

Changing perspectives on regeneration ecology and genetic diversity in western quaking aspen: implications for silviculture

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Abstract: A conventional view of regeneration ecology of quaking aspen (*Populus tremuloides* Michx.) in western North America holds that reproduction is strictly vegetative and, except on some marginal sites, only successful following high-severity disturbance. This view has strongly influenced silvicultural treatment of western aspen and has led to low expectations concerning genetic diversity of stands and landscapes. However, recent discoveries are fundamentally altering our understanding of western aspen regeneration ecology and genetics. For example, there are clearly multiple pathways of aspen regeneration and stand development. Research on a variety of fronts indicates that seedling establishment is common enough to be ecologically important and that genetic diversity is substantially greater than previously thought. We review conventional understanding of western aspen and put this into the context of silvicultural practice. We then review recent developments in aspen research and assess the silvicultural implications of these insights.

Résumé : Une vision classique de l'écologie de la régénération du peuplier faux-tremble (*Populus tremuloides* Michx.) dans l'Ouest de l'Amérique du Nord veut que la reproduction soit strictement végétative et, à l'exception de certaines stations marginales, ne réussissent qu'à la suite d'une perturbation sévère. Cette vision a fortement influencé la sylviculture du peuplier faux-tremble et suscité de faibles attentes quant à la diversité génétique des peuplements et des paysages. Cependant, des découvertes récentes sont en train de modifier en profondeur notre compréhension de l'écologie de la régénération et de la génétique du peuplier faux-tremble. À titre d'exemple, il existe clairement plusieurs modes de régénération et de développement des peuplements. Les recherches menées sur plusieurs fronts indiquent que l'établissement des semis est suffisamment fréquent pour être écologiquement important et que la diversité génétique est beaucoup plus grande qu'on l'avait précédemment imaginé. Nous passons en revue la perception classique du peuplier faux-tremble dans le contexte des pratiques sylvicoles. Nous passons ensuite en revue les avancées récentes de la recherche sur le peuplier et nous évaluons les implications sylvicoles de ces informations.

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Introduction

Quaking aspen (*Populus tremuloides* Michx.) (Salicaceae) is the most widely distributed tree species in North America. Its range extends entirely across the continent from Newfoundland to Alaska and south to Mexico (Little 1971). Quaking aspen is closely related to bigtooth aspen (*Populus grandidentata* Michx.) and four Eurasian species (Hamzeh and Dayanandan 2004). As a group, these species have a circumpolar distribution. In western North America, *P. tremuloides* (hereafter referred to as western aspen or simply aspen) has not only an extensive latitudinal range (Alaska to Mexico) but also the broadest ecological amplitude of any western tree species. In the central Rocky Mountains of the United States, for example, aspen occupies sites from less than 2500 to more than 3500 m elevation — all the way from the lower tree line

to the upper tree line (Mitton and Grant 1996). Within a given watershed, it can occupy sites ranging from xeric to mesic. Aspen has high aesthetic and recreational values (Mitton and Grant 1996) and is the most important deciduous forest type in western North America, with high value as forage for wildlife and domestic livestock, fiber (and potentially biofuels), biodiversity, and as a fuelbreak.

This review is focused on aspen of western North America, particularly the Rocky Mountains of Canada and the United States. There is a well-developed conventional wisdom concerning the regeneration ecology, genetics, and silviculture of western aspen that sometimes is in contrast with conventional wisdom concerning eastern aspen. In particular, the relative infrequency of seedling establishment and the large clone sizes in western aspen have dominated management perceptions and practices in western North America. The understanding of

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western aspen is based on more than 80 years of solid research and practical experience (e.g., Baker 1925; DeByle and Winokur 1985; Peterson and Peterson 1996). However, recent discoveries are dramatically and fundamentally altering our understanding of aspen regeneration ecology and genetics. These new insights have important implications for aspen silviculture in western North America.

In this paper, we briefly review conventional conceptualizations of regeneration ecology in western North American aspen and put these into the context of silvicultural practice. We then review recent developments in aspen research and assess the silvicultural implications of these new insights.

Aspen regeneration ecology, genetics and silviculture – conventional understanding

There are two basic tenets at the heart of the way silviculturists have thought about western aspen and the silvicultural systems appropriate for its management. The first tenet is that aspen is exceedingly intolerant and the second is that for all practical purposes, regeneration is exclusively vegetative, i.e., from root suckers. These tenets influence not only the choice of reproduction method and silvicultural system but also perspectives on conservation of genetic diversity, and even how stands are identified and delineated.

