Effects of diversity of tree species and size on forest basal area growth, recruitment, and mortality

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Abstract

The objective of this study was to determine the relationship, or lack thereof, between growth and diversity of tree species and size in conifer stands of western North America. Growth was measured by net basal area growth and its components: survivor growth, recruitment, and mortality. The analysis used inventory data from permanent plots in the Douglas-fir/western hemlock forest type in Oregon and Washington, and in the mixed-conifer forest type in California. The methods consisted of generalized least square regression with spatial autocorrelation, controlling for the effect of other stand characteristics. Other things being equal, in the two forest types under study there was a strong positive relationship between net basal area growth and tree-species diversity. This effect was associated with higher recruitment in stands of higher tree-species diversity. Neither mortality nor growth of survivors was related to tree-species diversity. The relationship between growth and tree-size diversity was less clear. For Douglas-fir/western hemlock, net basal area growth was negatively correlated with tree-size diversity, essentially because recruitment was lower on plots of high tree-size diversity. For mixed conifers, net basal area growth tended also to be lower in plots of high tree-size diversity, but this was mostly because mortality was higher in plots of higher tree-size diversity.
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1. Introduction

Does plant diversity increase ecosystem productivity? This question has attracted wide attention, both for theoretical and managerial reasons. Lately, positive correlations have been observed between vegetation productivity and species diversity in various terrestrial ecosystems, but the relationship may be transient and it varies across species assemblages and spatial scales (Schulze and Mooney, 1993; Huston, 1997; Chapin et al., 2000; Loreau et al., 2003).

Some grassland experiments suggest that diversity effects are neither transient nor explained solely by a few productive species. Tilman, among others, has noted that even the best-chosen monocultures cannot achieve greater productivity than higher-diversity sites (Tilman et al., 1996; Hector et al., 1999; Tilman et al., 2001). However, it remains unclear whether these results hold true at the landscape level, and across ecosystem types (Loreau et al., 2001; Cardinale et al., 2004).

In the case of forest ecosystems, there are still few studies of the relationship between forest productivity and tree diversity, due in part to the complexity and long life cycle of forest ecosystems (Caspersen and Pacala, 2001; Monserud, 2002; Vilà et al., 2003). The traditional view in forestry was that the clearcutting system with artificial regeneration (an even-aged monoculture) maximized volume productivity (e.g., Assmann, 1970; Gulden and Baker, 1988). However, Hasse and Ek (1981) and Haight and Monserud (1990) found that this maxim does not generalize. Using simulation with a widely-used forest management model (viz., Wykoff et al., 1982), Haight and Monserud (1990) compared long-term optimal forest stand productivity between a monoculture of western white pine (*Pinus monticola*) and a multi-age mixed-species management strategy that relied on periodic thinnings and natural regeneration (an uneven-aged shelterwood). The mixed-species stands had much higher species and size diversity, yet the optimal long-term productivity ($m^3 \, ha^{-1} \, year^{-1}$) of the two

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contrasting stands was essentially identical (Haight and Monserud, 1990).

The diversity of a forest stand may not be sufficiently described by tree species diversity alone. Structural diversity, resulting from recruitment of trees of different sizes into multi-layered canopies, should also be taken into account. This characteristic, which can be approximated by the diversity of tree size, affects the amount of light and precipitation received by subordinate trees and understory plants (Anderson et al., 1969), and may thus influence the productivity of forest ecosystems. In addition, silvicultural treatments are often defined by target stand states defined by the distribution of tree by size class (Smith et al., 1997). Thus manipulating tree-size diversity is a practical tool for forest managers who strive for greater biodiversity and/or greater productivity (Varga et al., 2005).

Studies dealing with tree-size diversity include Oren et al. (1987), and Lusk and Ortega (2003). Liang et al. (2005) consider the effects of both tree-species diversity and tree-size diversity on individual tree growth, mortality, and recruitment. However, most previous studies have dealt with tree-species diversity only. Insignificant or negative productivity–diversity relationships (Sterba and Monserud, 1995; Chen and Klinka, 2003; Vilà et al., 2003) are as common as positive ones (Kelty, 1989; Caspersen and Pacala, 2001; Liang et al., 2005). Much still needs to be learned on the effects of species and size diversity on forest growth.

