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Curtailing succession: Removing conifers enhances understory light and growth of young aspen in mixed stands around Lake Tahoe, California and Nevada, USA

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ABSTRACT

Aspen is a keystone species that is relatively rare in the Sierra Nevada Mountains and is undergoing succession to conifers in the absence of disturbance. In the presence of more conifers, recruitment of young aspen to replace aging overstory aspen is failing and diverse understory plant communities are being lost. We studied vegetation attributes and understory light in nine aspen-conifer stands in the Lake Tahoe Basin in California and Nevada, USA. Within each stand we measured and mapped trees in a one-hectare study area and collected 27–30 hemispherical canopy images on a grid that were used to estimate forest canopy variables and the amount of light reaching the understory. We also measured percent cover of herbaceous vegetation on the same sample grid. After restoration treatments cut smaller conifer trees at six of the nine sites, we repeated canopy images and began monitoring the growth of young aspen adjacent to sample grid points. Less light was reaching the understory beneath areas of forest canopy dominated by true firs. Understory light was enhanced by removal of conifers (pine and fir species). Stand density and species composition of trees surrounding a grid point where each hemispherical image was taken were useful predictors of understory light and forest canopy variables, herbaceous vegetation cover, and the morphology and growth of young aspen. Less herbaceous vegetation was found in the vicinity of true firs and pines, particularly in areas with less light being transmitted to the forest floor. In areas where the overstory was pure aspen, herbaceous vegetation cover remained high across the range of understory light levels measured. Greater conifer removal treatment intensity, in terms of proportion of stand density cut, enhanced crown ratio and growth of young aspen. Height and diameter increment of young aspen was negatively impacted by the presence of true fir trees in the vicinity. If the objectives of forest management include promoting understory vegetation cover or vigorous aspen regeneration, then removing conifers (especially true firs) from aspen-conifer stands appears to be a viable management tool; using such an approach should focus on removing as many conifers as possible within approximately 8–11 m of areas where an enhancement of understory light, herbaceous vegetation, and the growth and vigor of young aspen is desired.

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1. Introduction

Quaking aspen (*Populus tremuloides* Michx.) forest communities in the Sierra Nevada Mountains are undergoing succession to conifers (Jones et al., 2005; Shepperd et al., 2006; McCullough et al., 2013; Berrill et al., 2016). This process impacts aspen vigor and stifles natural regeneration (Pierce and Taylor, 2010;

Krasnow et al., 2012; Berrill and Dagley, 2012, 2014). A century of fire suppression has lengthened the return intervals of fire that can kill shade-tolerant conifers becoming established beneath aspen (Shepperd et al., 2006; Beaty and Taylor, 2008). Conifers eventually overtop even the tallest aspen and constrict their crowns causing lower branches to die (i.e., crown rise) and an associated loss of vigor (Berrill and Dagley, 2012). Within these stands, aspen root suckers (vegetative reproduction) are often abundant (Berrill and Dagley, 2014). However they remain small and are unlikely to replace the aging aspen canopy because of competitive exclusion from conifers (Pierce and Taylor, 2010; Berrill and

Dagley, 2014). Aspen stems are short-lived (typically < 200 years), but with successful vegetative reproduction aspen clones may live for millennia by regenerating continuously in all-aged stands or periodically after stand-replacing disturbances (Ally et al., 2008). Aspen are light-seeded pioneers capable of colonizing newly-disturbed areas (Mock et al., 2008; Krasnow and Stephens, 2015). However, the relatively small aspen stands of the Sierra Nevada are often isolated by dense stands of conifers that have experienced relatively few natural disturbances over the last century due to management activities (e.g., fire suppression) and thus prohibit the expansion of aspen. More intense disturbances such as stand-replacing fire create opportunities for aspen expansion, but can be difficult to implement safely, especially in sensitive areas or near dwellings in the wildland-urban interface.

Over time, different disturbances may have modified aspen stands in the Lake Tahoe Basin, California and Nevada, USA. Disturbances promoting aspen included a history of mixed-severity wildfire of varying return intervals killing young conifers less tolerant of fire that would establish beneath aspen (Beaty and Taylor, 2008). Aspen would also have colonized areas after stand-replacing disturbances (e.g., patches of high-severity fire, insect outbreaks, landslides, etc.). Other disturbances may have had mixed effects on aspen. Sheep grazing in the late 1800s may have led to excessive browsing of regenerating aspen that prevented recruitment of young aspen into the overstory (Rogers et al., 2007). Aspen stands were also disturbed by burning to clear land and stimulate forage production, logging and burning of logging residues, mining, or water diversion practices. These practices probably killed overstory aspen but may have promoted regeneration of new cohorts. Most aspen stands were then left undisturbed during the 1900s era of fire suppression (Shepperd et al., 2006), or only experienced small-scale disturbances that probably did not promote regeneration of aspen. Beavers cut pole-sized aspen near water in some stands. This might promote regeneration, but not if their dams alter hydrology and raise water levels excessively (McColley et al., 2012). Recently we have seen instances of damage to aspen regeneration from ungulate browsing in the Lake Tahoe Basin. However this level of damage is less than damage reported in other parts of the Sierra Nevada (Margolis and Farris, 2014) or other western regions (Endress et al., 2012; Britton et al., 2016). While there has been an increase in severity and size of wildfire disturbance in the 21st century (Miller et al., 2009), the overall extent and frequency of mixed severity fire is lower than what would be expected under natural fire regimes (Perry et al., 2011; Miller et al., 2012). Contemporary forest management efforts continue to focus on fuels reduction treatments with the hope that future wildfires are not as destructive or that prescribed fire may eventually be implemented.

In the Lake Tahoe Basin, aspen are found in small, isolated patches. These stands are relatively rare, covering less than two percent of the landscape. There is interest in preserving these aspen 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 Significant Areas because of their scarcity and the diversity of flora and fauna these habitats support (Manley et al., 2000). Habitat and forage value, and ground cover and soil stabilization are enhanced by a lush, diverse herbaceous vegetation layer found in stands where aspen dominate, but not in aspen stands undergoing succession to conifer (Kuhn et al., 2011). The occasional presence of presettlement fir and pine trees within aspen stands around Lake Tahoe is evidence that aspen and conifers have coexisted for centuries. Shinneman et al. (2013) describe situations where aspen persist in the absence of fire, but suggest that montane aspen-conifer mixtures are fire dependent. Therefore the 1900s era of fire suppression likely impacted aspen around Lake Tahoe by allowing shade-tolerant conifers to become established at high densities in many of the Lake Tahoe Basin aspen stands. These conifers, the majority of which are true firs, are forming a near continuous canopy layer beneath mature aspen (Shepperd et al., 2006). In some instances, the young conifers have grown to share or overtop the mature aspen canopy layer. The conifers tolerate higher stand densities than aspen, causing aspen to experience competition-induced mortality (Berrill and Dagley, 2014). Our previous simulations of stand development under such conditions indicated that complete succession to conifer could occur in 120 years (Berrill et al., 2016). Aspen may be lost sooner if the stresses of climate change and competition for limited soil moisture and growing space lead to health problems or sudden decline (Worrall et al., 2008; Rehfeldt et al., 2009). The U.S. Forest Service Lake Tahoe Basin Management Unit has defined 'desired conditions' for aspen stands, including that aspen comprise >75% of the overstory with conifers comprising <25% of the overstory. Additional desired conditions are that aspen stands are multi-layered with sufficient light to support abundant understory vegetation and aspen regeneration (USDA Forest Service, 2016). Conifer removal will be needed to restore these desired conditions (Berrill et al., 2016).

