Above- and below-ground effects of aspen clonal regeneration and succession to conifers

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Abstract: Above- and below-ground characteristics were measured and compared for six sets of paired trembling aspen (*Populus tremuloides* Michx.) clones on the Fishlake National Forest in central Utah. Three self-regenerating clones were compared with three non-regenerating clones and three pure aspen stands were compared with three mixed aspen–conifer stands. Regenerating clones had dense understories of younger aspen stems, which were not present in non-regenerating clones. Regenerating clones also had greater numbers of roots and greater total root surface area than non-regenerating clones. Aboveground biomass and growth of the aspen in mixed stands was less than that of pure stands. A corresponding difference in aspen root mass was not apparent, indicating that the decline of aspen in mixed stands had not yet affected the root system. Conifer height and basal area growth rates were clearly greater than those of aspen, suggesting that aspen will eventually disappear from these forests in the absence of stand-reinitiating disturbances.

Résumé : Les caractéristiques épigées et hypogées de six groupes appariés de clones de peuplier faux-tremble (*Populus tremuloides* Michx.) ont été mesurées et comparées dans la forêt nationale de Fishlake située dans le centre de l'Utah. Trois clones qui se régénèrent d'eux-mêmes ont été comparés à trois clones qui ne se régénèrent pas d'eux-mêmes et trois peuplements purs de peuplier ont été comparés à trois peuplements mélangés de peuplier et de conifères. Les clones qui se régénèrent ont un sous-étage dense de tiges de peuplier plus jeunes qui n'est pas présent chez les clones qui ne se régénèrent pas. Les clones qui se régénèrent ont aussi un plus grand nombre de racines et une plus grande surface racinaire totale que les clones qui ne se régénèrent pas. En peuplement mélangé, le peuplier a une croissance et une biomasse épigée moindre qu'en peuplement pur. Aucune différence correspondante n'est apparente dans la masse racinaire du peuplier, indiquant que le déclin du peuplier dans les peuplements mélangés n'a pas encore affecté le système racinaire. Les taux de croissance en hauteur et en surface terrière des conifères sont nettement plus élevés que ceux du peuplier, ce qui indique que le peuplier disparaîtra éventuellement de ces forêts en l'absence de perturbations qui renouvelleraient le peuplement.

[Traduit par la Rédaction]

Introduction

Trembling aspen (*Populus tremuloides* Michx.) is a species of primary importance in many ecosystems throughout the interior western United States, providing wood products, wildlife habitat, and highly desirable scenic resources. Aspen normally regenerates vegetatively via root suckering after mature stems die, either from a fire or disease outbreak, or from individual tree falls or other perturbances that initiate a suckering response. A previous study of aspen rooting characteristics (Shepperd and Smith 1993) found that root biomass did not decrease when even-aged, mature aspen clones in Colorado were successfully regenerated by removing all existing stems in a commercial clear-fell harvest.

However, in some instances, mature aspen clones appear to be in decline and have not successfully suckered, either because of repeated animal herbivory or competition from invading conifers. This raises the question of how the clonal root system and residual aspen stems are effected by clonal decline or conifer invasion. These relationships could have far-reaching management implications throughout the West, where interrupted natural fire regimes and high ungulate populations have altered natural disturbance patterns. Knowing how clonal root systems are affected when clones do not successfully sucker could help develop management guidelines to minimize clonal decline and rehabilitate those clones that are already affected. Quantifying the effect that invading conifers have on aspen clonal growth dynamics would be very useful in prioritizing and scheduling management activities to restore these stands to a pure aspen condition.

This manuscript reports the results of an investigation of the above- and below-ground growth dynamics of aspen in central Utah under two contrasting situations: (*i*) regenerating versus non-regenerating aspen clones and (*ii*) mixed aspen–conifer versus pure aspen stands. In the first case, our objective was to test the hypothesis that non-regenerating aspen clones that are not successfully reproducing by root suckering will have significantly less large-root biomass than adjoining clones that have successfully suckered. In the second investigation, our objective was to document how the presence of conifer trees affects aspen tree growth and root development in mixed aspen–conifer stands.

