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Integration of small-scale canopy dynamics smoothes live-tree structural complexity across development stages in old-growth Oriental beech (*Fagus orientalis* Lipsky) forests at the multi-gap scale

Eric K. Zenner [a,*], Khosro Sagheb-Talebi [b,2], Reza Akhavan [b,3], JeriLynn E. Peck [a,1]

[a] Department of Ecosystem Science and Management, The Pennsylvania State University, Forest Resources Building, University Park, PA 16802, USA
[b] Forest Research Division, Research Institute of Forests and Rangelands (RIFR), P.O. Box: 13185-116, Tehran, Iran

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ABSTRACT

Despite the need to identify managerially operational live-tree structural conditions that distinguish among the stages of the mosaic development cycle, no previous work has quantified the three-dimensional structural heterogeneity of different development stages in Oriental beech (*Fagus orientalis*) forests. We examined live-tree structural heterogeneity at the 1 ha scale in three replicates each of the Initial, Optimal, and Decay development stages in primeval Caspian beech forests in Iran. Typical uneven-aged structures (reverse-*J* shaped diameter distributions) were observed across the three development stages, which did not differ in live-tree density, basal area, the standard deviation of tree diameters, the diameter differentiation index, or the number of large and extra-large trees with diameters greater than 52.5 cm or 72.5 cm, respectively. The Optimal stage was only differentiated from the Decay stage by having more small (16.5–32.5 cm DBH) trees, greater spatial clustering, and lower variation in tree size mixture. In contrast, the Initial stage differed from the Optimal/Decay stages by having higher density of very-small (<16.5 cm DBH) trees, lower density of medium (32.5–52.5 cm DBH) trees, greater inequity in the diameter distribution (CV, Gini coefficient), neighborhood-scale tree sizes, and vertical size differentiation, and greater small scale structural complexity. Although large trees were necessary for high structural complexity, differences in development stages were mostly due to differences in the abundance and spatial pattern of very-small and small trees. As a consequence of small-scale gap dynamics in forests dominated by a long-lived and shade-tolerant species, the widespread intermixture of small and large trees established in the Initial stage persists throughout the Optimal stage and into the Decay stage before the development cycle repeats. Accordingly, rather than oscillations between stages of heterogeneous and homogeneous live-tree abundance (captured by density, basal area, and diameter distributions), the development stages instead reflected the cyclic appearance and disappearance of small canopy gaps (captured by spatial pattern and neighborhood scale size disparities). Due to such subtle differences in stand texture among development stages, the development stage model may not be managerially practical. However, given the constancy of large canopy trees and the subsequent greater relative importance of small trees, our findings indicate that nature-based management in Oriental beech forests may be best focused on utilizing continuous cover approaches (e.g., selection system, Swiss Femelschlag or irregular shelterwood) that recreate temporal cycles in the distribution of abundance among tree size classes rather than maintain constant patterns of total abundance.

1. Introduction

The spatiotemporal dynamics of natural European (*Fagus sylvatica* L.) and Oriental beech (*Fagus orientalis* Lipsky) forests are driven by frequent small-scale gap events interspersed with occasional intermediate and large-scale (wind) disturbances (Korpel, 1995; Sagheb-Talebi and Schütz, 2002; Nagel et al., 2006; Sefidi et al., 2011). The dominance of small-scale dynamics, which is referred to as the forest cycle concept (Watt, 1947), the mosaic-cycle

* Corresponding author. Tel.: +1 814 865 4574; fax: +1 814 865 3725.
E-mail addresses: eric.zenner@psu.edu (E.K. Zenner), saghebtalebi@rifr-ac.ir (K. Sagheb-Talebi), akhavan@rifr-ac.ir (R. Akhavan), peckj@psu.edu (JeriLynn E. Peck).
[1] Tel.: +1 814 865 4508.
[2] Tel.: +98 21 44580282.
[3] Tel.: +98 21 44580280.

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concept (Remmert, 1991; Podlaski, 2008), the forest patch dynamics concept (Shugart, 1984; Paluch, 2007) or the development phase (Leibundgut, 1959, 1993; Korpel, 1995), is typically idealized as a cyclic succession of development phases. Development phases are defined to reflect salient ecological processes (i.e., regeneration, growth and mortality) that shape the vertical (i.e., size distribution) and horizontal (i.e., spatial pattern) mosaic structure of a forest during its life cycle (Leibundgut, 1959, 1993; Korpel, 1995). The phases are a surrogate for several attributes of forest structure and provide a useful temporal context to improve our understanding how natural processes shape structural difference over time (e.g., Huber, 2011; Amiri et al., 2013). It has also been suggested that nature-based management could be used to restore the natural forest mosaic through the silvicultural creation of stands containing structural conditions associated with development phases that are otherwise rare on the managed landscape (e.g., 'fast-forwarding' stands through the optimal stage using thinning or into the Decay stage through artificial gap creation) and maintain restore a degree of old-growth character in managed forests (Sagheb-Talebi and Schütz, 2002; Bauhus et al., 2009).

