RESEARCH ARTICLE

Predicting Treatment Longevity after Successive Conifer Removals in Sierra Nevada Aspen Restoration

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ABSTRACT

Populus tremuloides (quaking aspen) stands throughout the Sierra Nevada Mountains are undergoing succession to conifers. Removal of conifers is being tested, however, little is known about treatment longevity—the time taken for stand density to return to pretreatment levels. To determine longevity of treatments removing conifers below different size limits, we developed tree growth equations from data collected in 1 ha plots around Lake Tahoe in *P. tremuloides* stands with varying amounts of conifer, and simulated stand development after treatment in two stands. At Ward Creek, cutting all conifer < 35 cm diameter at breast height (DBH) generated the most wood that could practically be piled and burned inside the stand, but only reduced stand density by 16%. After 13 years of predicted treatment longevity, a second treatment was simulated with options of light, medium, or heavy cutting (50, 60, or 75 cm DBH limits). This gave treatment longevity of 23, 29, and 40 years respectively but did not restore *P. tremuloides* dominance. At Cookhouse Meadow, cutting conifer < 35 cm DBH had 16-year treatment longevity, after which time two treatments were compared. Cutting conifers < 50 cm DBH enhanced *P. tremuloides*' representation from 27% to 37% of stand basal area and had 23-year treatment longevity. Raising the DBH limit to 60 cm left *P. tremuloides* representing 45% of stand basal area, and extended treatment longevity to 36 years. Our findings indicate that a series of treatments will be needed to restore and maintain *P. tremuloides* communities, and will eventually require removal of large conifers (> 75 cm DBH).

Keywords: conifer encroachment, diameter limit thinning, forest management, *Populus tremuloides*

Populus tremuloides (quaking aspen) forest communities in the Sierra Nevada mountains are undergoing succession to conifers which impacts *P. tremuloides* vigor and stifles natural regeneration (Jones et al. 2005, Shepperd et al. 2006, Pierce and Taylor 2010, Krasnow et al. 2012, Berrill and Dagley 2012, 2014, McCullough et al. 2013). Fire suppression has lengthened the return intervals of fire that can kill shade-tolerant conifers before becoming established beneath *P. tremuloides* (Shepperd et al. 2006, Beaty and Taylor 2008). Conifers eventually overtop *P. tremuloides* and constrict their crowns and vigor (Berrill and Dagley 2012). Within these stands, *P. tremuloides* root suckers (vegetative reproduction) are often abundant but they remain small and are unlikely to replace the aging *P. tremuloides* canopy because of competitive exclusion from conifers (Pierce and Taylor 2010, Berrill and Dagley 2014). *Populus tremuloides* stems typically live < 200 years, but with successful vegetative reproduction *P. tremuloides* clones may persist—by regenerating continuously in all-aged stands or periodically after stand-replacing disturbances—for millennia (Ally et al. 2008). Mock et al. (2008) found that *P. tremuloides* seedlings (sexual reproduction) were also an important mode of regeneration in the western US. *Populus tremuloides* are light-seeded pioneers that could evade replacement by conifers if they had newly-disturbed areas to colonize (Krasnow and Stephens 2015). However, the relatively small *P. tremuloides* stands of the Sierra Nevada are often surrounded by dense stands of conifers that experience relatively few natural disturbances and thus prohibit the expansion of *P. tremuloides*. More intense disturbances (e.g., stand-replacing fire) that could be simulated by management to create opportunities for *P. tremuloides* expansion are difficult to implement safely, especially in sensitive areas with high soil moisture favored by *P. tremuloides*, near waterbodies, or near dwellings in the wildland-urban interface.

Disturbances affecting *P. tremuloides* stands in the Lake Tahoe Basin, California and Nevada, USA, have changed over time. Historically, mixed-severity wildfire of varying

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Restoration Recap

- Sierra Nevada *Populus tremuloides* stands, which have ecological importance, are threatened by rapid succession to conifer primarily due to longer fire return intervals (i.e., fewer fires to kill competing conifers or clear new areas for *P. tremuloides* to colonize).
- Where land managers are restricted in the size of conifers that can be removed and equipment used in *P. tremuloides* stands, restoration currently involves hand cutting and piling of smaller conifer trees rather than mechanical removal of all (including large) conifers.
- Cutting smaller, younger conifers slows succession by leaving only slower-growing older trees, however many small trees must be cut to substantially reduce crowding. If cut wood cannot be extracted, frequent, repeated light cutting and pile burning overcomes the space limitations for piling cut wood inside dense stands.
- Cutting larger trees and cutting more trees will prolong treatment longevity but can generate too much woody debris to pile and burn in sensitive or inaccessible areas where it would otherwise accumulate as a dangerous fuel load in between the remaining trees.
- Additional restoration approaches are available. Clearing beyond stand boundaries provides space for wood disposal and migration of *P. tremuloides*. Girdling conifers to create snags leaves dead wood stored vertically until snags fall and become surface fuel. Removing seed-bearing conifers in/near *P. tremuloides* stands reduces seed supply needed to regenerate conifers that would otherwise have to be treated (or outcompete *P. tremuloides*) in future. Fire could be reintroduced to kill young conifers and promote *P. tremuloides* regeneration, but risks damaging *P. tremuloides* trees.
- Cutting conifers offers managers control over stand density and treatment longevity which vary between stands with different structure and species composition.