Conifers are being removed from aspen 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 intensities vary (e.g., complete conifer removal, partial conifer removal). Managers restoring aspen in the Lake Tahoe Basin are often unable to conduct intensive conifer removal treatments because of the limited conditions under which mechanical equipment (that removes large conifers) is permitted in aspen stands. Where hand equipment (e.g., chainsaw) is used to remove conifers, cut trees often cannot be removed from the stand which increases hazardous fuels on the forest floor and may affect aspen regeneration. Down wood decays relatively slowly in the dry Mediterranean climate and can lead to high-severity fire in riparian forests (Van de Water and North, 2011). Performing more frequent, less intensive restoration treatments such as partial conifer removal followed by piling and pile burning of cut wood alleviates some of these problems. However, burning is often a challenge to complete due to safety and burn weather restrictions. In the Lake Tahoe Basin, from 1998 to 2010 there was an average of 87 days per year, between 1 and 12 days per month, where air resources and weather aligned to allow for burning (USDA Forest Service, 2015).

Little is known about understory vegetation responses and growth of young aspen after conifer removal treatments, and if cutting alone can act as a surrogate for natural disturbances in aspen-conifer stands. We sought to understand how herbaceous vegetation and the development of young aspen in the understory of aspen-conifer stands might be influenced by stand density, understory light, canopy cover, tree species composition, and conifer removal treatments. Our objectives were to: (1) identify relationships among stand density, canopy cover, understory light, and herbaceous vegetation cover, and (2) identify factors influencing the growth of young aspen after different intensities of conifer removal. Specifically, we hypothesized that tree species composition and stand density estimates were useful predictors of understory light and forest canopy variables (canopy cover, and leaf area index), and that these variables were useful predictors of herbaceous vegetation cover and growth of young aspen.

2. Methods

2.1. Study area

The Lake Tahoe Basin covers over 134,000 ha in the Sierra Nevada Mountains of California and Nevada, USA. The basin has

63 tributaries delivering water to the lake. The majority of 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 present but rare (NRCS, 2007). A Mediterranean continental climate brings cold winters, and summers with cool nights and warm days. Precipitation generally increases with elevation and from east to west, and varies between years and seasons; most comes as snow or rain during winter months. Occasional summer thunderstorms bring short periods of rain (http://www.wrcc.dri.edu). Mixed aspen-conifer stands are scattered around the Lake Tahoe Basin. The average stand area is currently less than 2 ha, although a few stands are much larger. They are typically located alongside creeks (or other water sources such as seeps and springs) in deeper soils with more soil moisture than most of the Lake Tahoe Basin which is dominated by conifer forests (Shepperd et al., 2006).

2.2. Field data collection

From 2009 to 2015 we collected aspen and conifer tree size data in nine aspen-conifer stands on the east, west, and south shores of Lake Tahoe between 1900 and 2260 m elevation (Fig. 1; Berrill and Dagley, 2012). In 2009 and 2010 we established a 1-ha study area in each of the nine stands where we recorded the diameter-at-breast height (dbh) and mapped the location of all aspen trees ≥ 10 cm dbh and all conifer trees ≥ 20 cm dbh. Tree species present were aspen, two pine species: lodgepole and Jeffrey pine (*Pinus contorta* Douglas ex Loudon var. murrayana (Balf.) Engelm.; *P. jeffreyi* Grev. & Balf.), and two true firs: white and red fir (*Abies concolor* (Gord. & Glend.) Lindl. ex Hildebr.; *A. magnifica* A. Murr.). High spatial variability in species composition and stand density throughout these large study areas meant that trees and understory vegetation could experience a range of growing conditions within a single study area. In an attempt to study and describe this range of conditions, we established a systematic grid of sample points throughout each 1-ha study area. Sample grid points were located 10 m apart along transect lines spaced 25 m apart, for a total of 27–30 points per study area. Square 1-ha study areas accommodated three long transects and rectangular 1-ha study areas had five or seven shorter transects. Sampling at each grid point included: tallies of aspen and conifer trees < 10 cm dbh and conifers 10–20 cm dbh in 0.004 ha plots, ocular assessment of percent understory vegetation cover in 1 m² quadrats, and hemispherical photography of forest canopy (180° camera lens facing upward, 1.37 m above ground).

After collecting pre-treatment measurements, a varying number and size of conifers were cut from six of the nine 1-ha study areas. Each of these sites had a different size limit for conifers that were cut (i.e., upper limits ranged from approximately 20 cm to 50 cm dbh), according to land manager's prescriptions, between 2009 and 2011. The site-specific prescriptions were each designed to maximize removal of conifers (smallest first) without creating a fire hazard by generating excessive down wood or exposing residual aspen to undue risk of windthrow or breakage. After this treatment we repeated hemispherical images at each grid point, and began repeatedly measuring a subset of young aspen in the 0.004 ha plot at these locations as follows: At the end of the growing season, three young aspen (<10 cm dbh) closest to the grid sample point (<2 m distance) were tagged and measured for total height, live crown base height, and dbh if taller than 1.37 m breast height. If the tip was within reach, or the stem flexible enough to bend over, we measured length of the current seasons shoot extension. We repeated these measurements at the end of each growing season for four consecutive years, and a fifth year at one site where we suspected insect damage in 2012 had introduced unexpected variability in growth. We calculated annual growth increment as the difference between consecutive measurements of height and dbh.

2.3. Analysis

We used tree-size and mapping data to describe characteristics (i.e., species composition and stand density) of 'patches' of forest within the vicinity of each grid sample point within each 1-ha study area, as follows: We created a tree location map for each 1-ha study area by converting tree location data from distance and azimuth (as collected in the field) to an easting (x) and northing (y) for each tree. We used ArcGIS to query each tree location map and derive stand density and species composition in the vicinity of each grid sample point. This query was achieved by creating a buffer of 7.98 m radius around each grid sample point which gave a 0.02 ha circular plot area. We then clipped tree data within each buffer to extract tree data for a series of 0.02 ha circular plots throughout each study area. Tree data from each 0.02 ha plot were summarized, giving basal area (BA) per hectare and stand density index (SDI) for the aspen, pine, and true fir stand components. SDI was calculated by summing individual tree SDI because the dbh data were not normally distributed: $SDI = \sum(0.04 dbh_i)^a$ where dbh_i = dbh in cm of the ith tree in the plot, and $a = 1.605$ (Shaw, 2000). Species composition in each plot was calculated as the proportion of each of aspen, pine, and fir that comprised stand BA. To test for the influence of plot size and shape, the process was repeated for larger (0.04 ha) plots at each grid point, and for a 0.02 ha semi-circle (half of 0.04 ha plot) on the south side of each grid point. We analyzed hemispherical images of the canopy taken at each grid sample point using Gap Light Analyzer (GLA). This produced estimates for two understory light variables (percent above canopy light and total light transmitted to the understory for the May 28 – Oct 2 growing season) and two forest canopy variables (four-ring leaf area index (LAI) for zenith angle 0–60° and percent canopy openness) at each grid point.

We used regression analysis to study relationships among response variables (i.e., understory light and forest canopy variables, herbaceous vegetation cover, young aspen growth and morphology variables) and candidate explanatory variables (i.e., stand density and species composition, understory light and canopy variables, tree-size variables, conifer removal treatment variables). We tested time since conifer removal, and treatment intensity (in terms of proportional change in SDI or BA from cutting) as predictors of young aspen growth, stem taper, and crown ratio. Time since cutting (i.e., 0–5 years) was the number of growing seasons between the time of treatment and the beginning of the increment period (for growth analyses) or time of measurement (for taper and crown ratio analyses). Treatment intensity was the proportional change in BA or SDI from cutting in the 0.02 ha or 0.04 ha plot surrounding the grid sample point adjacent to each young aspen measured.