Although consensus exists regarding the exact definition, or even precise number, of development phases and no standardized set of criteria has been identified to distinguish among development phases (Leibundgut, 1959; Zukrigl et al., 1963; Mayer, 1984a,b; Emborg et al., 2000; Král et al., 2010), it is generally accepted that three main stages of development that encompass several development phases (*sensu* Korpel, 1995), but more broadly convey whether local stand biomass or volume is accumulating (Initial stage), culminating (Optimal stage), or breaking down (Decay stage) (Saniga and Schütz, 2002; Paluch, 2007; Vrška et al., 2009). The assignment of a particular patch of forest to a main development stage is not based on simple threshold values of parameters of stand structure, but considers an array of structural criteria simultaneously, such as tree size structure, canopy openness and presence of gaps, number of canopy strata, amount of dead wood, and occurrence of regeneration (Leibundgut, 1993; Korpel, 1995; Sagheb-Talebi et al., 2003, 2011; Podlaski, 2004; Sefidi and Marvie Mohadjer, 2010).

Despite the somewhat subjective nature of visually integrating multiple conditions in the field, a typical search image for the three stages in old-growth forests has emerged (Leibundgut, 1959; Mayer and Neumann, 1981; Korpel, 1995; Peterken, 1996). The Initial stage is envisioned to exhibit all three canopy layers, with dense regeneration and young trees locked in competition under gaps in the upper canopy, variable yet rising basal area and stand volume, and low overstory mortality with declining volumes of dead wood, yet increasing understory mortality. As the culmination of the processes at work in the Initial stage, the Optimal stage is expected to exhibit more homogenous conditions, with the highest stand volume and decreasing volume growth, and is characterized by decreasing tree densities as regeneration halts following the closure of canopy gaps and sapling densities decline as competition-induced mortality thins suppressed trees. Subsequently, the Decay stage is anticipated to have increasing canopy tree senescence and a growing number and size of persistent canopy gaps that permit the regeneration and recruitment of shade-tolerant tree species. This stage is expected to have decreasing basal area and stand volume and the highest volume of dead wood among the three stages.

Though no forest will contain all of the ideal conditions of each stage and any given stand may contain all stages or different phases of stages (i.e., early, mid and late Optimal phase) if the forest is in steady state (Boncina, 2000; Král et al., 2010), it is nonetheless possible to translate the continuous development process into discrete stages identified at a fixed point in time if the overall tendency of structural surrogates for these processes are seen to lean toward one or the other stage (e.g., Meyer, 1999; Tabaku, 2000). If the structural conditions of development stages are to be useful targets for nature-based silviculture (e.g., Huber, 2011), then at least some of these surrogates must be manipulable live-tree structures and it is widely assumed that the live-tree component that typifies these stages would exhibit distinctive vertical and horizontal structural differences, starting with differences in structural attributes (e.g., stand basal area, tree density, and size distributions), spatial point patterns, and three-dimensional stand structure (Akhavan et al., 2012). The live-tree component is hypothesized to oscillate between typically multi-layered canopies (Decay and Initial stages) separated in time by single-layered (Optimal stage) canopies (Rademacher et al., 2004). A comprehensive assessment of surrogate structures (i.e., forest texture), however, also requires an evaluation of the full vertical and horizontal structural mosaic, taking both magnitude and spatial pattern into consideration. Despite the importance of identifying reliable metrics based on simple field observations at an appropriate spatial scale, no studies to date have quantified the three-dimensional structural heterogeneity of different development stages and few have explored multi-canopy-gap scales in replicated stands. Although historically assessments of development stage have often been applied to relatively small sample plots (Korpel, 1995; Szwagrzyk et al., 1995; Jaworski and Paluch, 2001; Paluch, 2007), recent work has established that an area of 1 ha is sufficient to distinguish well among development stages (Sagheb-Talebi and Schütz, 2002; Eslami and Sagheb-Talebi, 2007; Akhavan et al., 2012) because it is large enough to capture small-scale disturbances resulting in canopy openings between 160 m^2 and 1680 m^2 in size (Sagheb-Talebi et al., 2005), yet small enough to be strongly dominated by one development stage (Korpel, 1995).

Our approach was to examine heterogeneity at the 1 ha scale in three replicates each of the Initial, Optimal, and Decay development stages. Old-growth Caspian beech forests in Iran provide a perfect setting for studying long-term small-scale natural stand dynamics processes, as the system is largely free from human manipulation (Sagheb-Talebi et al., 2005) and small-scale disturbance events that result in the death of 1–6 canopy trees and release advance regeneration of beech trees (Shanavazi et al., 2005; Mousavi et al., 2003; Sagheb-Talebi and Schütz, 2002) maintain a dynamic equilibrium that is characterized by more or less irregular and uneven-sized structures for a long time (Eslami and Sagheb-Talebi, 2007; Fallah, 2000; Sagheb-Talebi et al., 2005; Sefidi et al., 2011).

The specific objective of the current study was to characterize the developmental dynamics of primeval Caspian beech forests by (1) quantifying the texture of old-growth Caspian beech forests in the Initial, Optimal, and Decay stages of the development cycle; (2) determining which live-tree structural metrics can be used to differentiate among these stages; and (3) exploring these textural differences at the fine scale tree neighborhood level.

2. Materials and methods

2.1. Study area

The study was conducted on north-facing aspects of the Elborz Mountain range along the southern Caspian Sea in northern Iran. A remnant of the Tertiary era, the range supports 800 km of forests extending in an east–west direction that are characterized by regionally high diversity with more than 80 woody species (Sagheb-Talebi et al., 2014). Sampling plots were established in three study regions: Guilan in the west (37°28′N, 48°49′E), Kelardasht in the central region (36°33′N, 51°5′E), and Neka to the east