return intervals killed young conifers less tolerant of fire that would establish beneath *P. tremuloides* (Beaty and Taylor 2008). *Populus tremuloides* would also have colonized areas after stand-replacing disturbances (e.g., patches of high-severity fire, insect outbreaks, landslides, etc.). *Populus tremuloides* and associated vegetation may have been exposed to sheep grazing in the late 1800s, along with burning to clear land and stimulate forage production, logging and burning of logging residues, mining, or water diversion practices. Most *P. tremuloides* stands were left undisturbed during the 1900s era of fire suppression (Shepperd et al. 2006). Recently we have seen instances of damage to *P. tremuloides* regeneration from ungulate browsing around Lake Tahoe. However this level of damage is much lower than damage reported in other parts of the Sierra Nevada (Margolis and Farris 2014) or other western regions (Endress et al. 2012). Beavers cut pole-sized *P. tremuloides* near water in some stands, and may have ecological importance (McColley et al. 2012). *Populus tremuloides* and conifers have coexisted for centuries, as evidenced by the occasional presence of presettlement fir and pine trees within *P. tremuloides* stands. However in recent years, many of the Lake Tahoe Basin *P. tremuloides* stands have borne an unusually high density of shade-tolerant young conifers that form a continuous canopy layer beneath mature *P. tremuloides* (Shepperd et al. 2006). In some instances, the conifer understory has grown to overtop the mature *P. tremuloides* canopy.

In the Lake Tahoe Basin, *P. tremuloides* are found in small, isolated stands that are relatively rare, covering less than two percent of the landscape. There is interest in preserving these *P. tremuloides* stands for their scenic and recreational value, and for ecosystem services such as stabilizing soil in sensitive riparian areas and fostering biodiversity (Shepperd et al. 2006). They have been identified as Ecologically Sensitive Areas because of the biological diversity these habitats support (Manley et al. 2000). Conifers are being removed from *P. tremuloides* stands throughout the Sierra Nevada, including the Lake Tahoe Basin (Jones et al. 2005, Dagley et al. 2012, Krasnow et al. 2012), however, treatment approaches and intensity vary (e.g., complete conifer removal, partial conifer removal). Managers restoring *P. tremuloides* around Lake Tahoe are often constrained in their ability to conduct more intensive conifer removal treatments because of: 1) restrictions on the use of mechanical equipment that could remove larger conifers; and 2) the potential for excessive downed wood in the stand (which increases hazardous fuels and may affect *P. tremuloides* regeneration) because cut trees often cannot be removed from the stand. Performing more frequent, less intensive conifer removal and associated pile burning treatments would alleviate part of these problems. However, little is known about how treatment type and intensity affects treatment effectiveness and longevity. Specifically, how much growing space must we provide *P. tremuloides* trees and their root sucker regeneration for vigorous growth to be sustained until the next restorative treatment?

The overall objective of this study was to determine the effectiveness of restoring *P. tremuloides* dominance through removal of conifers under various diameter limits. Specifically, we wanted to compare the longevity of treatment types that varied based on the size of conifers that were removed. To do this, we developed growth models and performed a simulation study to compare responses to the various treatments applied in two representative Lake Tahoe Basin *P. tremuloides*-conifer stands. The effectiveness of each treatment was evaluated by determining treatment longevity and change in species composition.

Methods

Study Area

Lake Tahoe is centrally located in the Sierra Nevada Mountains of California and Nevada, USA. The Lake Tahoe Basin is a collection of watersheds encircling and draining into Lake Tahoe. The basin covers over 134,000 ha, and has 63 tributaries delivering water to the lake. Most soils formed in parent materials derived from igneous intrusive rocks (typically granodiorite) and igneous extrusive rocks (typically andesitic lahar). Soils derived from metamorphic rock are much less common (NRCS 2007). Cold winters and summers with cool nights and warm days characterize the Mediterranean continental climate. Precipitation generally increases with elevation, and varies between years and seasons; most comes as snow or rain during winter months. Occasional summer thunderstorms deliver rain and lightning (www.wrcc.dri.edu). The average area of individual *P. tremuloides* stands around Lake Tahoe is currently less than 2 ha, although a few stands are much larger. They are typically located alongside creeks (or other water sources) in deeper soils with more soil moisture than areas dominated by conifers (Shepperd et al. 2006).

