus *Populus*, section *Populus*, subsection *Tepidae*.

<table>
<thead>
<tr>
<th>Species</th>
<th>Region (#countries)</th>
<th>Estimated Range (M km²)</th>
<th>Elevation (m)</th>
<th>Maximum Height (m)</th>
<th>Maximum Diameter (cm)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>P. adenopoda</em>&lt;sup&gt;a&lt;/sup&gt;</td>
<td>East Asia (1)</td>
<td>1,522</td>
<td>300-2500</td>
<td>30</td>
<td>60</td>
</tr>
<tr>
<td><em>P. davidiana</em>&lt;sup&gt;a&lt;/sup&gt;</td>
<td>East Asia (3)</td>
<td>5,865</td>
<td>100-3800</td>
<td>25</td>
<td>60</td>
</tr>
<tr>
<td><em>P. grandidentata</em>&lt;sup&gt;b&lt;/sup&gt;</td>
<td>East North America (2)</td>
<td>4,826</td>
<td>0-900</td>
<td>24</td>
<td>25</td>
</tr>
<tr>
<td><em>P. sieboldii</em>&lt;sup&gt;c&lt;/sup&gt;</td>
<td>East Asia (1)</td>
<td>414</td>
<td>?</td>
<td>20</td>
<td>?</td>
</tr>
<tr>
<td><em>P. tremula</em>&lt;sup&gt;d&lt;/sup&gt;</td>
<td>Eurasia, North Africa (~70)</td>
<td>71,493</td>
<td>700-2300</td>
<td>35</td>
<td>75</td>
</tr>
<tr>
<td><em>P. tremuloides</em>&lt;sup&gt;b&lt;/sup&gt;</td>
<td>North America (3)</td>
<td>27,671</td>
<td>0-3500</td>
<td>30</td>
<td>40</td>
</tr>
</tbody>
</table>

<sup>a</sup> Flora of China  
<sup>b</sup> US Forest Service, Fire Effects Information Systems  
<sup>c</sup> Flora of Japan  
<sup>d</sup> Woody Plants of Czech Republic