Models were fitted using PROC GLIMMIX in SAS (SAS Institute, 2011). The nesting of samples within different 1-ha study areas was accounted for by specifying 'site' (study area) and 'subplot' (grid sample point) as random effects in generalized linear mixed-effects models. Temporal autocorrelation of repeated measures of tree size and growth increment was accounted for by specifying the following as random effects: tree tag number, and either calendar year or number of years since conifer removal treatment. Selection of variables for inclusion in the final model was based on Akaike's Information Criterion (AIC; Burnham and Anderson, 2002). To describe model goodness-of-fit, we calculated the average model prediction error in terms of root mean square error (RMSE; the square root of the mean of squared errors) in absolute and percent terms where the absolute prediction error for each observation (i.e., [predicted – actual]) was also converted to per-
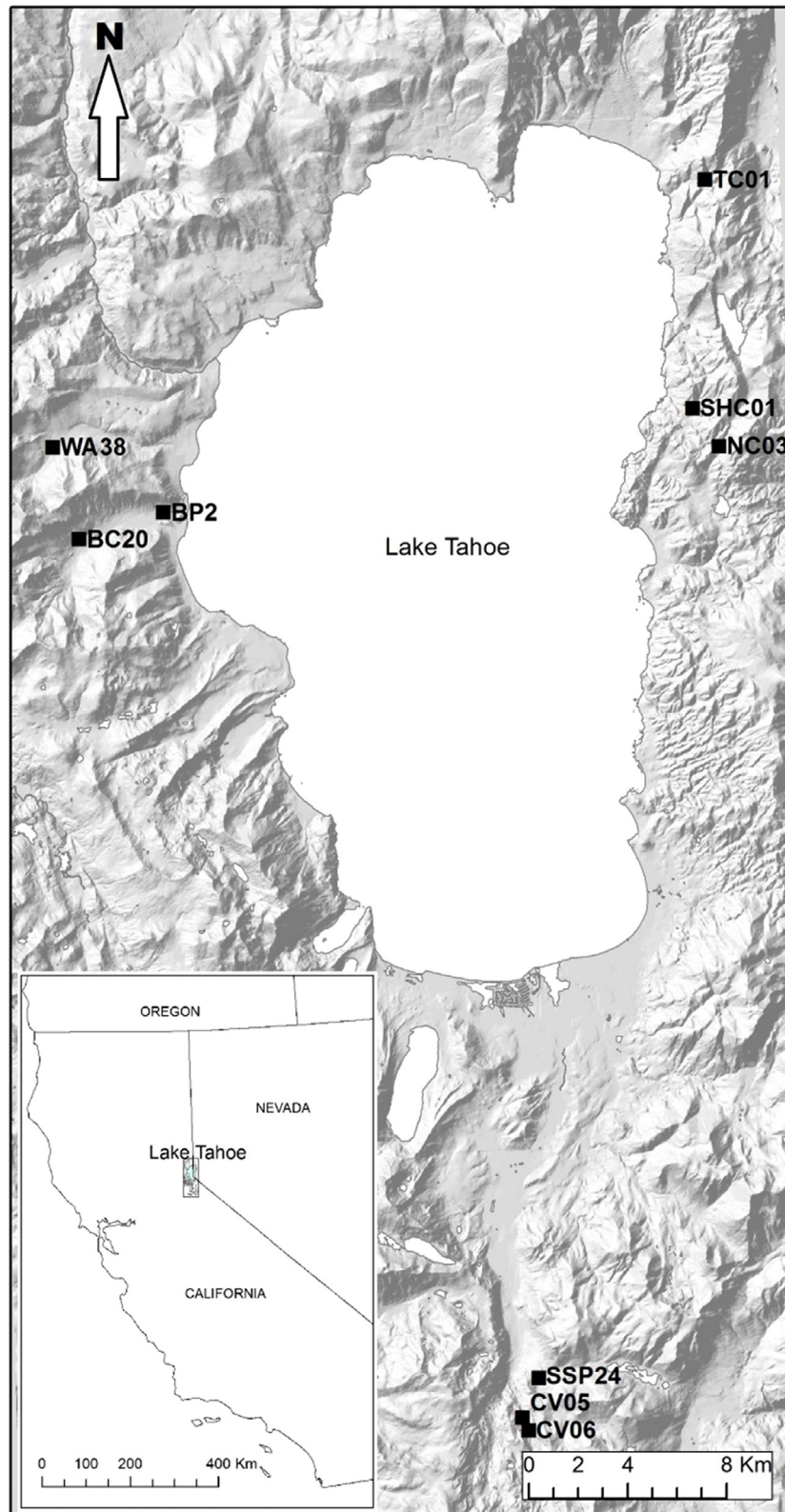
Fig. 1. Location of nine aspen-conifer study areas in the Lake Tahoe Basin, California and Nevada, USA. The six restored sites were Blackwood Creek (BC20) and Ward Creek (WA38) on the west shore, Secret Harbor Creek (SHC01) and North Canyon (NC03) on the east shore, and two sites at Christmas Valley (CV05 and CV06) on the south shore. Untreated sites were Barker Pass Road (BP2), Tunnel Creek (TC01), and Cookhouse Meadow (SSP24).

cent error (i.e., [(predicted − actual)/predicted] × 100). To depict the influence of explanatory variables and their interactions on response variables we used the final models to generate average (expected) values of the response variable across the range of data collected in the nine aspen-conifer mixtures. For each model, we also calculated standardized estimates for the fixed effects because

their respective sizes indicated relative importance of each predictor variable. These are estimates produced when the response and predictor variables were standardized to mean zero and standard deviation one (SAS Institute, 2011).

3. Results

Summary data for each 1-ha study area indicated that aspen represented less than half of stand BA, and that conifer removal treatment intensity differed among stands (Table 1). The systematic grid sampling stand density, species composition, understory light, canopy variables, and herbaceous vegetation generated plot data representative of 215 localized areas within nine aspen-conifer stands in the Lake Tahoe Basin. Summary data for 0.04 ha plots at each grid sample point exhibited high variability indicative of spatial heterogeneity in stand density and species composition within each 1-ha study area. Like tree species composition ranging from pure aspen to pure conifer at different densities throughout the nine aspen-conifer stands, estimates of understory light, canopy variables (LAI and percent openness), and herbaceous vegetation cover for each grid sample point also varied widely (Table 2).

3.1. Understory light

More light was reaching the understory at lower stand densities (SDI) and – to a lesser extent – beneath aspen as opposed to conifer. These relationships were similar for both metrics of understory light: percent of above canopy light (PACL) and total light transmitted to the understory. SDI was 5.8 times more influential than percent aspen BA on understory light which was impacted by trees within 11.28 m (i.e., radius of 0.04 ha plots) in all directions, not just trees south of each grid point where light was sampled. Removal of smaller conifers within six 1-ha study areas enhanced understory light for any given level of SDI and percent aspen BA (Table 3; Supplemental File, Table S1). Given that estimates of SDI were calculated using data for trees >10 cm dbh in each plot, our finding indicated that conifers <10 cm dbh were impacting understory light. For example, expected values (i.e., model predictions) of PACL for SDI = 1000 in an aspen-dominated stand indicated that treatment (removal of smaller conifers) raised understory light from 22% to 31% PACL (i.e., an enhancement of 40%) (Fig. 2).