Stand Structure and Growth Data

To meet our objective of evaluating conifer removal treatment effectiveness, we needed *P. tremuloides* and conifer tree data for model development and to use as starting points for growth model simulations. We collected tree data in nine *P. tremuloides*-conifer stands on the east, west, and south shores of Lake Tahoe at elevations of 1,900–2,260 m (Berrill and Dagley 2012). Between 2009 and 2010, we established a 1 ha plot in each of the nine stands within which we recorded the DBH, height, and height to the base of the live crown, and mapped the location of all *P. tremuloides* trees ≥ 10 cm DBH. Within the 1 ha plot we also measured the DBH and mapped the location of all conifer trees ≥ 20 cm DBH. We measured the total height and live crown base height of over 75% of conifers: all large conifers and a subsample of the abundant smaller conifers (that we expected would be cut). For all trees (*P. tremuloides* and conifer), we recorded instances of damage or poor health (e.g., forked, crown damage, leaning) and used this information to withhold from analysis any data for trees with substantial damage. We re-measured the DBH of all sampled trees three years later in five of the nine 1-ha plots, giving DBH growth data for *P. tremuloides* and conifer trees in unmanaged stands on the east, west, and south shores of Lake Tahoe, and DBH growth after conifer removal in stands on the east and west shores of Lake Tahoe. Spatial variations in species composition and stand density throughout these large plots meant that trees experienced a range of growing conditions. We tallied smaller *P. tremuloides* (< 10 cm DBH) and conifer (< 20 cm DBH) in a grid of subplots throughout each 1 ha plot, because they were so numerous, and re-measured a subsample of these for DBH growth in five of the nine 1 ha plots.

Growth Models

We used existing growth models, and developed new models as needed, to estimate the expected growth rate for *P. tremuloides* and conifer species present within *P. tremuloides* stands at Lake Tahoe. For conifers, we developed a set of predictive equations for DBH growth and crown ratio (CR) for each species present in our sample stands: *Pinus contorta* (lodgepole pine), *Pinus jeffreyi* (Jeffrey pine), *Abies concolor* (white fir), and *Abies magnifica* (red fir). To test for and to model the effects of competition on tree growth, we included one of three stand density metrics in the growth model: BA, stand density index (SDI), or SDI of larger trees (SDIL, calculated using SDI data for sample tree and plot trees of same or larger size). Stand density metrics were calculated for trees in 0.02 ha plots centered on each sample tree.

We developed height-diameter equations for each species, after excluding data for trees with broken or dead tops, forks, and leaning trees, and used these models to predict total tree height (HT) from DBH for trees without height data. To estimate wood volume cut in simulated treatments, we applied tree volume equations to DBH and HT which gave stemwood volume for conifers cut in each restoration simulation (McLean and Berger 1976, Fowler and Hussain 1987). Additionally, we developed "sapling growth models" to predict growth of regenerating *P. tremuloides* and conifer ranging in size from zero DBH up to the smallest size of tree measured for data used to develop the tree DBH growth models for *P. tremuloides* and conifer.

We generated data summary tables to define the range of applicability of the various tree and sapling models, and provide these summary data and model formulations in an online appendix (Supplementary Materials). We fitted these models as linear and multiple linear regression models using PROC REG and generalized linear models that included species as a categorical variable using PROC GLM in SAS (SAS v. 9, SAS Institute, Cary, NC).

We had existing models available to simulate *P. tremuloides* DBH growth and CR. These models had the following attributes: DBH growth was predicted in terms of tree basal area increment (BAI) from inputs of DBH, CR, stand density in terms of BA, geographic location (east or west shore of Lake Tahoe), and elevation; *Populus tremuloides* CR was predicted as a function of stand density and species composition predictor variables (Berrill and Dagley 2012). Using these existing and newly developed models, we simulated *P. tremuloides* and conifer tree growth to determine how *P. tremuloides*-conifer stands changed over time with and without conifer removals.

Simulating Stand Growth and Restoration Treatment Longevity

We used the *P. tremuloides* and conifer growth models to simulate stand development in *P. tremuloides*-conifer mixtures, using real tree data collected in two representative sample stands as starting points for the growth projections. We selected these two particular stands because succession to conifer was advanced (conifers comprised > 75% of TPA, BA, and SDI), yet they differed in terms of stand density, structure, and species composition.

1. The Ward Creek stand (WA38) was located in a remote, inaccessible part of the Ward Creek drainage at 2,033 m elevation on the west shore of Lake Tahoe. It had an abundance of *A. magnifica* and *A. concolor* 0–15 cm DBH, no *P. jeffreyi*, and *P. contorta* of all sizes. Each conifer species outnumbered and outsized *P. tremuloides*.
2. The stand at Cookhouse Meadow (SSP24) was at 2,165 m elevation adjacent to Highway 89 near Luther Pass, south of Lake Tahoe. It had 33% higher stand density and no pine regeneration <10 cm DBH. *Abies concolor* dominated and was abundant in all sizes > 15 cm DBH. *Populus tremuloides* outnumbered the occasional *P. jeffreyi* and *P. contorta* found at SSP24.