Stand development

In silvicultural terms, *tolerance* relates to the capacity of trees to “grow satisfactorily in the shade of, and in competition with, other trees” (Helms 1998). Aspen is typically considered to be more *intolerant* than any of the tree species with which it is commonly associated. It requires high levels of light for successful establishment and is, therefore, dependent on periodic high-severity disturbance. In the long absence of high-severity disturbance such as fire or clearfelling, aspen is at risk of successional displacement by more tolerant tree species — typically conifers (Long 1994). Conifer-dominated stands with even a few “remnant” mature aspen are thought to be indicative of a once aspen-dominated site where aspen is now in imminent danger of being entirely lost (Bartos and Campbell 1998).

In the predominant stand development pathway, aspen is strictly a pioneering, disturbance-dependent species; however, an important alternative is the “stable aspen” pathway. Successionally stable, multicohort stands have been observed on some environmentally marginal sites where either a seed source for late-successional species is absent or conditions are so limiting that the late-successional species are unable to establish (Baker 1925). Under these conditions, aspen, because of its ability to sucker, is able to maintain itself even in the absence of high-severity disturbance (Fetherolf 1917; Barnes 1966).

Regeneration

Root suckers result from the sprouting of preformed or adventitious shoot primordia (termed “sucker buds” by Wan et al. 2006). For intact trees, the suppressed sucker buds are prevented from sprouting by a combination of growth regulators produced in the aboveground tissue, primarily the stems, and the failure of sucker-promoting growth regulators, produced in the roots, to accumulate to sufficient concentrations (Schier 1973). Following decapitation, the supply of inhibiting

auxins is eliminated, and with the cessation of transpiration, there is a buildup in the roots of the growth regulators that promote the growth of root suckers (Frey et al. 2003; Wan et al. 2006 and references therein).

Following high-severity disturbance, the production of abundant suckers, with rapid height growth compared with seedlings, confers tremendous regeneration potential even in harsh environments. This reproductive strategy can give aspen a competitive advantage over the more tolerant conifers with which it is typically associated. In addition, while ramets (individual stems) have low resistance to disease and herbivory, suckering gives genets (genetically unique individuals, i.e., clones) as a whole remarkable resistance and resilience (Stevens et al. 2007 and references therein). The tendency to sucker can vary dramatically by clone (Farmer 1962; Zufa 1971; Schier 1974) and neither defoliation nor stem girdling illicit as strong a suckering response as decapitation (Wan et al. 2006).

Generally, all ramets in a clone are either male or female, although some perfect flowers can exist. It is also the case that ramets and clones sometimes produce different combinations of perfect, male, and female flowers within trees and clones and between years (Erlanson and Hermann 1927; Einspahr and Winton 1976; McDonough 1979). Contrary to what was commonly believed for many years, female clones do produce abundant viable seed, e.g., >90% viability (Mitton and Grant 1996). The barrier to seedling establishment is neither the quantity nor the quality of seeds but the short window of seed viability and the rarity of environmental conditions necessary for germination and seedling survival (Perala 1990 and references therein). The necessary combination of a mineral soil seedbed and ample spring and summer moisture during at least the first year is not common throughout the range of aspen in western North America (McDonough 1979).

Sexual reproduction, the successful establishment of seedlings, has long been assumed to be extremely rare and therefore simply not a factor in western aspen regeneration. To some extent, this conclusion may have become a self-fulfilling prophesy. Because seedlings are indeed rare, the burden of proof for identifying successful sexual reproduction has been very high (Ellison 1943; Larson 1944). Essentially, it had to be determined beyond a reasonable doubt that a putative seedling really could not possibly be a sucker. Because aspen seedlings can sucker within 4–6 years following germination (Shepperd and Mata 2005), there is a narrow temporal window during which seedling status is obvious without root system excavation and comparison of ring numbers for roots and stems (e.g., DesRochers and Lieffers 2001). Occasionally, aspen shoots do meet the standard of proof without root system excavation, e.g., a seedling established in the middle of a phosphate mine dump (Williams and Johnston 1984), seedlings established on a reservoir shoreline (Larson 1944), or post-fire seed germination events yielding a high density of similar-aged seedlings against a backdrop of mineral soil (Barnes 1966).