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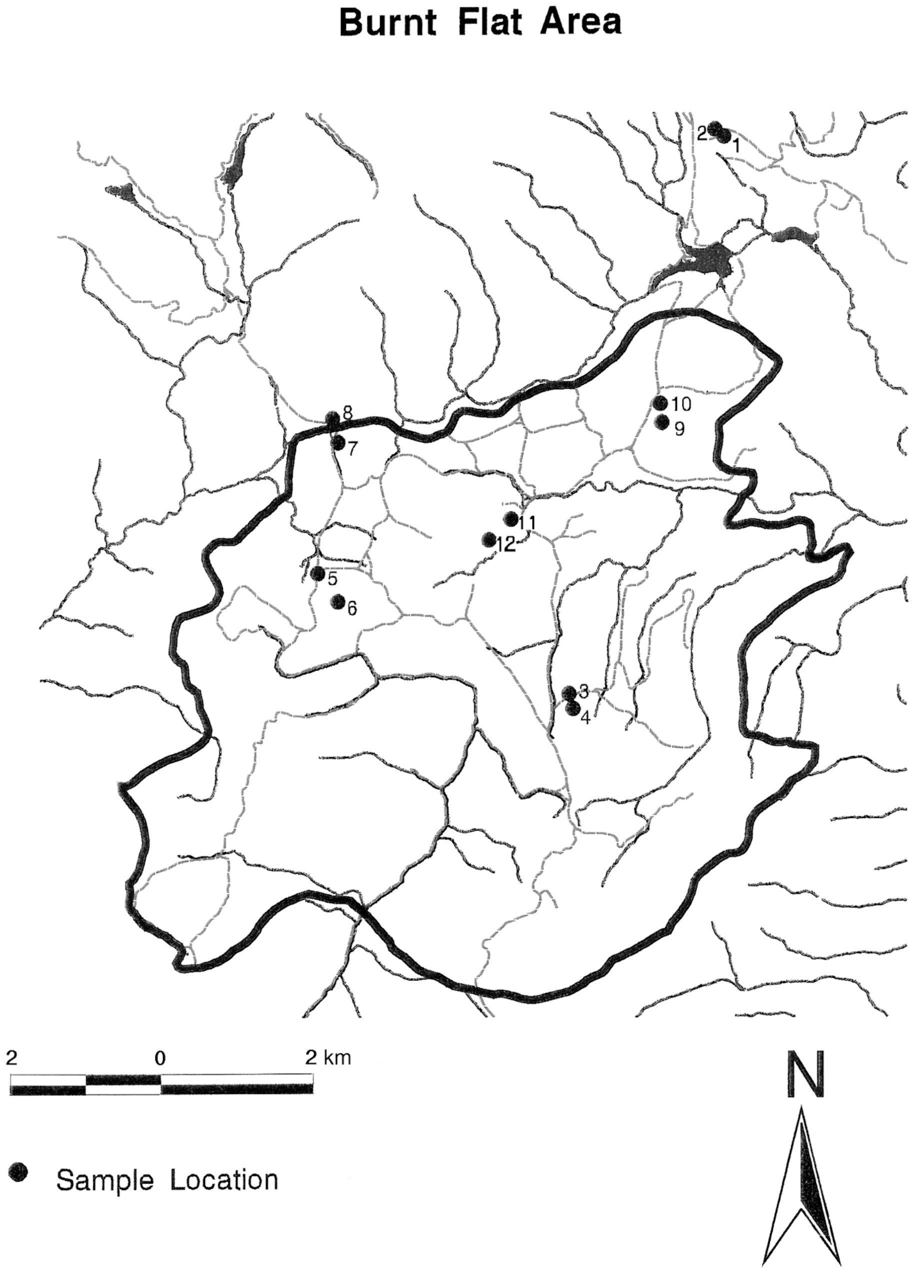
Fig. 1. Map of the Burnt Flat study area. Numbers are the paired locations that were sampled.