The heterogeneous spatial pattern of tree locations introduced variability in the relationship among understory light, stand density, and tree species composition (Table 3). It followed that estimates of stand density and composition from larger plots (0.04 ha) were better predictors of understory light, composed of direct and diffuse light reaching the sampling point at different angles, over the entire growing season. For example, in 132 plots within six 1-ha study areas treated by removal of smaller conifers, estimates of SDI and percent aspen BA from 0.04 ha circular plots were superior predictors of PACL ($R^2 = 0.45$) at grid sample points when compared to estimates from 0.02 ha circular plots ($R^2 = 0.34$) and 0.02 ha semi-circles on the southern side of the light sample point ($R^2 = 0.28$). In aspen-dominated stands, PACL was expected to reach only 70% at zero SDI (i.e., no trees in 0.04 ha circle surrounding the point of understory light assessment; Fig. 2A). According to estimates of sky area at our low-lying study areas in this mountainous terrain, we only expect 72–86% of available sunlight to reach the forest floor if trees were completely absent (Table 2). Of this 'above-canopy light', the proportion reaching the understory (i.e., breast height, 1.37 m above ground) was reduced by trees within the vicinity of the sample point, and by what appears in the hemispherical imagery to be a 'wall' of conifer trees encircling each aspen-conifer stand. Solutions for the random site effects indicated that understory light was higher for any stand density and species composition at sites adjacent to openings (e.g., roads or meadows) or sites where aspen had shorter crowns carrying less leaf area (low crown ratios) due to excessive competition (Supplemental File, Table S1 and S2).

3.2. Canopy variables

Modeled estimates of expected LAI and canopy openness depict responses to change in predictor variables (Fig. 2). LAI estimates derived from hemispherical images taken throughout nine study areas were higher in areas of greater stand density and relatively more conifer BA (Table 3). After the smaller conifers were cut, the six treated study areas had less LAI for a given SDI due to the removal of numerous smaller conifers not included in calculation of plot SDI. Standardized estimates for the fixed effects correlating with LAI indicated that SDI was 4.4 times more influential than percent aspen BA.

The canopy was more open in aspen-dominated areas and in treated stands after removal of conifer leaf area obstructing clear view of the sky from our hemispherical lens (Table 3). SDI was 12 times more influential than percent aspen BA. Solutions for the random effects revealed site-specific differences in the relationship between canopy openness and its predictors (Supplemental File, Table S2).

3.3. Herbaceous vegetation cover

Percent herbaceous vegetation cover was highly variable, ranging from 0 to 100%, with an average of 34% (Table 2). The mixed-effects analysis revealed that herbaceous cover was scant in areas of low light beneath conifers and higher in aspen-dominated areas at understory light levels of 10–25 Mol m^2 (Fig. 3 and Table 3; Supplemental File, Table S3).

Table 1
Stand summary data for all trees > 20 cm dbh in nine 1-ha study areas surrounding Lake Tahoe, California and Nevada, USA.

Stand	Pre-treatment data						Treatment data	
	Density (stems ha^{-1})	SDI (metric)	Stand BA (m^2 ha^{-1})	Aspen BA (%)	Fir BA (%)	Pine BA (%)	Year cut	Trees cut (%)
BC20	400	1290	89.8	4.8	86.1	9.1	2011	73.3
BP2	424	819	49.6	43.7	39.5	16.9	No cut	–
CV05	306	778	50.7	48.2	33.3	18.5	2010	18.0
CV06	255	739	52.2	13.5	63.1	23.4	2010	1.2
NC03	261	407	23.9	21.7	53.3	25.0	2010 & 11	15.3
SHC01	300	631	41.9	22.2	48.4	28.5	2010	16.3
SSP24	510	1075	69.0	22.4	66.6	11.0	No cut	–
TC01	397	738	46.1	29.9	62.9	3.6	No cut	–
WA38	325	783	51.6	12.8	58.5	28.8	2009	43.1

Table 2
Summary data for stand density and species composition in 0.04 ha plots, and canopy variables, understory light, and herbaceous vegetation cover at the center of each plot (n = 215) systematically located throughout nine 1-ha study areas.

Variable	Mean	Std. Dev.	Min.	Max.
Basal area (m^2 ha^{-1})	51.61	27.09	3.24	164.00
SDI (metric)	809.17	419.98	64.56	2556.50
AScomp	0.32	0.31	0.00	1.00
FIRcomp	0.49	0.31	0.00	1.00
PINEcomp	0.19	0.25	0.00	1.00
Sky area (%)	82.20	4.07	72.01	85.69
Canopy openness (%)	18.80	7.36	6.73	36.58
Leaf area index (m^2 m^{-2}; 4-ring 0–60°)	1.90	0.62	0.87	3.94
Transmitted light (Mol m^{-2})	14.67	6.54	2.89	31.99
PACL (%)	30.84	13.81	6.24	69.10
Herbaceous vegetation cover (%)	33.85	33.35	0.00	100.00

Note: AScomp/FIRcomp/PINEcomp = species composition in terms of aspen/fir/pine BA as proportion of total stand BA; Sky area = percent of 360° hemisphere not obstructed by landforms; transmitted light is total understory light over 4.2-month growing season (May 28-Oct 2), used to calculate percent above-canopy light (PACL).

Table 3
Coefficients for generalized linear mixed models of understory light, canopy variables, and understory vegetation, fitted to data collected in 215 plots systematically located throughout nine 1-ha study areas (6 sites with conifer removal and 3 sites without).

		Models				
		PACL$^{0.5}$	Transtot$^{0.5}$	Ln(LAI + 1)	PCO$^{0.5}$	PHerbC
Fixed effects	Intercept	7.3791	5.0783	0.8954	5.2644	−80.606
	SDI$^{0.5}$	−0.0971	−0.0668	0.0106	−0.0543	–
	AScomp	0.3965	0.2752	–	0.1004	91.872
	AScomp^2	–	–	−0.0626	–	–
	Transtot$^{0.5}$	–	–	–	–	41.244
	Transtot	–	–	–	–	−3.617
	Transtot$^{0.5}$ × AScomp	–	–	–	–	−13.641
	Conifers cut (Yes/No)	0.8591	0.5977	−0.1999	0.6755	–
RMSE	(actual)	9.43 PACL	4.47 Mol m^{-2}	0.42 m^2 m^{-2} LAI	5.28 PCO	30.2 PHerbC
	(%)	32.8%	32.9%	22.9%	29.4%	30.2%

Note: Response variables were percent above-canopy light (PACL), total light transmitted to the understory over growing season (May 28-Oct 2) (Transtot; Mol m^{-2}), leaf area index (LAI; 4-ring, estimated for zenith angle 0–60°), percent canopy openness (PCO; 0–100%), and percent cover of herbaceous vegetation (PHerbC; 0–100%). Predictor variables were stand density index (SDI) and species composition in 0.04 ha plots (AScomp = percent basal area in aspen, range 0–1), and Transtot. Model fit in terms of RMSE given in absolute and percent terms. Models can be rearranged to make predictions for untransformed response variables, e.g., *PACL* = (7.3791−0.0971*SDI* + 0.3965*AScomp* + 0.8591*Cut*)^2 where *Cut:* Yes = 1, No = 0.

3.4. Growth of young aspen

Data for height and diameter growth of young aspen (<10 cm dbh) in the understory indicated that some aspen were growing rapidly while others scarcely grew after conifer removal treatment at each study area (Table 4; Supplemental File, Table S4). Mixed-effects analyses of annual growth increments revealed strong positive correlations of aspen growth with crown ratio. The proportion of neighbor trees that were true firs (red fir and white fir; in terms of BA) correlated negatively with growth of young aspen which also varied between years at each study area.

Primary growth was assessed in terms of extension of the dominant vertically-oriented leader (apical, tip) over the growing season. This shoot extension was greater among smaller aspen with longer crowns (Table 5). Higher proportions of neighbor trees that were true firs in close proximity (within 0.02 ha plot) negatively impacted the shoot extension of young aspen. Plots with higher LAI also had less aspen shoot extension. Shoot extension was only modestly correlated with treatment intensity. It proceeded at a somewhat steady rate over the first five years after cutting, with better and worse seasons that were not consistent among sites (i.e., interaction of random effects: site and season; Supplemental File, Table S5). Standardized coefficients for the fixed effects indicated that shoot extension correlated most strongly with crown ratio (std. est. = 0.89), followed by tree height (−0.60), LAI (−0.44), fir BA as a proportion of total BA in the 0.02 ha sample plot (−0.44), and was least correlated with proportional change in SDI from cutting (0.25). Modeled estimates of expected shoot extension depict responses to change in predictor variables (Fig. 4).