Genetic diversity

The presumed rarity of seedling establishment by western aspen has influenced not only the perception of regeneration ecology but also assumptions about genetic diversity in this forest type. There is the presumption that both stand and landscape genetic diversity are exceptionally low because in-

dividual stands are comprised of one or a few large clones. Also axiomatic has been the assumption that clonal differences, and therefore genetic diversity, can be readily recognized based on coarse visual characteristics, e.g., bark color, phenology, etc. This view is reinforced by what appear to be obvious clonal boundaries that exist between stands. Based on such perceptions, an aspen stand is often seen as consisting of a single, or at most a couple, of clones, and even fairly large watersheds with an abundance of aspen have been considered to contain only a handful of clones. The celebrated “Pando” clone in southern Utah (Kemperman and Barnes 1976), touted as the largest (by weight) organism on the planet (Grant et al. 1992), reinforces this perspective.

The apparent absence of successful sexual reproduction has led to the conclusion that many, and even most, clones are very old, perhaps dating from a cooler, wetter Pleistocene climate (Einspahr and Winton 1976; McDonough 1985). There has even been speculation that individual clones might date back to the early Pleistocene, reaching “ages in excess of 1 million years” (Mitton and Grant 1996, p. 27). Furthermore, the size of clones has been thought to correlate with relative clonal age (see discussion in Ally et al. 2008).

This conceptual model of ancient clones dominating western landscapes presents some problems in explaining persistence of clones over millennia. For instance, in the absence of sexual recombination, very ancient clones would be expected to accumulate deleterious mutations that would eventually have negative fitness consequences that could not be purged through sexual reproduction (Klekowski 1984; Charlesworth 1993; Moorad and Promislow 2008; Ally et al. 2010). Additionally, landscape conditions since the Pleistocene have changed dramatically, and it is difficult to explain the persistence of aspen clones in situ over such vast time periods and ecological shifts in the absence of genetic recombination and seedling establishment.

Silvicultural methods

Because of its relative intolerance and the predominance of vegetative reproduction, the default reproduction method and silvicultural system for aspen has always been strictly even-aged management based on simple coppice wherein the entire mature stand is clearfelled in anticipation of vegetative reproduction. Suckering is induced by clearfelling or high-severity prescribed fire (Baker 1925; DeByle 1976; Long 1994; Peterson and Peterson 1996; Shepperd 2001). When fire is used as a silvicultural tool, care is taken to avoid a fire hot enough to damage roots, which are effectively the only source of regeneration (Shepperd 2001). Whether treatment is mechanical or via fire, attention is focused on obtaining an abundance of suckers and then, where necessary, protecting them from browsing by ungulates.

Timely regeneration of aspen stands is considered critical. A combination of settlement-era disturbance, i.e., logging and fires, in combination with post-settlement fire exclusion has, at least in the central Rocky and Sierra Nevada Mountains of the United States, resulted in an unusually high proportion of mature aspen stands (Rogers et al. 2007; Shaw and Long 2007). There is concern that many stands may currently be approaching, or even be beyond, a “tipping point” of resilience, where dramatic shifts in species composition can occur (Bartos and Campbell 1998).

Because of the large size of stands putatively containing a very low number of clones, and because seedlings are not considered to be a factor, there has essentially been no attention given to the influence of regeneration treatments on genetic diversity in western aspen. In the West, the presumption has been that since reproduction is entirely vegetative, silvicultural practices do not have the potential to influence, either positively or negatively, the genetic makeup of stands. Within-stand genetic diversity is considered to be low or absent, and essentially moot. Silviculturists are, of course, concerned with conservation of aspen genetic diversity. The focus of this conservation, however, is on timely regeneration, and therefore continued presence, of the large clones. The assumption is that as clones are lost from western landscapes, genetic diversity inevitably declines over time, and aspen can only be restored via vegetative spread from extant or adjacent stands. Therefore, if aspen is absent from a large landscape, it will remain absent regardless of disturbance regimes.

Updating our view of western aspen

Recent discoveries are subtly and in some cases dramatically altering and extending our understanding of aspen regeneration ecology and genetics. These new insights have important implications for silvicultural approaches to aspen maintenance and restoration in western North America.