In each stand, we simulated a range of different diameter limit cuts (hereafter referred to as "partial cutting" treatments to signify that only a portion of trees in the stand were cut) to allow for comparison of diameter limits. First, we simulated cutting by removing records from the plot data for conifers below the diameter limit and then recalculating density and average tree size after this partial cutting. We then input this new post-treatment data into the tree growth models and simulated post-treatment growth. This approach ensured that model simulations were based on realistic pre- and post-treatment starting values. In addition to starting values, the growth models needed inputs of stand density and CR to make predictions of tree growth. As tree growth proceeded in the simulations, stand density increased accordingly, and this (competition from neighboring trees) invoked the CR models, causing tree crowns to rise in the simulations. However, after partial cutting reduced stand density we held the live crown base of each tree at a steady height until sometime after the treatment when stand density had again reached a level where CR models predicted that the process of density-induced crown rise had resumed. To simulate development of regeneration initiated by each partial cutting treatment, we invoked sapling growth models. We assumed this regeneration numbered 150 *P. tremuloides*, 200 fir, and 10 pine stems ha^{-1} with these *P. tremuloides* and conifer attaining heights of 1.37 m (breast height, i.e., DBH = 0 cm) at age 5 and 10 years, respectively (J-P. Berrill and C.M. Dagley, Humboldt State University, unpub. data), at which time they started to contribute to stand density in terms of SDI and began DBH growth predicted by the sapling growth models. Summing stand density for trees and regeneration of each species gave total SDI for every year after partial cutting. This allowed us to determine treatment longevity for each partial cutting treatment—defined here as the time taken for stands to return to their pre-treatment level of crowding in terms of SDI—under different diameter limits. We also reported the proportion of stand BA represented by *P. tremuloides* to describe change in species composition over time and how *P. tremuloides* representation was enhanced by conifer removal treatments, and provide a summary table of simulation results in Supplementary Materials.

Results and Discussion

Ward Creek Simulations

Tree summary data collected in 2009 from the 1 ha plot at Ward Creek showed that before partial conifer removal, *P. tremuloides* represented only 14% of stand BA (Stand BA = 43.5 m^2 ha^{-1}), *A. magnifica*, *A. concolor*, and *P. contorta* representing 25%, 33%, and 29% of stand BA, respectively. *Populus tremuloides* density for trees > 20 cm DBH (52 trees ha^{-1}) was lower than that of all conifers present. Of the conifers present, *A. magnifica* and *A. concolor* (93 and 117 trees ha^{-1}, respectively) were more common than *P. contorta* (63 trees ha^{-1}). Using these data as starting values, growth model projections showed that, in the absence of any treatment or other disturbances to reduce conifer tree and regeneration densities, *A. magnifica* and *A. concolor* dominated in large part due to fast growth among younger fir trees. As the stand succeeded to conifers, *P. tremuloides* dropped from 14% to 5% of stand BA after 66 years and 2% after 88 years. During this time, stand density was predicted to rise above SDI = 1000 (metric) leading *P. tremuloides* to enter the so-called "zone of imminent mortality" (i.e., > 60% of maximum SDI; Long 1985) where mortality gradually reduced *P. tremuloides* densities in approximate balance with *P. tremuloides* growth. At year 67, total SDI exceeded the upper limit of SDI = 1700 (metric) for *P. tremuloides* leading to rapid *P. tremuloides* decline and replacement by conifer (Berrill and Dagley 2014). *Pinus contorta* also exhibited gradual decline as more growing space became occupied by the more shade-tolerant fir in both the overstory and understory.

In the fall of 2009, the U.S. Forest Service treated the Ward Creek unit by removing all conifer trees < 35 cm DBH, generating cut conifer wood manually piled in relatively small burn piles (average pile diameter = 2.8 m; range = 2.0–4.3 m) numbering 124 piles per hectare (Dagley et al. 2012). The stemwood volume (excluding branches/foliage) of cut conifers > 20 cm DBH totaled ~ 42 m^3 ha^{-1}. Conifers < 20 cm DBH were plentiful and presumably contributed a