Estimates of shoot extension over the growing season overestimated how tall each aspen was becoming because young aspen were sustaining repeated instances of top damage and shoot dieback that reduced their total height. Browsing damage on smaller aspen or tip breakage during winter (e.g., from weight of snowpack) was common. Shoot tip death was also common, accompanied by lateral branches turning upward to become new leaders. Therefore, if we summed predictions of height development from our shoot extension model over multiple growing seasons, we would ignore losses in total height resulting from top damage, and over predict height development of young aspen. To solve this problem, we developed a height increment model fit to repeated measures of total height. These height increment data represented 'net annual height growth' resulting from shoot extension minus any losses. The difference between this net height increment and measured shoot extension in the same season averaged −0.05 m (i.e., 5 cm loss in height), with 95% of observations exhibiting losses <0.23 m, and the most extreme five observations suffering losses from 0.40 to 0.80 m height in one year. Logistic mixed-effects regression analysis of the probability of sustaining top damage did not reveal any combination of tree- or stand-level variables that were useful predictors of top damage in young aspen.

Height increment was weakly correlated with post-treatment stand density (−) or PACL (+), but models without these effects had lower AIC. The best height increment model indicated that growth was more rapid among aspen with longer crowns (higher crown ratio) and slower when fir trees represented a greater proportion of stand BA in the immediate vicinity (in 0.02 ha plots). Greater height growth was measured in parts of the stand that
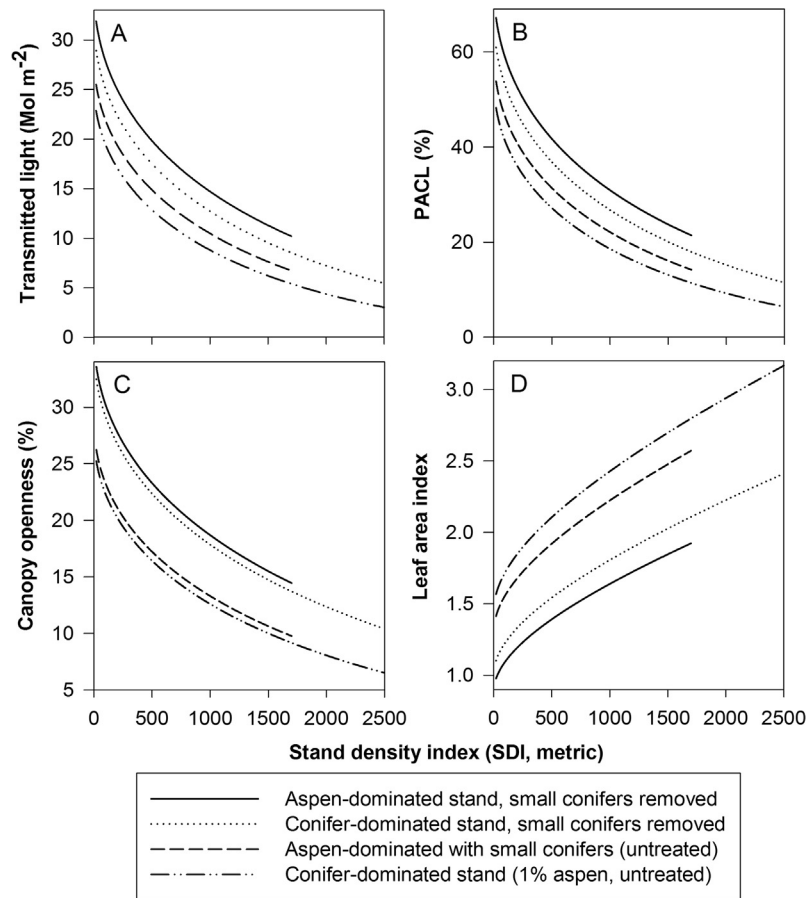
Fig. 2. Relationship between stand density index (SDI), species composition, and parameter derived from hemispherical images: (A) total light transmitted to the understory and (B) percent above canopy light (PACL) over growing season (May 28-Oct 2), (C) percent canopy openness, and (D) leaf area index (LAI) for 0–60° view angle, with and without conifer removal. Predictions show aspen at 99% of BA in aspen-dominated stand and 1% in conifer-dominated stand, across range of observed SDI and species composition in 0.04 ha plots (n = 215). Equations taken from Table 2, rearranged to predict untransformed response variable, e.g., $PACL = (7.3791 - 0.0971SDI + 0.3965AScomp + 0.8591Cut)^2$ where Cut: Yes = 1, No = 0.
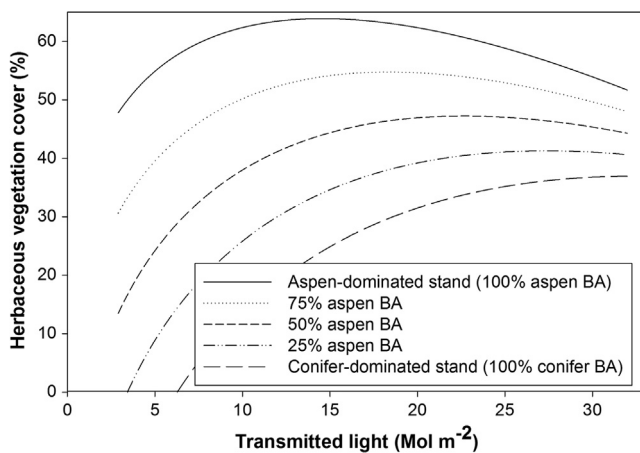

Fig. 3. Relationship between percent cover of herbaceous vegetation and total light transmitted to the understory over growing season (May 28-Oct 2), and tree species composition in terms of percent aspen BA, across range of understory light levels and species composition in 0.02 ha plots (n = 215).

had undergone heavier cutting (Fig. 4 and Table 5). These predictor variables were all strongly correlated with height increment of young aspen. However, height development was highly variable. Unexplained residual variation outsized other components of variation in height increment including an interaction between season of measurement and site (Supplemental File, Table S6).

Young aspen had diameter (dbh) growth ranging from 0.5 to 11.0 mm year^{-1} (Table 4). The mixed-effects analysis indicated that annual dbh increment was rapid among aspen with longer crowns, impacted by the presence of true firs in the vicinity, and slower in areas where a lower proportion of stand density was removed (Fig. 4). Dbh increment peaked two years after cutting (in the third growing season), and was lowest in the fourth year (fifth growing season) since cutting (Table 5). Standardized coefficients for fixed effects indicated that crown ratio (1.80) was more strongly correlated with dbh increment than composition in terms of fir BA (−1.44) and proportion of stand density removed (0.95) in the vicinity (0.04 ha plot). After random error, the most important random effect was an interaction between site and season which indicated that growth rate of all young aspen sampled at a particular site varied together with some sites exhibiting better or worse growth in the same climate year. Conifer removal treatments occurred in different years. After accounting for variations in treatment response over time using the variable years-since-treatment as a fixed effect, there were additional variations between calendar years at specific sites (i.e., aside from conifer removal treatment response) (Supplemental File, Table S7).

3.5. Stem taper and crown ratio of young aspen

We developed basic allometric equations predicting stem taper and crown ratio to support implementation of the young aspen growth models. Aspen stem taper, in terms of height-to-dbh ratio, correlated most strongly with SDI in close proximity (0.02 ha

Table 4
Summary data for young aspen (<10 cm dbh) sampled for growth and morphology variables: shoot extension, total height increment, dbh increment, height-diameter ratio (H:D ratio = (total height − 1.37 m)/(0.001 dbh)), and crown ratio.