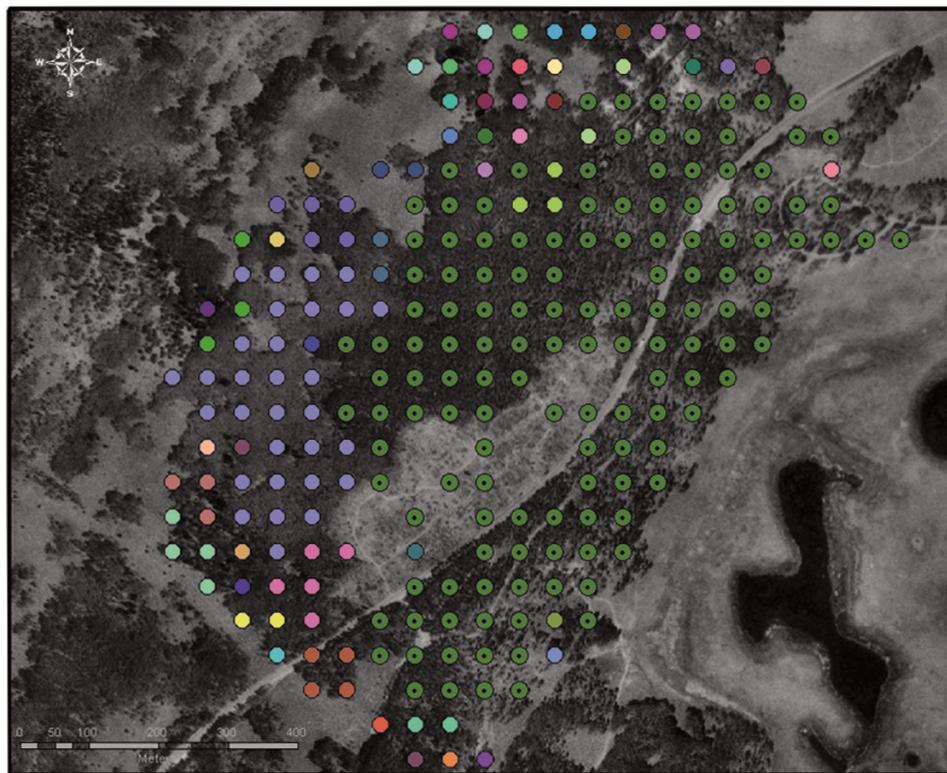
Stand development: multiple pathways

In contrast with the conventional view that aspen is strictly a pioneer on all but marginal sites, studies have shown that even on productive sites, there are multiple pathways of aspen regeneration and stand development. Aspen can be part of late-seral mixed-species stands and has been observed to persist at low densities in small gaps of conifer-dominated stands that have not experienced high-severity disturbance for centuries (Cumming et al. 2000; David et al. 2001). In old-growth Engelmann spruce (*Picea engelmannii* Parry ex Engelm.) and subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) stands on the T.W. Daniel Forest in northern Utah, Long (2003) described aspen suckers colonizing small gaps (e.g., <300 m²) within the matrix of conifer forest. The aspen ramets ranged from 1 to 300 years old (J.D. Shaw, unpublished data (2009)). Obviously, this gap-phase behavior is fundamentally different from the conventional model of aspen regeneration ecology.

Regeneration: importance of sexual reproduction

An even more striking challenge to the conventional view of aspen regeneration ecology and genetics relates to the presumed near exclusivity of vegetative reproduction and the resulting low genetic diversity. There are now well-documented examples of pulses of aspen seedling establishment following high-severity disturbances such as the Yellowstone fires of 1988 (Kay 1993; Elliott and Baker 2004; Romme et al. 2005). This suggests that patches of aspen arising from contemporary seeding events might also occur following smaller-scale disturbances and may be more common than traditionally presumed. Such seeding events also have implications with respect to long-distance dispersal of aspen. Since both pollen and seed are highly mobile, it is reasonable to assume that sexually produced aspen progeny can be widely dispersed. For example, Kay (1993) found aspen seedlings several kilometres from the nearest seed

Fig. 1. Genotype-specific map of the stand containing “Pando” near Fish Lake, Utah. The quaking aspen (*Populus tremuloides*) “Pando” genotype is shown in green with a black dot. Other distinct genotypes in the stand ($n = 53$) are shown in different colors. Most genotypes were observed only once with sampling on a 50 m grid. Adapted from Mock et al. (2008).



source. Landhäusser et al. (2010) have demonstrated that upslope expansion of aspen in response to climate change is occurring through seedling establishment following both anthropogenic and natural disturbance.