Methods

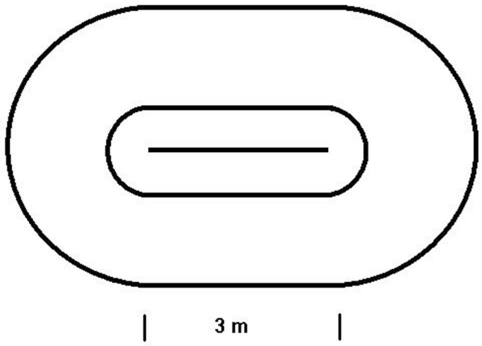
To test these two hypotheses, 12 paired aspen clones were selected within the Burnt Flat aspen analysis area of the Monroe Mountain Demonstration Area on the Fishlake National Forest in central Utah (Fig. 1). This area was selected because of the wealth of data available on the history of aspen in the area (Bartos and Campbell 1998) and the availability of numerous isolated aspen clones of various conditions that could be accessed with the equipment we needed to sample aspen roots. Burnt Flat is located between 2770 and 2930 m elevation on an isolated high mountain range in central Utah. It is a relatively dry high-elevation plateau intersected by small streams in rolling terrain. Vegetation within the study area is dominated by three general cover types: sagebrush–grass–forb communities (42%), aspen (20%), and mixed aspen–conifer (34%) (Mrowka and Campbell 1997). Undergrowth vegetation is much less abundant in mixed aspen–conifer stands compared with that under pure aspen stands.

Twelve sampling sites located in either pure aspen or mixed aspen–conifer stands were evaluated on the Burnt Flat area. Subsequently, these same plot locations were used to evaluate changes in soil properties associated with aspen succession (Bartos and Amacher 1998). Soil types of the 12 sample plots have been described by personnel on the Fishlake National Forest. Bartos and Amacher (1998) detailed the various soil types that are associated with the aspen and mixed aspen–conifer stands in this area. In the western United States, soils associated with stable aspen are Mollisols, whereas those developed under conifer are primarily Alfisols. Soils under mixed aspen–conifer usually have intermediate properties (Bartos and Amacher 1998) that are strongly affected by the persistence of vegetation that occupies the sites (Jones and DeByle 1985).

Regenerating versus non-regenerating clones

We selected three locations within the Burnt Flat area where we could find healthy successfully suckering aspen clones (Fig. 1,

Fig. 2. Diagram of 46.3- and 9.1-m^2 oval plots surrounding the central 3-m root trench.



clones 1, 4, and 10) located near aspen clones that were non-regenerating as evidenced by a lack of successful suckering (Fig. 1, clones 2, 3, and 9). Clonal boundaries were identified by bark color, leaf, branching, and other morphologic characteristics (Shepperd 1982). Each pair of clones was in the same physiographic position and had similar soils and associated vegetation. All of these clones were pure aspen with no conifer component and were of similar size. Overstory stems in both types of clones originated in the mid-1800s, following a major fire[2] that swept through the Burnt Flat landscape.

Each clone was sampled using a combination of nested oval-shaped fixed area plots surrounded a 3 m long root sampling trench (Fig. 2) (Shepperd and Smith 1993). The large oval plot was used to sample stems greater than 10 cm diameter at breast height (DBH, 1.37 m) that occurred within 3 m of the trench (46.3-m^2 plot size). The smaller oval plot encompassed the area within 1 m of the trench (9.1-m^2 plot size) and was used to sample stems less than 10 cm DBH. Three plot trenches were randomly located in each clone that was selected to be sampled.

Stem height, DBH, and 5-year radial growth (from three radial increment borings) were obtained from all live stems within each of the nested plots. All sound trees were also increment cored to the pith at DBH on opposite sides of the stem to obtain age and yearly growth data. Three vigorous trees in a dominant canopy position were sampled at each location for site index determination (Edminster et al. 1985). Increment cores were steamed to remove twist, glued in wooden core mounts with the grain aligned vertically and ring widths measured using a computerized microscope stage. Aspen cores were stained with Fehling's solution (USDA Forest Service 1962) to allow rings to be seen for measurement.

Root trenches were installed by splitting the soil surface with two parallel axe lines and excavating the soil between them. The 3-m trench was excavated to 0.2 m depth, which was sufficient to sample nearly all the large root biomass. Roots along one wall of the trench were exposed by washing the soil away using a high-pressure water hose and sampled using a plane intercept method previously used in studies of aspen roots (Shepperd and Smith 1993). Cross-sectional diameters of all tree roots larger than 4 mm were measured along a plane projected down the side of the trench to a depth of 0.2 m.