Variable	n	Mean	Std. Dev.	Min.	Max.
Shoot extension (m year^{-1})	459	0.31	0.23	0.02	1.20
Height increment (m year^{-1})	330	0.27	0.21	−0.05	1.04
Dbh increment (mm year^{-1})	240	3.68	2.09	0.50	11.00
H:D ratio	274	77.60	16.55	35.46	117.86
Crown ratio	395	0.67	0.15	0.21	0.98

Table 5
Coefficients for generalized linear mixed models of young aspen (<10 cm dbh) growth and morphology over 3–4 consecutive growing seasons (i.e., 4–5 annual measurements) for growth over the 2nd, 3rd, 4th and 5th growing seasons following removal of smaller conifers (Post-cut seasons #2-#5).

		Models				
		$Ln(GI+1)$	$Ln(HTI+1)$	$(DBHI+1)^{0.5}$	$Ln((HT-1.37\ m)+1)$	$Ln(CR/(1-CR))$
Fixed effects	Intercept	−0.3096	−0.7986	0.8700	−0.6681	1.7897
	$(HT+1)^{0.33}$	–	–	–	–	−0.1742
	$Ln(HT+1)$	−0.0706	–	–	–	–
	$Dbh^{0.5}$	–	–	–	0.3357	–
	Dbh	–	–	–	−0.0092	–
	$(CR+1)^{0.5}$	0.6253	0.6121	–	–	–
	CR	–	–	1.0365	–	–
	0.02 ha Fircomp^2	−0.0599	−0.1087	–	–	–
	0.04 ha Fircomp^2	–	–	−0.3498	–	–
	$Ln(SDI+1)$	–	–	–	0.0478	–
	$(LAI+1)^{0.5}$	−0.1695	–	–	–	–
	$Ln(LAI+1)$	–	–	–	–	−2.6486
	$(HT+1)^{0.33} \times Ln(LAI+1)$	–	–	–	–	0.5223
	$(Prop.\ cut+1)^{0.5}$	0.1112	0.2623	–	–	1.0365
	$Ln(Prop.\ cut+1)$	–	–	0.3295	–	–
	Post-cut season #2	–	–	0.5984	–	–
	Post-cut season #3	–	–	0.7448	–	–
	Post-cut season #4	–	–	0.6156	–	–
	Post-cut season #5	–	–	0.0000	–	–
RMSE	(actual)	0.196 m year^{-1}	0.186 m year^{-1}	1.82 mm year^{-1}	0.58 m HT	0.14 CR
	(%)	71.7%	73.9%	56.6%	12.7%	20.0%

Note: Response variables were shoot extension (GI; m year^{-1}), height increment (HTI; m year^{-1}), dbh increment (DBHI; mm year^{-1}), total height (HT), and logit-transformed crown ratio (CR; range 0–1). Predictor variables were height, dbh, CR, species composition as proportion of basal area in fir species within 0.02 ha or 0.04 ha plots (Fircomp, range 0–1), stand density index (SDI) within 0.02 ha plots, leaf area index (LAI) estimated from hemispherical images, and proportional change in SDI from cutting in vicinity (within 0.04 ha plot) during treatment (Prop. cut, range 0–1). Model fit in terms of RMSE given in absolute and percent terms. Models can be rearranged to make predictions for untransformed response variables, e.g., $HTI = e(−0.7986 + 0.6121(CR+1)^{0.5} − 0.1087 Fircomp^2 + 0.2623(Prop.cut+1)^{0.5}) − 1$.

plots). The second best predictor of stem taper was LAI. After heavier cutting, young aspen had slightly more taper (larger dbh for a given height) but this effect was not important. We selected a simpler model without treatment intensity (2 points lower AIC) as the final model (Fig. 5; Table 5; Supplemental File, Table S8). This model predicted aspen height as a function of dbh$^{0.5}$, dbh, and SDI in 0.02 ha plots, and represented a significant improvement in model fit (26 AIC points) over a basic bivariate model without SDI where: $Ln(HT-1.37\ m) = −0.1881 + 0.2455\ dbh^{0.5}$.

Crown ratio of young aspen averaged 0.67 with a narrow interquartile range (0.19) from 0.58 to 0.77. A few extremely low crown ratios suggested that top damage or competition-induced crown rise had left some young aspen with short crowns, and that crown ratio data may reflect past conditions as opposed to the current post-treatment stand and understory light conditions. Therefore we discarded data collected over the two years immediately following cutting, leaving data for three to four consecutive measurements. Crown ratio of young aspen was only weakly correlated (−) with stand density. Crown ratio was correlated with understory light (+), and most strongly correlated with LAI (−) derived from hemispherical images taken at sample points where young aspen were measured. Crown ratio of shorter aspen was more sensitive to LAI than taller aspen. We used an interaction between tree height and LAI to model this effect. Higher crown ratios were also found related to heavier cutting in the vicinity (0.04 ha plot) (Fig. 5 and Table 5). High variability characteristic of crown ratio data

impacted overall model performance in terms of RMSE, and solutions for random effects revealed important site-to-site differences and variability between measurement years (Supplemental File, Table S9).