Genetic diversity: many genets, patchy distribution

Dramatic new insight into aspen regeneration ecology and genetics has come with the application of practical molecular tools for identifying unique genets. In the past, it has been necessary to rely exclusively on phenological and morphologic characters to differentiate putative clones, and it turns out that these characterizations can be misleading. The underestimation of clonal diversity was first brought to light through the use of allozymes (Cheliak and Pitel 1984; Jelinski and Cheliak 1992). More recently, hypervariable genetic markers such as microsatellites have been used to identify unique genets in plants and to map them precisely (Miwa et al. 2001). Recent landscape surveys of genetic diversity based on microsatellite analysis in western aspen clearly indicate that clonal diversity within stands can be quite high (Hipkins and Kitzmiller 2004; De Woody et al. 2009). In a particularly striking example, 189 distinct clones were identified across a 2100 ha landscape in northern Utah containing 30 aspen stands. Most of these clones were only encountered once on a 50 m sampling grid (Mock et al. 2008). Subsequent studies in other western states (Zeigenfuss et al. 2008) have found similar patterns. Even the stand containing the well-known “Pando” clone turns out to be an illustration of high genetic diversity (Fig. 1). “Pando” was genetically confirmed

to be a single genetic clone (De Woody et al. 2008), as originally described morphologically by Kemperman and Barnes (1976), but a total of 52 additional distinct genets were found in the same stand when sampled on a 50 m grid (Mock et al. 2008). Again, most of these clones were only encountered once, and they were clustered at the edges of the “Pando” clone. These estimates of clonal richness far exceed expectations based on morphological attributes. Further, the very small spatial extent of many of the individual clones in these clusters suggests that seeding events may be occurring on a modern time scale and that relatively recent episodic events (i.e., hundreds of years, not thousands or hundreds of thousands) may be responsible for a large proportion of the genetic variation in current western landscapes (Jelinski and Cheliak 1992; Mock et al. 2008).

If sexual reproduction is much more common than previously thought, there are implications for several thorny ecological and genetic issues. For example, sexual reproduction calls into question presumptions about the great age of most clones and, therefore, reduces the need to invoke heroic assumptions about how the inevitable accumulation of deleterious mutations in ancient clones might be overcome. Similarly, sexual reproduction provides a mechanism to explain the persistence and adaptation of aspen over millennia of climate change (see below). Additionally, the ability of western aspen to colonize new sites has almost certainly been underestimated (e.g., Kay 1993; Elliott and Baker 2004; Landhäusser et al. 2010).

Fig. 2. Quaking aspen (*Populus tremuloides*) in northern Utah several weeks after a hard spring frost in 2007. Clones experiencing early budbreak show extensive frost damage and defoliation. Photograph by Ron Ryel, used with permission.



Alongside the realization that genetic diversity is pronounced and highly patchy in western aspen is an increasing awareness that different aspen genets can have strikingly different traits (Fig. 2). This is obvious within landscapes in terms of phenological phenomena such as budburst and leaf senescence and often in terms of morphological variation, but this variance among genets also extends to growth rates (Kanaga et al. 2008), herbivore defenses (Stevens et al. 2007), suckering ability (Schier 1974), and even litter decomposition rates (Madritch et al. 2006). Such clonal differences clearly have important ecological implications (Madritch et al. 2009) and if unrecognized could lead to confusing results in regeneration and restoration studies. Further, this adds credence to the idea that genetic diversity is an important aspect of aspen management.

Climate change, range shifts, and local adaptation

Western North American climates are generally expected to become warmer and drier in the coming century, with an accompanying increase in the frequency and severity of fires (Flannigan and Van Wagner 1991; Rehfeldt et al. 2009). These changes are expected to present both risks and opportunities for aspen, with anticipated range shifts.

Aspen has certainly experienced dramatic range shifts in response to past climate changes, given that the great majority of its current range was glaciated approximately 20 000 years B.P. (Clark et al. 2009). Long-distance seed dispersal is an important mechanism in range shifts (Landhäusser and Wein 1993), and evidence suggests that aspen, at least locally, is currently undergoing a rapid upslope expansion mediated by seed dispersal in the northern Rocky Mountains (Landhäusser et al. 2010). In the central Rocky Mountains, climate envelope

modeling predicts dramatic range contraction in the absence of adaptation (Rehfeldt et al. 2009).