Data from the three trench plots in each clone were summed and expressed on a per-hectare basis. Aboveground volumes of trees larger than 10 cm DBH were estimated using whole stem equations for the central Rockies (Edminster et al. 1982). Root density, diameter, and volume were estimated using equations originally derived for sampling downed woody fuels (Van Wagner 1968) that were adapted to sample aspen roots (Shepperd and Smith 1993). These summaries were then analyzed using analysis of variance, comparing self-regenerating versus non-regenerating clones and pure versus mixed aspen–conifer stands. Each pair of clones was treated as a statistical block, and plots within clones served as subsamples assigned to a single block. The block by treatment interaction served as the error term in the analysis.

Pure aspen versus mixed aspen–conifer stands

We again selected three locations within the Burnt Flat area where we could match pure healthy aspen clones that did not contain conifers (Fig. 1, clones 6, 8, and 12) to nearby clones where conifers had invaded the overstory canopy (Fig. 1, clones 5, 7, and 11). Conifers in the mixed stands were predominately (85%) subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) with some (13%) Engelmann spruce (*Picea engelmanii* Parry ex Engelm.) and a few (2%) Douglas-fir (*Pseudotsuga menziesii* var. *glauca* (Beissn.) Franco)

Paired stands were again located in similar physiographic positions and had similar soils; however, understory vegetation was quite depauperate in the mixed stands compared with the pure aspen. Each of these six stands was sampled using three trench plots as described above and the same above- and below-ground data were collected.

Results

Our data from all 12 study clones are consistent with the known disturbance history of the Burnt Flat area; most of the oldest aspen originated in the 1880s following the last recorded fires in the area.[2] Overall, the aspen clones that we studied reflect the somewhat marginal growing conditions within the study area. Aspen site indices (Edminster et al. 1985) ranged from 7.6 to 13.7 m (base 80 years), meaning a dominant tree in the canopy could be expected to achieve these heights in 80 years. Average size, stocking, and volume of the study clones also reflected the less than optimal capability of this site. Study clones contained between 648 and 5472 stems/ha, with quadratic mean diameters ranging from 9.2 to 25.0 cm. Average stand volumes ranged from 80 to 440 $m^3 \cdot ha^{-1}$, and 10-year radial growths ranged from 1.7 to 9.6 mm.

Regenerating versus non-regenerating clones

Although dense understories were a defining characteristic of self-regenerating clones, our data revealed several additional features that distinguished these stands from their non-regenerating neighbors. A histogram of diameter-class distributions (Fig. 3) illustrates that our self-regenerating stands have the characteristic "inverse J" distribution of uneven-aged forests, where smaller and presumably younger diameter classes are much more abundant than larger and presumably older diameter classes. The non-regenerating stands exhibit a more normal distribution typical of that found in even-aged forests, but skewed to include a few large trees.

A height–age plot of cored trees (Fig. 4) reveals that the three non-regenerating clones contained 70- to 130-year-old stems that appeared to be clustered into two broad age-classes. The three self-regenerating clones contained stems that were 10–150 years of age that were clustered into several broad but distinct age-classes, including two distinct younger age-classes that were not present in non-regenerating clones (Fig. 4). The distribution of stem heights and ages

[2] Chappell, L.M. 1997. A fire history study conducted on the Monroe Mountain Demonstration Area, Richfield district, Fishlake National Forest and Bureau of Land Management. Unpublished report. Fishlake National Forest, Richfield, Utah.

Fig. 3. Mean stem density per hectare by 5-cm diameter classes in three regenerating aspen clones that were paired with three non-regenerating aspen clones.

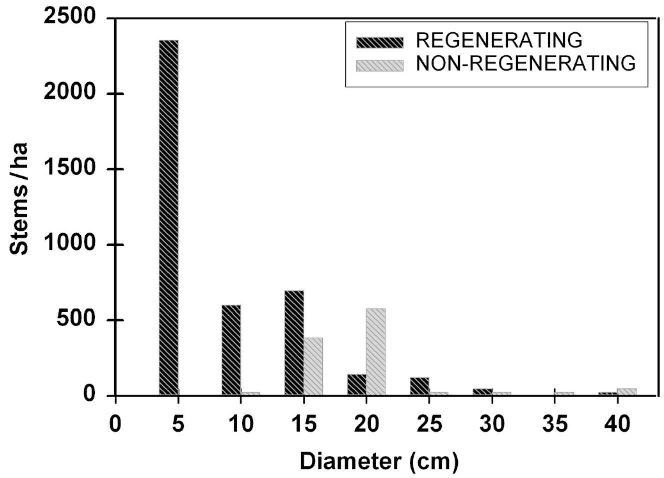


Fig. 4. Stem heights and breast-height ages of aspen trees sampled in regenerating and non-regenerating clones.

