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ARTICLE

Twelve-year responses of planted and naturally regenerating conifers to variable-retention harvest in the Pacific Northwest, USA

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Abstract: We studied patterns of conifer regeneration over 12 years as part of a regional-scale experiment in variable-retention harvest in the Pacific Northwest, the DEMO Study. We compared survival and height growth of planted conifers and density and seral composition of natural regeneration among treatments with differing retention levels (15% versus 40%) and patterns (dispersed versus aggregated) replicated across a range of latitudes and forest zones. We also assessed plot-scale relationships of natural regeneration with overstory density and basal area, competing vegetation, and slash accumulations. Early (1- to 2-year) survival of planted seedlings was greater in dispersed treatments (*Pinus monticola* Douglas ex D. Don, *Abies* spp.) or unaffected by retention level or pattern (*Pseudotsuga menziesii* (Mirb.) Franco). Later (5- to 12-year) survival did not differ (all species), but growth was distinctly reduced in dispersed treatments and (or) at higher levels of retention. Density of natural regeneration was 1.5–2.5 times greater in dispersed treatments than in the cleared areas of aggregated treatments. Low-level dispersed retention promoted *Pseudotsuga*, the early-seral dominant, presumably by enhancing seed rain within a relatively high-light environment. Dispersed retention favored late-seral conifers. The ability to manipulate retention pattern and level to influence regeneration density and composition provides managers with flexibility in developing structurally complex and compositionally diverse forests.

Résumé : Nous avons étudié les patrons de régénération de conifères pendant 12 ans dans le cadre de l'étude DEMO, une expérience régionale sur les coupes à rétention variable dans la région du Nord-Ouest de l'Amérique du Nord. Nous avons comparé la survie et la croissance en hauteur de plants de conifères ainsi que la densité et la composition de la régénération naturelle entre des traitements se distinguant par le niveau (15% ou 40%) et le type (dispersée ou en bouquet) de rétention et qui ont été répétés sous une gamme de latitudes et dans une variété de zones forestières. Nous avons aussi établi des relations à l'échelle de la placette entre la régénération naturelle et la densité ainsi que la surface terrière du couvert dominant, la végétation concurrente et l'accumulation de débris de coupe. À court terme (1 à 2 ans), la survie des plants était meilleure dans les traitements à rétention dispersée (pour *Pinus monticola* Douglas ex D.Don et *Abies* spp.) ou n'était pas influencée par le niveau et le type de rétention (pour *Pseudotsuga menziesii* (Mirb.) Franco). À plus long terme (de 5 à 12 ans), la survie de toutes les espèces était la même, mais la croissance a été clairement réduite dans les traitements à rétention dispersée ou à niveau élevé de rétention. La densité de la régénération naturelle était de 1,5 à 2,5 fois plus forte dans les traitements à rétention dispersée que dans les aires coupées des traitements à rétention en bouquet. Les faibles niveaux de rétention dispersée ont favorisé *Pseudotsuga*, une espèce dominante de début de succession, probablement en favorisant la pluie de graines dans un environnement avec une luminosité relativement forte. La rétention dispersée a favorisé les conifères de fin de succession. La capacité à manipuler le type et le niveau de rétention de façon à influencer la densité et la composition de la régénération donne de la flexibilité aux gestionnaires pour aménager des forêts structurellement complexes et dont la composition est différente. [Traduit par la Rédaction]

Introduction

Variable-retention harvest has become integral to ecologically sustainable forest management worldwide (Lindenmayer et al. 2012). It emphasizes retention of forest structures through harvest to mimic the processes and outcomes of natural disturbance and succession (Franklin et al. 1997). An implicit goal of variable retention is to balance the ecological and economic values of managed forests (Lindenmayer et al. 2012). Although variable retention can be implemented in diverse ways (Gustafsson et al. 2012), two elements of forest structure, the level (amount) and spatial distribution of retained trees, are hypothesized to play important roles in post-harvest regeneration (Franklin et al. 1997). Studies that isolate the individual and joint effects of retention level and pattern are rare, however (Rosenvald and Lõhmus 2008).

Partial retention of the overstory is hypothesized to have direct and indirect effects on the survival, growth, density, and composition of the regenerating cohort. Retained trees can provide direct benefits by ameliorating understory microclimate (Vanha-Majamaa and Jalonen 2001), increasing seed rain (Beach and Halpern 2001), or facilitating access to mycorrhizae (Luoma et al. 2006). Conversely, they can inhibit regeneration by reducing light (Mitchell 2001), soil moisture, or nutrients (Boyden et al. 2012). Moreover, these influences can change over time, enhancing seed availability early in succession but reducing survival in the longer term (Temesgen et al. 2006). Pattern of retention can also influence the composition of the regenerating cohort. Dispersed retention is thought to favor shade-tolerant species and the harvested matrix among forest aggregates, shade-intolerant species (Franklin et al 1997).

Partial retention can also shape patterns of regeneration indirectly through effects on post-harvest ground conditions and competing vegetation. For example, variation in cover and depth of logging slash can affect survival of advanced regeneration or post-harvest germination and establishment (Halpern and McKenzie 2001). Retention level and pattern can also influence the growth of herbs and shrubs that compete with regenerating trees (Halpern et al. 2012). Where physical or biotic conditions create barriers to

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