At regional scales, extant genets are often presumed to be adapted to local climatic conditions, particularly with respect to phenological traits (e.g., Brisette and Barnes 1984; Reighard and Hanover 1985). Concerns about such local adaptation underlie the development of regional seed transfer guidelines for many tree species (Morgenstern 1996; McKenney et al. 2009). Climate change, however, is expected to shift geographic optima for many species (Parmesan 2006), creating an “adaptational lag” in tree species (Hamrick 2004; Aitken et al. 2008). Recent studies involving aspen provenance trials of sources across western Canada and the upper midwestern United States suggest that, indeed, an adaptational lag exists in the northern range of aspen (Gray et al. 2011).

Western aspen mortality

The issue of geographically widespread dieback and decline in western aspen has received a great deal of attention in the last 10–15 years (Hanna and Kulakowski 2012). Frey et al. (2004) provided a useful framework for summarizing observations of aspen dieback. They organized contributing factors into those that are largely predisposing (e.g., succession, age), inciting (e.g., drought, insect defoliation), and contributing (e.g., pathogens, windthrow). There has been particular focus on the influence of drought across multiple years and at the xeric fringe of aspen distribution (Hogg and Hurdle 1995; Hogg et al. 2008; Rehfeldt et al. 2009; Hanna and Kulakowski 2012). Acute water stress resulting from xylem cavitation may often be the proximate cause of dieback (Frey et al. 2004; Anderegg et al. 2011).

An extremely important distinction with respect to dieback of mature stems in a clone is whether or not the dieback is accompanied by suckering. Rapid dieback of mature stems is likely to be accompanied by suckering and, therefore, survival of clones. In contrast, prolonged, gradual dieback of the overstory may occur without suckering, resulting in loss of clones (Frey et al. 2004). An additional factor important in some areas is the loss of regeneration, and the potential loss of clones, to excessive ungulate, especially elk, browsing (Kashian et al. 2007; Binkley 2008; DeRose and Long 2010). Very high populations of elk are a fairly recent phenomenon in the Rocky Mountains (White et al. 1998). In his classic monograph, Baker (1925) had already recognized the need to protect regeneration from excessive browsing by sheep and cattle but did not perceive elk to be a problem worth mentioning.

How will these evolving insights impact silviculture in western aspen?

Mixed-species and multicohort management

The most common reproduction method employed for western aspen is, and will undoubtedly remain, simple coppice wherein the entire mature stand is clearfelled in anticipation of suckering. New insight into the regeneration ecology of western aspen, however, clearly suggests that more silvicultural options exist than have been previously appreciated, and silviculturists should at least consider a broader range of management practices. For example, MacIsaac et al. (2006) examined the fate of relatively small regeneration gaps that originated following clearfelling of aspen stands in northwestern Alberta. They concluded that the gaps would likely be long-lived (i.e., not likely to natural fill in) but suggested that if planted with white spruce (*Picea glauca* (Moench) Voss), the resulting heterogeneity might be a desirable component of mixed-wood management. A pre-harvest example of a broader silvicultural perspective would be modification of the traditional simple coppice method to include retention of small groups of aspen as seed sources (i.e., coppice-with-standards or coppice-with-reserves). The cost of retaining seed trees is small, but the value of the increased genetic diversity represented by even a few successful seedlings could potentially be great, given the importance of sexual recombination in adaptation.

Variations on uneven-aged methods could be used across the range of aspen stand composition, from pure aspen to mixed species, and across a wide range of site quality. For example, group selection might be useful in maintaining an aspen component in late-successional conifer-dominated stands (David et al. 2001; Long 2003; Kurzel et al. 2007). Group selection refers to a method of regeneration where mature "trees are removed and new age classes are established in small groups" (e.g., the width of the opening might be twice the height of the mature trees) (Helms 1998). The previously underestimated occurrence of aspen in mixed-species and uneven-aged stands has important implications for management of some western landscapes. For example, even small amounts of aspen in conifer-dominated stands and landscapes have been shown to contribute to avian species richness (Li and Martin 1991; Griffis-Kyle and Beier 2003; Hollenbeck and Ripple 2007).

Aspen restoration

The emerging view of aspen regeneration ecology requires a broader perspective of aspen restoration. For example, recognition that aspen can exist in mixed-species, multicohort stands (Cumming et al. 2000; David et al. 2001; Long 2003; Kurzel et al. 2007) raises questions about the contention that even one mature aspen stem per hectare is *prima facie* evidence that aspen was once dominant in a particular landscape. It is clear that aspen is, and was, an important component of stands representing a wide spectrum of natural disturbance regimes and conditions. Management intended to recreate or maintain an historical condition must be based on a reasonable approximation of what that historical condition represented in terms of species composition and stand structure (Long 2009). The identification of appropriate restoration objectives may also be confounded in situations where the apparent reference condition is the legacy of a unique combination of climatic and human disturbance influences (Rogers et al. 2007).