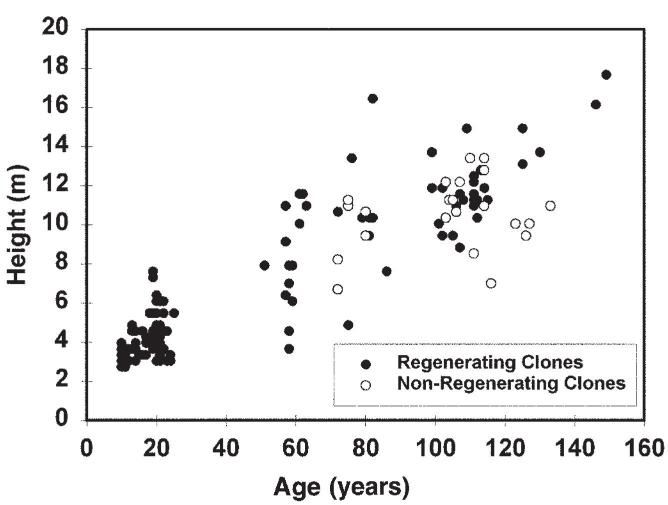
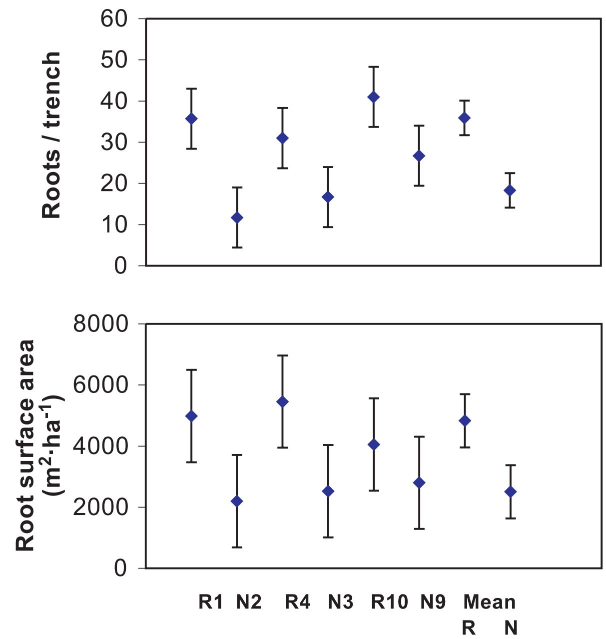


Fig. 5. Mean root density (per 3 m of trench) and root surface area of three pairs of regenerating (R) and non-regenerating (N) aspen clones (with 95% confidence intervals). Overall means appear at right.



does not appear to differ between the regenerating and non-regenerating clones, indicating that both types of clones are growing at similar rates.

Two differences in belowground growth characteristics were also apparent between regenerating and non-regenerating clones. All of the self-regenerating clones had greater numbers of roots and a greater root surface area than their non-regenerating neighbors (Fig. 5). Average root diameter and volume did not differ significantly overall between regenerating and non-regenerating clones but were significantly greater in one regenerating clone of the three pairs studied.