The literature on diversity in ecology is vast (Dennis et al., 1979). Three measures of diversity are prominent. Species richness, a simple count of the number of species, is straightforward but it ignores species frequency. Shannon's (or Shannon–Wiener's) index of diversity was originally a measure of entropy (Boltzmann, 1872), later applied to information theory (Shannon, 1948; Shannon and Weaver, 1949). The Simpson (1949) (or Gini–Simpson) index of ecological diversity had in fact been used earlier to measure economic inequality (Gini, 1912). All three indices are closely related and they can be derived from the same one-parameter family of diversity indices (Patil and Taillie, 1979; Keylock, 2005). Both Shannon's and Simpson's indices have stood the test of time "and are still generally regarded as the premier measures of ecological diversity" (Gorelick, 2006). We chose Shannon's index because it reflects both evenness and richness of species (Magurran, 1988, p. 34), without favoring either dominant or rare species. Simpson's index gives more weight to dominant species. We also found that with our data the explanatory power of Shannon's index was superior to the species count.

In the present study we examined the effects of diversity of tree species and size on the net basal area growth of forest stands. We also investigated diversity effects on the components of net basal area growth, namely, survivor growth, recruitment, and mortality. The data were from forests in the U.S. west coast region, which stretch over a vast area from northern Washington to southern California, and cover several ecoregions (Omernik and Gallant, 1986).

To check the consistency of the diversity effects in different ecosystems, we examined two forest types: the Douglas-fir/ western hemlock type, and the mixed conifer type in California.

The Douglas-fir/western hemlock (*Pseudotsuga menziesii*/*Tsuga heterophylla*) forests are among the most productive in North America. They thrive in the moist temperate rainforest west of the crest of the Cascade Mountains in Oregon and Washington. These forests are mostly in seral stages but there are still areas of old-growth with massive Douglas-fir (*P. menziesii*) and western hemlock (*T. heterophylla*). Although Douglas-fir and western hemlock are most abundant, they coexist with many other tree species in natural stands, in particular *Alnus rubra*, *Thuja plicata*, and *Acer macrophyllum* (Franklin and Dyrness, 1988).

Farther south along the Pacific coast, mixed-conifer forests cover 13% of California's land area. The dominant tree species are *Pinus ponderosa*, *Pinus jeffreyi*, *Pinus lambertiana*, *P. menziesii*, *Abies concolor* and *Libocedrus decurrens* (Barbour and Major, 1977).

2. Data and methods

Data were obtained from 2.5 ha circular forest plots in the PNW-FIA Integrated Database (IDB 2.0, Hiserote and Waddell, 2005). This is the most complete database to date for the Douglas-fir/western hemlock and the mixed-conifer forest types. The plots covered a large area from northern Washington, along the Cascades, the Klamath Mountains and the Sierra Nevada, down to southern California (Fig. 1). The database assembles past inventories from the USFS National Forest System (R5, R6), Bureau of Land Management, and Forest Inventory and Analysis,
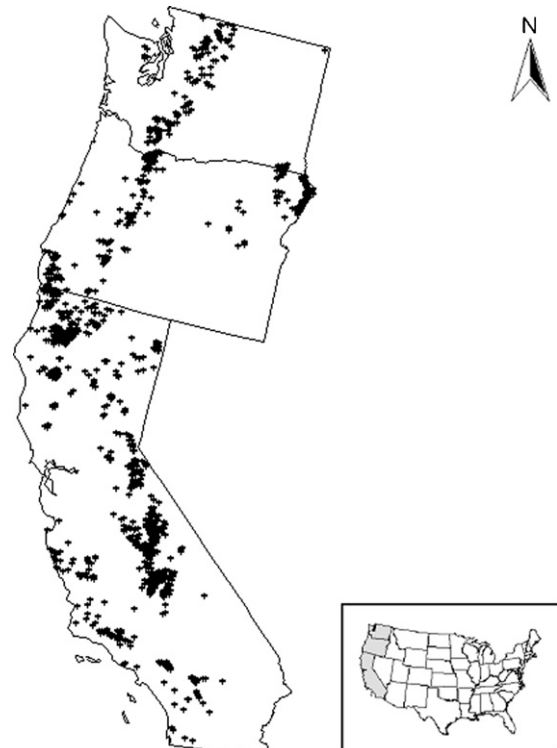

Fig. 1. Geographic distribution of the 1160 FIA plots and location of the study regions in the United States (dark shaded area of the inset at lower right). All the plots were reserved from human interference. In Washington and Oregon (two states to the north), all the plots belonged to Douglas-fir/western hemlock type. In California, all the plots were in mixed conifer type.