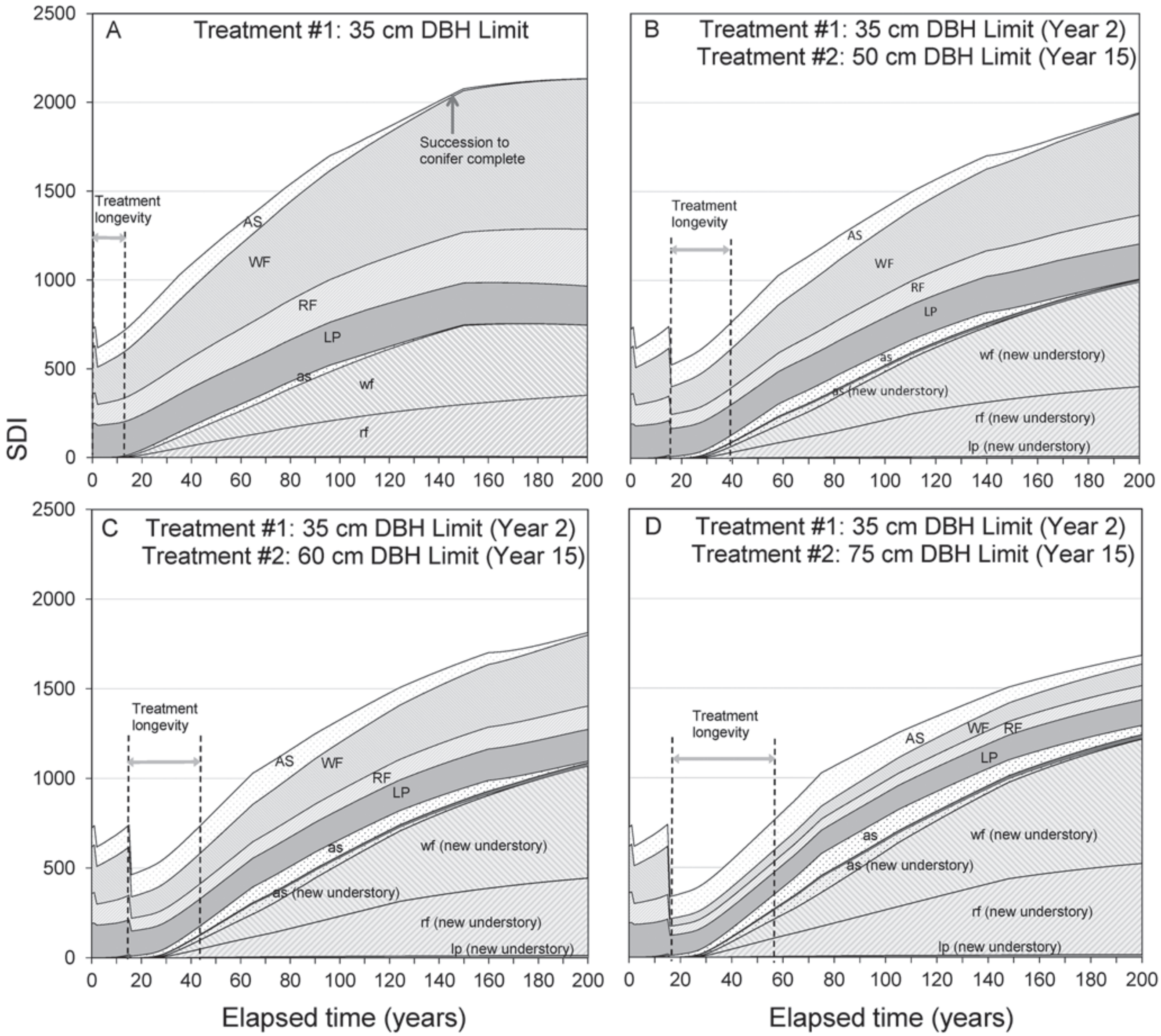

Figure 1. Treatment scenarios at Ward Creek (WA38)—simulated change in stand density index (SDI) and relative contribution to stand SDI of each species in the overstory and understory. AS = *Populus tremuloides* (aspen), JP = *Pinus jeffreyi* (Jeffrey pine), LP = *Pinus contorta* (lodgepole pine), RF = *Abies magnifica* (red fir), WF = *Abies concolor* (white fir).

large volume of additional cut wood, branches, and foliage to these piles. Thinning more heavily would likely have created an unacceptable fire hazard from excessive down wood in this inaccessible area. The treatment only reduced SDI by 16% (from SDI 737 to 617), with a modest "boost" in average conifer DBH by removing the smallest individuals of each conifer species (DBH increase for *P. contorta*: 9 cm; *A. magnifica*: 10 cm; and *A. concolor*: 19 cm). The conifer removal treatment produced a large reduction in the number of (smaller) trees per acre (reduced density of *P. contorta*: 26%; *A. magnifica*: 65%; and *A. concolor*: 44%) but only reduced stand BA by 4 m^2 ha^{-1}. Our growth model output indicated that the WA38 stand returned to pre-treatment SDI after about13 years, at which time *P. tremuloides* represented 15% of stand BA giving only 1% improvement over pretreatment composition of 14% *P. tremuloides* BA. These results indicate that primarily removing small conifers slows the process of *P. tremuloides* stand succession to conifer because the remaining older conifers are predicted to have slower growth than younger trees. In the absence of repeat treatment, the models projected a decline in *P. tremuloides* to 5% of stand BA in Year 100 (86 years after the stand had returned to pre-treatment SDI) and < 2% in Year 120 (Figure 1A).