Mixed versus pure clones

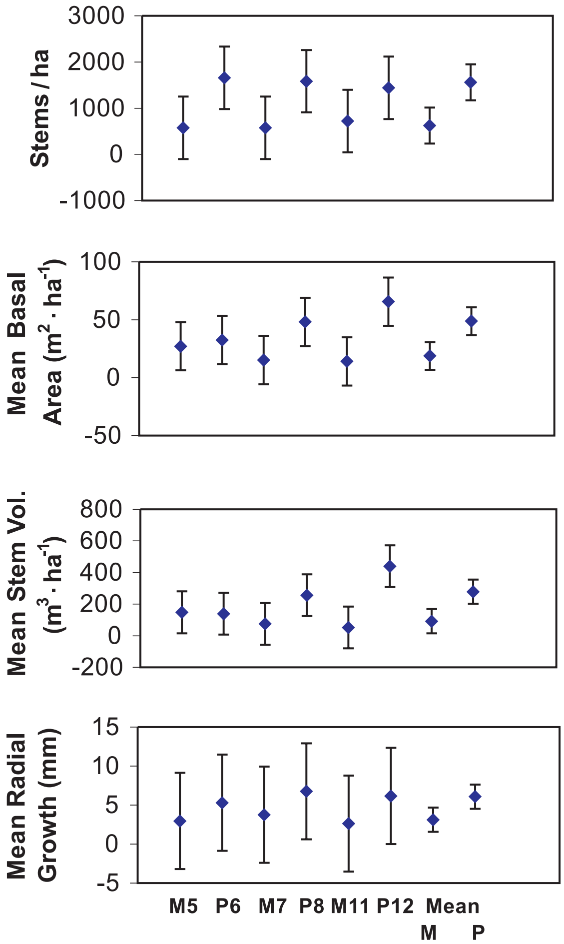
All six of the clones sampled in this part of the study were well stocked and with the exception of some recent aspen mortality (which unfortunately was not measured) in mixed clones, did not show observable signs of decline. Mixed clones did not contain significantly greater total numbers of trees (aspen plus conifer) than pure clones (1632 vs. 1608 tress/ha) nor were there significant differences in overall average basal area, height, or biomass between the pure and mixed clones.

However, the situation changed when only the aspen component was compared among mixed and pure clones. All of the mixed clones contained far fewer aspen (Fig. 6) than their corresponding pure clones (624 vs. 1560 aspen/ha, p = 0.01). Mean aspen basal areas, stem volumes, and radial growth in mixed stands were significantly less than in pure clones, but these differences were not obvious in all clonal pairs (Fig. 6).

Belowground characteristics did not significantly differ between pure and mixed clones. Pure clones averaged 26.5 roots (aspen + conifer) per trench compared with 42.8 roots in mixed clones, but the difference was not significant. Similarly, mean root diameters (12.3 vs. 10.0 mm), root volumes (31.5 vs. 33.5 $m^3 \cdot ha^{-1}$), and root surface areas (4234 vs. 6065 $m^2 \cdot ha^{-1}$, p = 0.02) did not significantly differ between pure and mixed clones. Mixed clones also contained a mean of 17.8 conifer roots per trench, which had an average volume of 7.98 $m^3 \cdot ha^{-1}$. In contrast to the aboveground data, subtracting this conifer root component did not result in significant differences in any measured aspen root characteristics between pure and mixed clones, indicating that the decline of aspen in these mixed stands had not yet affected the root system.

Aspen comprised 51, 58, and 67% of the total basal area in the three mixed clones. The pattern of yearly basal area increment for aspen and conifers growing together in these mixed stands was quite revealing. Average yearly basal area increment of conifer trees in mixed stands overtook that of aspen in the 1920s and remained consistently greater until the 1980s, when it rapidly dropped (Fig. 7). Average yearly basal area increment of aspen in pure stands followed a pat-

Fig. 6. Mean stem density, basal area, stem volume, and radial growth of the aspen component of three mixed (M) conifer–aspen stands compared with those of adjoining pure (P) aspen stands (with 95% confidence intervals). Overall averages appear at right.



tern similar to that of conifers in mixed stands (Fig. 7), indicating that the presence of conifers markedly reduced the productivity of the aspen in mixed stands. This was further evident when the total yearly basal area increment (aspen plus conifer) from mixed stands was plotted with that of the pure stands (Fig. 8). Total basal area production in the two types of stands over the past 120 years was quite similar.

We combined data from all stands measured in the study to compare height–age relationships for conifers and aspen growing in this landscape. Aspen can typically reach breast height in a couple of years, but spruce and firs in the southern Rockies can take 40 years to grow to breast height under partial shade (Alexander 1987). The oldest conifers in our data were about 40 years younger than the oldest aspen indicating that the oldest cohorts of aspen and conifer trees originated at the same time. Given that we aged trees at DBH, we added 40 years to the measured ages of conifer trees to obtain a better estimate of their true ages. The resulting patterns of height–age data are clearly different for aspen and conifers (Fig. 9). To help assess these differences, LOESS curves were fit to both aspen and conifer height–age data. LOESS curves are derived by fitting a series of weighted linear regressions to data, where the weights decrease with distance from the point of interest (Cleveland 1993). The curves indicate a relatively steady height growth rate for aspen, whereas conifers grow slower than aspen at early ages but increase in height rapidly as trees age, eventually overtaking and surpassing the growth rate of aspen (Fig. 9).