A silvicultural strategy intended to address issues of mature stem dieback coupled with regeneration failure must be based to the extent possible on stand-specific causes (sensu Frey et al. 2004). A broad generality, however, is that disturbance (e.g., clearfelling or prescribed fire) must be of sufficient severity to promote suckering and must occur before the regeneration capacity of the root system is too degraded (Shepperd 2001). The issue of timing is more complicated for stands where ungulate browsing pressure limits successful regeneration. In such cases, treatment should probably be delayed until the browsing problem has been addressed (Bartos and Campbell 1998). Treatment to promote suckering without first dealing with excessive browsing (e.g., by fencing or reducing ungulate numbers) could result not only in the repeated loss of new regeneration but also in the eventual loss of the root system's capacity to produce new suckers (Bartos and Campbell 1998). Another aspect of timing relates to the season of treatment. For stands in which the regeneration potential is thought to be marginal, treatment during the dormant season should provide the best response possible (Shepperd 2001).

Conservation of genetic diversity

Increased awareness of the importance of seedling establishment in western aspen is coupled with an increased appreciation of genetic diversity and the need for its conservation. Silviculturists should routinely monitor areas that have experienced high-severity disturbance such as stand-replacing fire, particularly when the sites did not have a pre-disturbance aspen component. With limited suckering, such areas may represent the best opportunity to identify and protect seeding events. Identifying and protecting these "catches" of aspen sexual reproduction is worthwhile because they represent new genetic combinations and, therefore, an opportunity for adaptation through selection. They may also represent potentially important range expansions, e.g., upslope migration in the face of climate changes (e.g., Landhäusser et al. 2010).

A challenge for silviculturists that is likely to become more common in the future is development of strategies for the management of aspen in areas even where it has historically been absent. Obviously, where aspen is present prior to catastrophic disturbance and not subjected to excessive post-disturbance browsing pressure (DeRose and Long 2010), it can be an im-

portant part of reforestation. However, there may also be a silvicultural role for aspen where its establishment may require assisted migration (*sensu* Gray et al. 2011). Such human-aided movement will demand careful matching of environment and source material (e.g., Li et al. 2010; Gray et al. 2011). Guidelines, analogous to seed transfer zones that exist for many western conifer species, will need to be developed for aspen.

Current research trajectories likely to impact future management

A variety of new technologies and analytical approaches are emerging that are likely to further enhance our understanding of clonal dynamics of aspen in the coming years. We have summarized a few of them.

One of the more intriguing questions about aspen is that of clonal age. Establishment of absolute clonal ages could greatly enhance our understanding of landscape histories and adaptation processes and mechanisms. Recently, researchers have been using molecular markers in an attempt to ascertain relative and absolute ages for particular aspen clones. While estimates using this approach still have very broad confidence intervals, Ally et al. (2008, 2010) have demonstrated the utility of microsatellite markers for this purpose and have shown (1) a trend of declining male fertility (pollen viability) with increasing clone age and (2) that clone size is not a simple predictor of clone age. We are hopeful that in the near future, this research will lead to a metric of clone age useful for managers. Such a metric could be used to more closely associate aspen establishment with particular environmental conditions or disturbances.

Clonal dynamics at large landscape scales would also be more tractable if clonal boundaries and clonal richness could be detected using remote sensing technologies. While these technologies have been successfully used to describe species composition (Martin et al. 1998; Key et al. 2001), the use of multispectral and hyperspectral data to describe intraspecific clonal diversity is currently being explored in aspen and other clonal species (M. Madritch and K. Kettenring, personal communication (2011)). The ability to detect clonal diversity remotely would reduce the need for large-scale genotyping and would enable the analysis of clonal richness in the context of landscape histories and climate change.

Molecular tools are also enabling the examination of belowground processes in aspen. Jelínková et al. (2009) have recently demonstrated that root grafting between aspen genets occurs. There are two novel implications here. First, genets in a stand may be functionally interconnected, potentially sharing nutrients and hormonal signals. Second, it may be the case that some genets are maintained solely as belowground tissue with no aboveground ramets. While the importance of these phenomena in aspen ecology and regeneration is not clear, these findings may have important implications for the resilience of aspen stands and the maintenance of genetic diversity.