To forestall this future decline, we simulated a second conifer removal treatment in Year 15. We simulated and compared three alternative prescriptions: "light conifer removal" (removing all conifers up to 50 cm DBH), "medium conifer removal" (60 cm DBH limit), and "heavy conifer removal" (75 cm DBH limit). These treatments had 23-, 29- and 40-year longevity, respectively (Figures 1B–D). The "light conifer removal" cut all conifer trees < 50 cm DBH, reduced SDI by 29%, and removed 67 stems ha^{-1} of residual conifer and 200 trees ha^{-1} of regenerating conifer saplings. This enhanced *P. tremuloides*'s representation in the stand from 15% to 21% of total stand BA. The stand returned to pre-treatment stand density in Year 38, resulting in treatment longevity of 38 – 15 = 23 years (Figure 1B). The "medium conifer removal" treatment (cutting all conifer < 60 cm DBH) produced a 38% reduction in stand density. Removing 92 stems ha^{-1} residual conifers and 200 stems ha^{-1} regenerating fir saplings shifted species composition in favor of *P. tremuloides* from 15% up to 23% of stand BA represented by *P. tremuloides*. The stand returned to pre-treatment SDI in Year 44, giving treatment longevity of 44 – 15 = 29 years (Figure 1C). The "heavy conifer removal" treatment (cutting all conifer < 75 cm DBH) extended treatment longevity but generated a lot of cut wood that would need to be removed or piled. The heavy cutting resulted in removal of 289 residual overstory conifers and all fir regeneration arising after the first treatment. Regenerating *P. contorta* (10 stems ha^{-1}) were not cut because they were rare. In total, the partial cutting reduced SDI by 54%. The remaining conifers comprised six *A. concolor* trees ha^{-1} averaging 84 cm DBH, four *A. magnifica* trees ha^{-1} averaging 123 cm DBH, and 14 *P. contorta* stems ha^{-1} averaging 91 cm DBH. These very large 24 trees ha^{-1} collectively represented 69% of stand BA. Therefore the most intensive treatment, after which only 24 very large conifers persisted, did not restore *P. tremuloides* dominance. *Populus tremuloides* was left representing only 31% of stand BA. Nevertheless, this meant that *P. tremuloides*' representation had doubled which was a better outcome than less intensive treatments but indicated that larger tree removal would improve *P. tremuloides* representation in stand BA. After this second treatment in Year 15, the stand did not return to pre-treatment SDI again until Year 55 (i.e., treatment longevity of 55 – 15 = 40 years). At that time, in Year 55, the young firs regenerating after the Year-15 treatment comprised one third of stand density (Figure 1D). After 55 years, three age classes of *P. tremuloides* totaled one third of stand BA, indicating that changes in stand structure and composition persisted beyond the calculated treatment longevity.

The "heavy conifer removal" in year 15 generated the most cut wood (~ 64 metric tons ha^{-1} of dry cut wood). The volume of conifer stemwood cut during this 75 cm DBH limit treatment amounted to 212 m^3 ha^{-1}. The cut conifer trees averaged 48 cm DBH and 1.71 m^3 stemwood per tree (not counting cut branches and foliage). This massive volume of cut conifer wood greatly surpassed the large volume cut in the prior treatment (with 35 cm DBH limit) where 124 piles of cut conifer collectively covered 10% of the ground area within the 1-ha plot at Ward Creek (Dagley et al. 2012). Therefore we infer that the simulated treatment with 75 cm DBH limit created too much down wood to be piled and burned at this remote, inaccessible location.

Cookhouse Meadow Simulations

Tree data from the 1 ha plot at Cookhouse Meadow showed there to be fewer small conifer saplings than the Ward Creek stand but more conifer density in terms of BA and SDI. *Populus tremuloides* represented 24% of stand BA and *A. concolor* represented 65% of stand BA before treatment (Stand BA = 55.6 m^2 ha^{-1}, SDI = 990). In terms of average DBH, the *P. tremuloides* were outsized by all conifer species. *Populus tremuloides* (128 stems ha^{-1}) were outnumbered by *A. concolor* > 20 cm DBH (354 stems ha^{-1}). *Pinus contorta* (28 stems ha^{-1}) was more common than *P. jeffreyi* (8 stems ha^{-1}) > 20 cm DBH. In the absence of treatment, model projections showed that *A. concolor* would continue to dominate at the expense of *P. tremuloides* and eclipse *P. tremuloides* completely in about 120 years (Figure 2A).

Here, removal of conifers first to the 35 cm DBH limit was expected to provide the greatest possible relief from crowding without creating too much cut wood and risk of windthrow which can be a problem after heavy cutting in such a crowded stand. Therefore in Year 2 of the simulation, we cut all small conifer < 35 cm DBH (235 stems ha^{-1}cut). This improved *P. tremuloides*' representation in the stand from 24% to 29% of stand BA. The stem wood volume (not counting branches and foliage) of cut conifers > 20 cm DBH totaled ~ 75 m^3 ha^{-1}. Conifers < 20 cm DBH were not common at SSP24 and presumably contributed a relatively small amount of additional cut wood, branches, and foliage for disposal. SDI was reduced by 23%. However, this treatment was short-lived with SDI returning to pre-treatment levels around Year 18, equating to a predicted treatment longevity of 18 – 2 = 16 years. After Year 18, residual *A. concolor* trees and a new cohort of *A. concolor* were predicted to progressively replace *P. tremuloides* once SDI exceeded 1000 (metric; lower limit of zone of imminent mortality for *P. tremuloides*). Later, *P. tremuloides* would decline more rapidly once SDI exceeded *P. tremuloides*' upper limit of 1700 (Figure 2B).

We simulated a second conifer removal treatment in Year 18, removing conifers below 50 cm DBH. This treatment reduced total SDI by 27%, and shifted species composition from 27% *P. tremuloides* to 37% *P. tremuloides* in terms of stand BA. Volume of conifer stemwood cut was similar to the first treatment, totaling ~ 76 m^3 ha^{-1} not counting branches and foliage. SDI had once again returned to pre-treatment levels by Year 41, giving a predicted treatment longevity of 41 – 18 = 23 years (Figure 2C).