Discussion

Regenerating versus non-regenerating clones

The ability of aspen to sucker and successfully introduce new cohorts into the stand appears to be paramount in maintaining overall clonal vigor. The paradigm that clonal root systems remain stable and persist for long periods of time until a disturbance event triggers a new generation of trees to sucker is not apparent in our data. Both regenerating and non-regenerating clones contain stems of various age-classes, indicating that periodic sucker events occurred in these clones. The fact that all of the non-regenerating clones that we measured had less fewer roots than their regenerating neighbors indicates that root systems decline when clones do not periodically self-regenerate.

Reasons for the occurrence of regenerating and non-regenerating clones in the Burnt Flat study area are not readily evident but cannot be attributed to climate or site characteristics. Each of the three pairs of regenerating and non-regenerating clones adjoined one another and had been subjected to identical growing conditions. It is possible that non-regenerating clones were more susceptible to disease or animal herbivory. Another possibility is that non-regenerating clones may be genetically less suited to the environments where they are growing or require a substantially greater disturbance to initiate a successful suckering event.

From a management standpoint these clones will need intensive management if they are to persist in this landscape. Because root systems under them are less extensive, cutting or burning these clones cannot be expected to produce as many suckers as would similar treatments in regenerating clones. Complete harvest of the clone, mechanical root stimulation (Shepperd 1996), prescribed burning, or other treatments to enhance suckering may be needed. Fewer initial suckers would mean that a greater portion would have to be protected from browsing and other causes of sucker mortality to achieve a fully stocked condition or, perhaps, even to achieve minimal numbers of mature trees in the next clonal generation. Fencing to protect suckers may be the only viable option that will permit clones in advanced stages of decline to regenerate successfully.

Mixed versus pure clones

Although all the mixed clones that we studied still contained numerous aspen trees, it was clearly apparent that the conifers were significantly impacting the growth of the surviving aspen stems. This was especially evident in the long-term growth patterns of aspen and conifers in the mixed stands. The distinct differences in basal area increment between conifers and aspen growing together in mixed stands (Fig. 7) illustrate the competitive advantage that shade-tolerant spruce and fir have over aspen. The recent decline in basal area increment of conifers (Fig. 7) might indicate that biomass production in these mixed stands has culminated. Barring another fire disturbance, aspen appears destined to

Fig. 7. Yearly mean basal area increment ($m^2 \cdot ha^{-1}$) of pure aspen stands versus the aspen and conifer components of mixed clones.

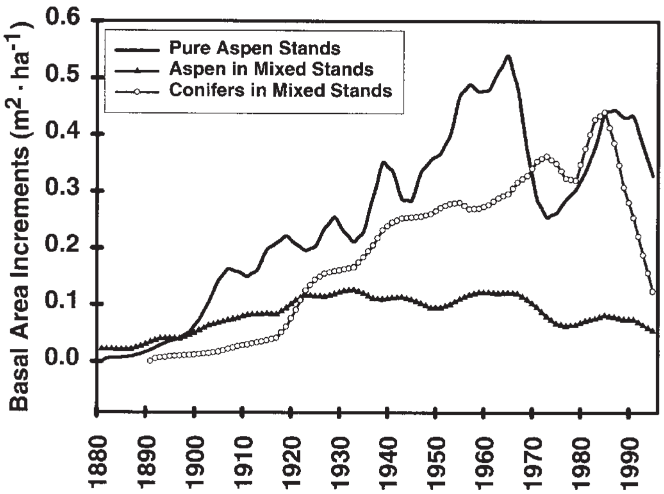
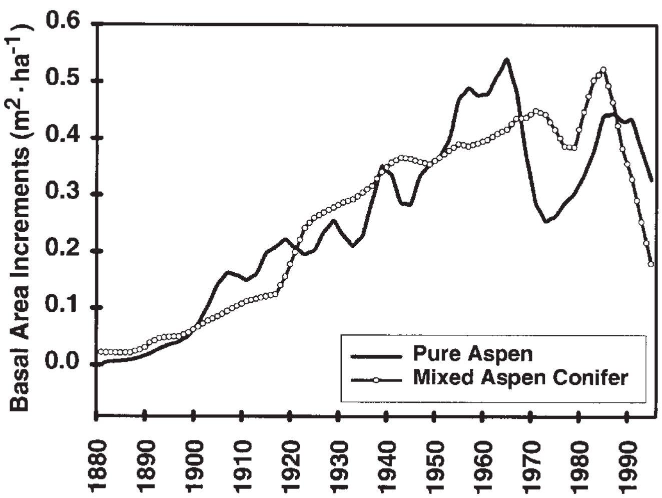


Fig. 8. Yearly mean basal area increment ($m^2 \cdot ha^{-1}$) of pure aspen stands versus that of mixed stands (aspen plus conifers).