An interesting corollary to the new insight regarding sexual reproduction has to do with the potential importance of triploids. Using microsatellite analysis, the finding of three different variants at a locus suggests that a sampled ramet may be a triploid (i.e., three copies of the genome, rather than the two copies found in diploids). Such evidence for triploidy was noted in two study areas in Utah, including the “Pando” clone (Mock et al. 2008), and one in Colorado (Zeigenfuss et al.

2008). Triploid clones have been described previously in Utah (Every and Wiens 1971), but the more recent findings suggest that they occur at a high frequency and occupy a substantial portion of western landscapes (Mock et al. 2012). Triploid clones are expected to have reduced fertility but perhaps greater vegetative vigor than diploid clones (Singh 2003). Triploids may be favored by natural selection in certain landscapes, either because of their vegetative vigor or because their triploid genome buffers them against the negative effects of mutation accumulation over time (see Comai 2005 and references therein). In southern Utah and Colorado, triploid aspen make up over 50% of the genets (Mock et al. 2012): the physiological and management implications of these findings are active topics of research.

Understanding the genetic basis of specific traits, such as disease resistance, has long been a goal of silviculturists. Such understanding can lead to the development of cultivars and hybrids that can be grown for specific wood characteristics and ecosystem services (e.g., disease resistance or carbon sequestration). The rapid development of genomic tools along with the complete sequencing of black cottonwood (*Populus trichocarpa* Torr. & A. Gray ex Hook.) (Tuskan et al. 2006) have stimulated a great deal of research on specific traits and environmental responses in *Populus* species (e.g., Tsai et al. 2006; Wilkins et al. 2009; Wegrzyn et al. 2010; Raj et al. 2011; Mock et al. 2013) including western aspen. Efforts to characterize specific genes expressed in forest species have accelerated in recent years with improvements in technology and computation, and recent efforts to understand gene expression and function (e.g., US Forest Service Western Forest Transcriptome Survey and Genome Canada) are including aspen as a target species. We anticipate that this work will ultimately lead to an improved understanding of stress responses, mortality, plasticity, and adaptive capacity in aspen and ultimately to improved management for production and persistence of the species in western landscapes.

Finally, rapid advances in climate modeling are already providing researchers and managers with insights about broad patterns of aspen mortality (Rehfeldt et al. 2009). As more detailed climate-related data become available, and as the predictive power of climate models increases, we anticipate the ability to identify locations where aspen could successfully be used in reforestation or afforestation and where appropriate source material might be obtained (Li et al. 2010). These developments will likely shape future transfer guidelines for western aspen.

Summary

Perspectives on western aspen are being fundamentally altered by a growing body of research on multiple fronts, ranging from disturbance ecology to molecular genetics. For example, while a conventional view has been that western aspen is strictly a pioneer on all but marginal sites, it has become clear that even on productive sites, there are multiple pathways of aspen regeneration and stand development and that aspen can even be part of late-seral mixed-species stands. Another challenge to the conventional view of regeneration ecology and genetics of western aspen relates to the presumed near exclusivity of vegetative reproduction and the resulting low genetic diversity. These shifts in understanding represent, at least to some extent, a view of western aspen that is more in

line with the conventional view of eastern aspen. It has become clear that germination and establishment of western aspen seedlings is more common than previously thought and that stand-level genetic diversity is substantially greater than previously recognized. Episodes of seedling recruitment have considerable ecological importance with respect to adaptation, persistence, and range expansion. There is also a growing understanding and appreciation of genetic diversity in western aspen, including the prevalence and potential importance of triploids. Finally, climate change is creating opportunities for expansion of aspen onto sites where it was previously absent, due to either interspecific competition or physiological limitations. Climate change is also creating adaptational lag, leading to recommendations concerning assisted migration.

In light of these research findings, there are clearly alternatives to the simple coppice silvicultural system traditionally used for aspen management in western North America. We suggest that silviculturists managing aspen forests should consider incorporating techniques that have been well established for other forest tree species (e.g., management for multiple stand development pathways, retention of seed trees, protection of areas with seedling establishment, and development of transfer guidelines). There is also opportunity for developing new approaches that may be specific to aspen (e.g., monitoring and protection for seeding events, targeted establishment of stands in areas where aspen does not currently exist, and development of planting stock production protocols).

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