Figure 2D depicts an alternative 'heavier' partial cutting treatment simulated in Year 18, removing conifers below a 60 cm DBH limit including regenerating firs (10 stems ha^{-1} of regenerating pines were retained). This treatment

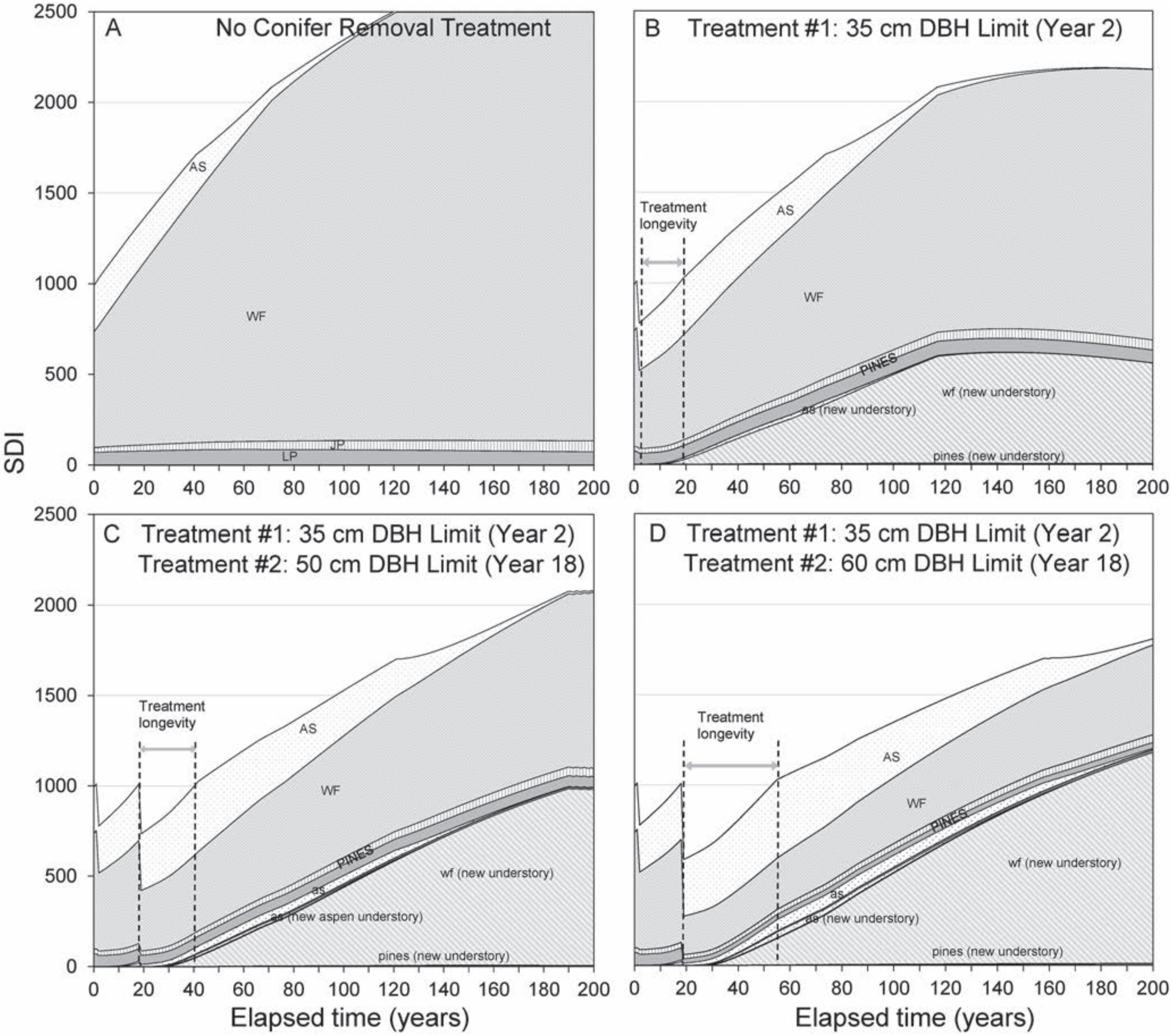

Figure 2. Treatment scenarios at Cookhouse Meadow (SSP24)—simulated change in stand density index (SDI) and relative contribution to stand SDI of each species in the overstory and understory. AS = *Populus tremuloides* (aspen), JP = *Pinus jeffreyi* (Jeffrey pine), LP = *Pinus contorta* (lodgepole pine), RF = *Abies magnifica* (red fir), WF = *Abies concolor* (white fir).

reduced total SDI by 42% and shifted composition in favor of *P. tremuloides* from 27% to 45% of stand BA represented by *P. tremuloides*. Volume of conifer stemwood cut was double the volume cut in the first treatment, totaling ~ 151 m^3 ha^{-1} not counting branches and foliage. Under this 60 cm DBH limit partial cutting treatment, stand density had once again returned to pre-treatment levels by Year 54, giving a predicted treatment longevity of 54 – 18 = 36 years. By year 54, all residual conifers had grown > 75 cm DBH. At this time, the regenerating conifers collectively represented only 14% of SDI, with the remainder being *P. tremuloides* or large residual conifers. Therefore any prescription calling for stand density to be reduced more than 14% would necessarily involve cutting/killing some conifer trees > 75 cm DBH. Reducing SDI by only 14% would have short treatment longevity, which highlights the need to revise or remove administrative restrictions such as diameter limits to avoid handicapping stand management. Without further treatment, stand growth (i.e., per hectare growth of *P. tremuloides* and conifer combined) was predicted to slow beyond year 60, likely because so much growing space would be occupied by large old conifers with declining DBH growth and *P. tremuloides* growing slowly under the partial shade they cast.