4. Discussion

4.1. Factors impacting growth and vigor of young aspen

The negative impact of high stand density on understory light and growth of young aspen suggests that aspen at Lake Tahoe are not faring well in the absence of disturbance or management that would otherwise reduce tree crowding. More understory light and herbaceous vegetation was measured beneath aspen as opposed to conifers (pine and fir species). However understory light in terms of PACL or total light transmitted to the understory was less useful than tree species composition (i.e., percent fir) in predicting growth of aspen. This discrepancy suggests that firs may also exert influence below ground. Pierce and Taylor (2010) detected repulsion between aspen saplings and neighboring white fir in northern California. Smith and Smith (2005) found that aspen regeneration was not long-lived and rarely advanced to the sapling stage in the presence of conifer at higher stand densities in Colorado. Conifers may be impacting aspen root development and suckering (Shepperd et al., 2001). Changes in soil chemistry associated
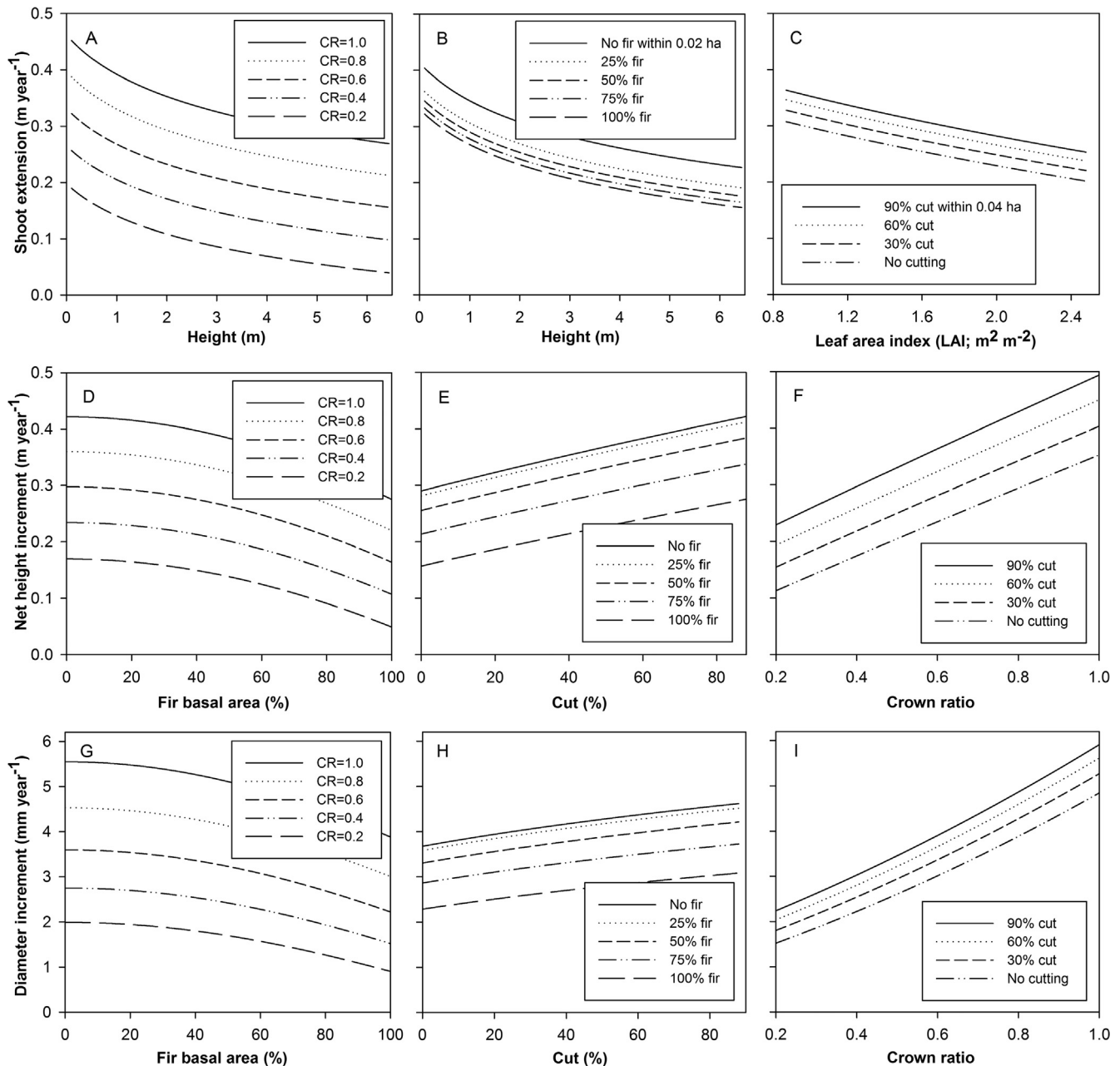
Fig. 4. Young aspen growth: expected annual shoot extension (A,B,C), net height increment (D,E,F), and annual diameter (dbh) increment over second growing season after conifer removal (G,H,I), across range of data for predictor variables: tree height, crown ratio, species composition in terms of true firs as percent of total basal area in the vicinity (0.02 ha), leaf area index, and percent change in stand density index (SDI) from cutting within 0.04 ha area. Unless otherwise stated, predictions based on crown ratio held constant at 0.67, percent fir BA at 50%, and percent change in SDI from cutting at 18% (average values).

with the presence of conifers among aspen might be leading to reduced growth in young aspen (Calder et al., 2011). Unknown is why percent fir BA within the immediate vicinity (within surrounding 0.02 ha) of young aspen was the most useful species composition variable for predicting shoot extension and net height growth, whereas percent fir BA within 0.04 ha was a better predictor of aspen dbh increment. One hypothesis to be tested is that secondary (diameter) growth in aspen proceeds later in the season than primary (shoot) growth, over a time period when soil moisture becomes limited and competition with conifers for this limited resource intensifies over a wider area. Conversely, primary growth, which appears to be determined by competition in the immediate vicinity, could be driven by energy stored over the

preceding growing season and shared via root grafts (Jelinkova et al., 2009, 2012), to be allocated to young aspen with long crowns in openings where the presence of neighboring fir trees cannot be sensed by aspen. An alternate hypothesis is that fir trees establish preferentially on microsites less favorable for aspen growth, where slower aspen growth was measured by coincidence and was not impacted by the fir trees as suggested by results of our regression analysis. Therefore aspen and conifers might coexist in close proximity, consistent with a "fire-initiated semi-stable aspen" type proposed by Shinneman et al. (2013). But after accounting for the influence of stand density and percent fir composition in regressions of aspen growth, the additional positive influence of treatment intensity (Table 5) lends further support to removal of
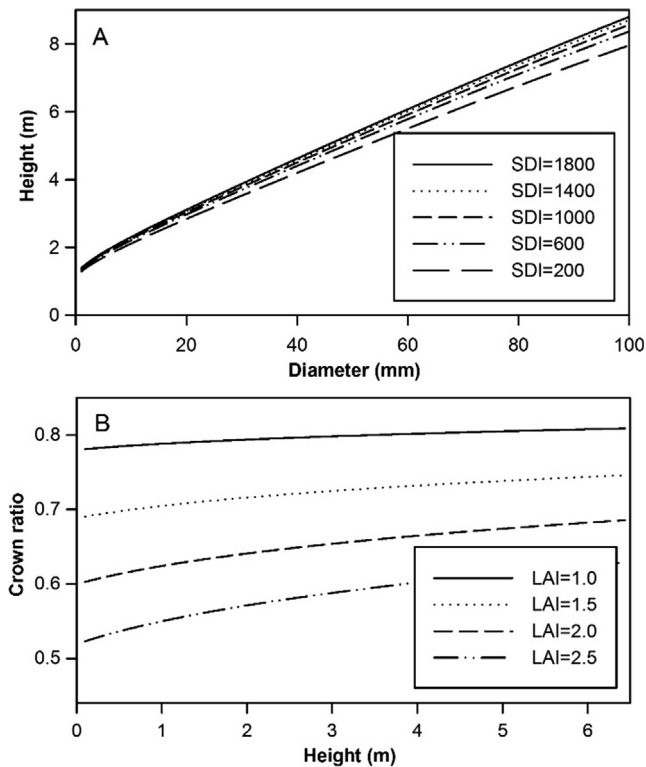
Fig. 5. Allometric equations for young aspen height and crown ratio: (A) stem taper relationship between total height, dbh, and stand density index (SDI) in the surrounding 0.02 ha area, and (B) relationship between crown ratio, tree size (height), and leaf area index (LAI) derived from hemispherical images > 2 years after conifer removal.

most conifers – especially true firs – to curtail succession in crowded aspen-conifer stands. Succession to conifer is a common pathway for many, but not all, aspen-conifer stands (Zier and Baker, 2006; Mittanck et al., 2014). This outcome is undesirable in the Lake Tahoe Basin where aspen communities are rare and ecologically important (Manley et al., 2000).

After removal of smaller conifers, stand LAI was a useful predictor of shoot extension and crown ratio among young aspen around the Lake Tahoe Basin. We developed regression equations that predicted LAI, canopy openness, and understory light from SDI which is easily calculated from basic forest inventory data. The mean prediction error of ±22.9% RMSE indicated that SDI calculated from our plot data was a useful predictor of LAI. The other variables derived from hemispherical photo analysis were not as well predicted by SDI: understory light (RMSE 32.9%), PACL (RMSE 32.8%), or canopy openness (RMSE 29.4%) (Table 3). PACL was a useful predictor of growth in coast redwood (*Sequoia sempervirens* (Lamb. ex D. Don) Endl.) vegetative stump-sprout regeneration after partial cutting (O'Hara and Berrill, 2010). With aspen being more light-demanding than redwood, we expected PACL to also explain variations in growth of young aspen (Perala, 1990). The diameter increment of young aspen correlated with PACL, however a simpler model without PACL was favored. This model indicated that dbh increment of aspen in the understory of treated stands was most strongly correlated with crown ratio – itself a function of stand LAI – and proportion of trees that were true fir in the immediate vicinity (Table 5). Shepperd et al. (2001) and Berrill and Dagley (2012) also recorded decreased growth of aspen in the presence of conifers. Timely removal of conifers, especially true firs, to reduce competition is advisable, so that young aspen might retain longer crowns and grow quickly to replace aging aspen in the overstory (Berrill and Dagley, 2012).