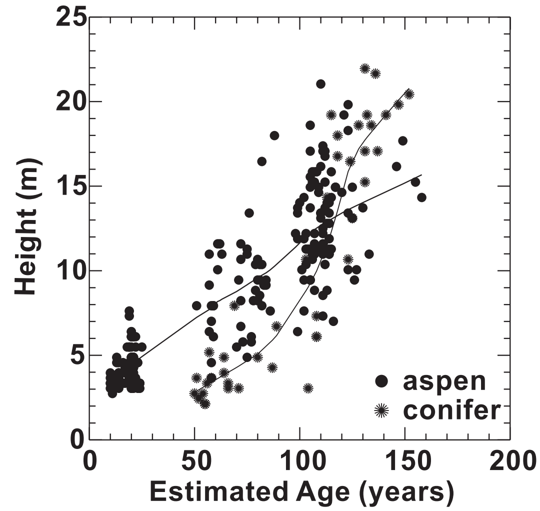


become an increasingly minor component of these mixed stands in the future.

We believe the observed age difference between the oldest conifers and aspen was merely a result of extra time needed for the conifers to grow to breast height, where the increment cores were taken. Adjusting for this, it appears that the oldest conifers and aspen both established immediately following the last major fire in this landscape (Fig. 9). The oldest conifers are taller than most of the oldest aspen, but younger conifers are the same height or shorter that younger aspen (Fig. 9). Therefore, the height–age growth pattern of conifers is steeper than that of aspen (Fig. 9). This dichotomy means that aspen trees are unable to compete with conifers that initially grow slower but eventually overtake the aspen. The remaining aspen are stressed and susceptible to the many factors that can kill them.

Both pure and mixed stands had similar total root biomass, and we did not observe significant reductions in aspen root biomass between the pure and mixed aspen stands that we studied. Although our mixed clones were not in ad-

Fig. 9. Heights and estimated total ages of 268 cored aspen and conifers (all clones) with nonparametric LOESS running means fit to the data. Forty years were added to conifer ages measured at breast height (1.37 m) to estimate total age.



vanced stages of decline, our data clearly show that conifers can make up at least half of the stocking in mixed stands without apparent harm to the aspen clonal root system. Further research is needed in clones where succession is more advanced to identify the point at which aspen root biomass decreases.

Even though the mixed aspen conifer stands that we studied were mature and not growing at optimum rates, the need for management intervention does not seem to be as immediate as in the non-regenerating clones. The aspen component appeared to be in decline, but the root system appeared to be intact. Although conifers may eventually exclude aspen in these stands, the aspen component is not in eminent danger of disappearing. Because these mixed stands do not contain a younger aspen component and the remaining overstory stems are overmature, it would propably be desirable to either regenerate some mixed stands in the Monroe Mountain landscape, or stimulate the introduction of new aspen age-classes within existing mixed stands. Replacing mixed stands could be accomplished by clearfell harvesting or prescribed stand replacement fire. Introducing new aspen age-classes into these mixed stands could be accomplished by selection harvesting or prescribed underburning to remove conifers and stimulate aspen suckering.

Conclusions

This limited study of above- and below-ground characteristics of contrasting aspen clonal conditions in central Utah indicates that significant differences do exist between both self-regenerating aspen clones and non-regenerating clones and between pure aspen clones and those containing conifers. We believe that similar patterns could be observed in many western landscapes where comparable conditions exist. The relationships that we have documented will improve our understanding of the vegetative regeneration process of aspen. This knowledge will help managers maintain these valuable resources within western landscapes, especially in designing intensive silvicultural techniques to rehabilitate declining and late-successional conifer–aspen forests. At the very least, the patterns we observed justify the need for additional research to verify these results in other areas.

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