Implications for Policy and Practice

This study provides insight into treatment longevity with and without partial cutting treatments to remove conifers from *P. tremuloides* stands succeeding to conifer. Although partial cutting appears to slow succession to conifer in *P. tremuloides*-conifer stands, our simulations indicated that benefits were short-lived unless treatments involved heavy cutting. Our results suggest that managers and policy makers defining diameter limits for *P. tremuloides* restoration should consider treatment longevity, and the inevitable advance in conifer size, age, seed production, and growing space occupancy at the expense of *P. tremuloides*. From an economic standpoint, higher diameter limit cuts might be desirable if this enhanced operational efficiency, if more merchantable wood could be extracted, or because fixed costs (e.g., planning, permitting, contract administration) were incurred less frequently when greater treatment longevity was achieved by reducing conifer SDI more than a lower diameter limit. Heavier cutting relieves crowding for longer and effects greater shifts in species composition in favor of *P. tremuloides*. Longer intervals between treatments also align with presettlement fire return intervals. Fire disturbances were less frequent in *P. tremuloides* stands occupying low-lying areas with higher soil moisture than in upland conifer stands (Beaty and Taylor 2008).

Our findings show that the current practice of removing numerous smaller conifer trees (e.g., < 35 cm DBH) instead of larger diameter conifers present in these stands slows down succession of a *P. tremuloides* stand to conifer, but without great reduction in SDI. As a result, cutting of only the smaller diameter trees may inadvertently leave enough larger conifers for SDI to remain at levels that impact *P. tremuloides* growth and vigor. Meanwhile, the remaining large conifers—that tolerate higher SDI than *P. tremuloides*—continue to grow towards practical or administrative thresholds for removal. Some managers in the Lake Tahoe Basin are evaluating options to remove larger trees (> 75 cm DBH) when removal would be critical to restoration efforts. Jones et al. (2005) recorded an abundance of vigorous *P. tremuloides* regeneration soon after removing all conifers of all sizes within nine meters of existing *P. tremuloides* stems. This treatment involved mechanical extraction of cut conifers, and did not impact the nearby stream environment (Jones et al. 2013). In areas inaccessible to machinery, consideration should be given to alternative methods of wood extraction or disposal. It is possible that cut wood could be moved to cleared areas beyond stand boundaries or recovered using portable mills. Extracting larger more-valuable conifers could offset high costs of helicopter logging. Girdling would relieve crowding and leave the dead trees standing for a time. Another alternative would be to create snags by strategically placing burn piles near unwanted live conifers (i.e., heat from burning pile could kill conifer). Since large pieces of wood are difficult to move and pile manually, a few large conifers could also be cut and left lying intact as woody debris. After managers have reduced stand density and fuel loading sufficiently, ground fire could be tested as a means of keeping fuels and conifer regeneration at low levels while stimulating regeneration of *P. tremuloides* (Krasnow et al. 2012, Margolis and Farris 2014). Fire and fuels could be kept away from certain areas to protect existing *P. tremuloides*; their thin bark and shallow roots are susceptible to damage by heat (Jones et al. 2005, Dagley et al. 2012).

A more comprehensive restoration strategy could attempt to mimic mixed-severity fire by incorporating alternative complimentary approaches: 1) create disturbances adjacent to *P. tremuloides*-conifer stands, giving *P. tremuloides* opportunities to colonize new areas via seedlings and by lateral root spread and suckering (Krasnow and Stephens 2015); 2) regenerate existing stands via stand-replacing disturbances that favor fast-growing *P. tremuloides* root suckers over conifer seedling regeneration (Krasnow and Stephens 2015); and 3) progressively replace aging *P. tremuloides* by implementing a series of disturbances designed to control stand density and conifer regeneration and promote ongoing recruitment of *P. tremuloides* to the overstory (Jones et al. 2005, Krasnow et al. 2012, Berrill and Dagley 2014).

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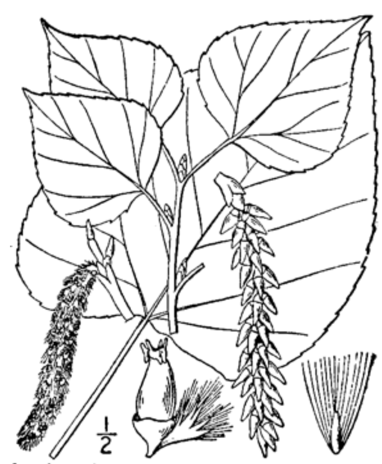

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