4.2. Sensitivity of young aspen to climate and disturbance

Diameter growth is a low priority for carbon allocation in trees, so we expect it to be more sensitive to changes in conditions and competition than height growth (Oliver and Larson, 1996). However, aspen height development was most sensitive to change and disturbances. The random effect for season × site interactions indicated that height growth of young aspen was sensitive to changes occurring at different sites in different seasons. This could be caused in part by different growing season lengths on the xeric east shore where moisture may become limiting in the year after a reduced winter snowpack versus more mesic sites on the west shore which could benefit from a longer growing season following earlier snowmelt (i.e., 2013, 2014, and 2015). The greatest inter-annual variations in height growth were measured at the only two of our nine study sites not classified as Stream Environment Zones (SEZ; a designation used in the Lake Tahoe Basin to classify wet meadow and riparian areas), possibly demonstrating aspen's sensitivity to biotic and abiotic stressors on more xeric sites (Rehfeldt et al., 2009; Yang et al., 2015; Chen et al., 2017). For example, the lowest rates of shoot extension were measured in 2013 at one of these sites where satin moth (*Leucoma salicis* Linnaeus) caterpillar damage was visible on most aspen throughout the stand in autumn 2012. Slow shoot extension in 2015 at the other dry site may have been in response to, or caused by, the unidentified insect or disease that killed the vertical shoots of numerous aspen root suckers the preceding year, causing forking where two or more laterals turned upwards to replace the dead top. Unknown is whether rapid growth or drought stress may have predisposed these young aspen to health problems. Climate-moisture indices can be useful predictors of aspen health problems (Brandt et al., 2003; Hogg et al., 2005), and wood-boring insects are known to damage aspen and slow their growth (Hogg et al., 2008). We had also measured rapid shoot extension of young aspen in 2012 and 2013 after treatment at this relatively dry site where succession to conifer was far advanced (i.e., aspen represented <5% of basal area of all trees >20 cm dbh; Berrill and Dagley, 2014) and the highest intensity of cutting was undertaken (Supplemental File, Table S5). Witnessing such a positive response to treatment encourages us to further investigate whether restoration will consistently be successful after succession has reached advanced stages. Unlike the other treated sites where only conifers were cut, approximately 40% of aspen trees were cut during this operation, and it was the only site to receive mechanized treatment. Either the cutting of aspen trees or heavy machine traffic disturbing aspen root systems could have incited hormone responses that stimulated rapid growth of aspen root sucker regeneration (DeByle and Winokur, 1985). The importance of the treatment intensity variable in our models of young aspen growth is consistent with findings of Krasnow et al. (2012) and Krasnow and Stephens (2015), and suggested that aspen may respond favorably to removal of greater numbers of fir trees, with less importance – in the short-term – placed on residual stand characteristics such as stand density. Presumably this treatment intensity effect will be short-lived, and stand density will once again become an important determinant of aspen tree growth and vigor (Berrill and Dagley, 2012).

4.3. Application to management

Vigorous young aspen are needed to replace old aspen that have experienced high levels of competition and crown rise in aspen-conifer stands undergoing succession to conifer (Berrill and Dagley, 2012). Managers interested in promoting shoot extension and promoting retention of long live crowns among young aspen would aim to reduce the density of fir trees and reduce overstory

LAI (Table 5), and reduce stand density with the objective of increasing the densities of regenerating aspen (Pierce and Taylor, 2010; Berrill and Dagley, 2014). Crown ratio can serve as an easily-obtainable field-based indicator of young aspen growth and vigor. Fostering aspen regeneration and growth through the removal of conifers will enhance understory light and herbaceous vegetation cover. Heavier cutting may be warranted in and around stands where light does not penetrate from adjacent openings such as roads or meadows. Conifer removal, especially of true firs, in a buffer extending at least 11.28 m (radius of 0.04 ha circle) beyond areas of aspen regeneration should promote height and dbh development of young aspen, and retention of live crown. Maintaining low stand densities through management is advisable if the goal of management is continuous recruitment of young aspen to the overstory. However, once aspen dominance has been restored, higher densities of aspen could be retained to meet other objectives such as providing shade or habitat without the loss of understory vegetation cover expected if conifers dominated (Fig. 3; Kuhn et al., 2011).

We designed our models to predict outcomes of conifer removal prescriptions based on inputs of post-treatment stand density and species composition. These variables can be obtained from basic forest inventory data. Using regression equations presented in Table 5 to predict growth of young aspen, we simulated two alternate conifer removal scenarios. In the hypothetical stand with 50% aspen and 50% fir (no pine) at 1500 SDI, we either: 1) cut smaller conifers to reduce SDI by 20% (leaving 1200 SDI remaining of which 62.5% was aspen), or 2) we cut all conifers to leave a pure aspen stand at 750 SDI. After five years, our height increment model predicted that new aspen root suckers reached 1.6 m height after the lighter cutting and 2 m (i.e., 27% taller) after the heavier cutting. This is consistent with post-treatment data from the nearby Lassen National Forest where new aspen suckers took four years to grow above the browse line (i.e., 1.4 m) (Jones et al., 2005). We also simulated height and dbh growth of young aspen that were present at the time of cutting. After five years, an aspen that was 2 m tall at the time of cutting had grown to 3.38 m height and 24 mm dbh with 0.68 crown ratio after lighter cutting and 3.63 m height (7% taller) and 29 mm dbh (18% larger) with 0.75 crown ratio after heavier cutting. The light and heavy cutting scenarios were predicted to result in growing season understory light of 12.5 versus 17.0 Mol m^{-2} and herbaceous vegetation cover of 47% versus 64%. These simulations demonstrate how treatment intensity affects the understory environment, and the crowns, stem taper, and growth of young aspen. We expect these relationships among influential variables to apply in aspen stands throughout the Sierra Nevada, but that actual growth rates may be greater or less than predicted for the Lake Tahoe Basin because of the inherent variations and sensitivity of aspen tree growth to biotic and abiotic factors in the dry Mediterranean climate of the Sierra Nevada (Jones et al., 2005; Pierce and Taylor, 2010; Berrill and Dagley, 2012; Krasnow et al., 2012).

5. Conclusion

Our regression analysis indicated that understory light was enhanced by removal of smaller conifers, and that more light reached the understory at lower stand densities and in areas with a higher proportion of aspen as opposed to conifer trees. Within these aspen-conifer stands, less herbaceous vegetation was found in the vicinity of conifers, particularly in areas with less light being transmitted to the forest floor. In areas where the overstory was pure aspen, herbaceous vegetation cover percent remained high across the range of understory light levels measured. LAI impacted the shoot extension of young aspen. Modeling the net height

increment of young aspen accounted for occasional loss in height from top damage. Unlike shoot extension which was greater among smaller aspen, height increment remained approximately constant across the range of tree sizes sampled, suggesting that damage to the tree tip was less frequent or severe among taller trees. Height and dbh increment of young aspen were greatest among aspen with long crowns, with proportionally fewer true fir trees in the vicinity, and following heavier conifer removals. Diameter increment peaked over the third growing season after conifers were cut. At lower stand densities, young aspen stems were more tapered (i.e., greater dbh for a given height) and presumably sturdier and more resistant to damage. Crown ratio of young aspen was a useful predictor of growth. Crown ratio was more strongly affected by LAI than stand density or any understory light variables. Crown ratio decreased gradually as the young aspen trees grew taller, and was enhanced by heavier cutting of conifer. We conclude that succession to conifer can be curtailed by reducing stand density through conifer removal. Our results support heavier cutting, focused on true firs, to promote rapid recruitment of young aspen to the overstory within aspen-conifer stands in the Lake Tahoe Basin.

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2017.06.001.

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