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Assessing environmental factors in red spruce (*Picea rubens* Sarg.) growth in the Great Smoky Mountains National Park, USA: From conceptual model, envirogram, to simulation model

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ABSTRACT

This study provides a method for assessing a multiplicity of environmental factors in red spruce growth in the Great Smoky Mountains National Park (GSMNP) of Southeastern USA. Direct and indirect factors in the annual growth increment are first organized into a schematic input–output envirogram (ARIRS), and this information is then used to construct a simulation model (ARIM). The envirogram represents a structured conceptualization of most environmental factors involved in growth, as developed from relevant literature. This interdisciplinary synthesis distinguishes direct vs. indirect factors in growth and takes account of the systems ecology concept that indirect factors may be as important as or more important than direct ones in regulating growth. The ARIRS envirogram summarizes hierarchically organized, within- and cross-scale, local-to-global interactions, and its construction makes it obvious that growth is influenced by many cross-scale spatiotemporal interactions. More research on genecology is still needed to clarify the role of phenotypic plasticity and adaptive capacity in nutrient cycling, global change, and human disturbance.

1. Introduction

Red spruce (*Picea rubens* Sarg.) is a commercially and ecologically important boreal tree species that for half a century has experienced radial growth decline and high mortality in Eastern North America (e.g., Deusen, 1988; Dumais and Prévost, 2007; McLaughlin et al., 1987; Peart et al., 1992; Webster et al., 2004). Dendrochronological studies in the Southern Appalachians suggest the declines are symptomatic of more broadly based changes in the species (Deusen, 1988; Cook and Zedaker, 1992; Johnson et al., 1992; Webster et al., 2004). Air quality, climate change, forest disturbance, and nutrient cycling have all been implicated as possible causes. Some research correlates declines with air pollution and physiological processes (DeHayes et al., 1999; Dumais and Prévost, 2007; Hawley et al., 2006; Johnson et al., 1992, 1995; Lazarus et al., 2006; LeBlanc et al., 1992; LeBlanc, 1993; Reams and Deusen, 1995; Richardson et al., 2004; Schaberg et al., 2000; Schaberg and Hawley, 2010; Strimbeck et al., 1995; Webster et al., 2004). These studies did not, however, address the many factors involved in different rates of decline in different habitats (Busing, 2004; Deusen, 1988; LeBlanc et al., 1992; McLaughlin et al., 1987; Reams et al., 1993; Schuler et al., 2002; Webster et al., 2004).

Methods to do this are reductionistic and mechanistic and do not treat organized complexity very well. Organized complexity is a ubiquitous feature of the living world. Systems methods that integrate relationships between system elements may be more appropriate for its study (Bertalanffy, 1969; Bertalanffy, 1975). In ecology, Odum (1962) and Patten (McIntosh, 1986) have advocated the use of such systems methods. They consider that living systems are open systems exchanging energy and matter with their environments (Bertalanffy, 1975; Lambers et al., 1998; White et al., 1992). This paper uses a systems approach to account for direct and indirect factors that influence the distribution and abundance of organisms.

In ecosystems, indirect interactions have been postulated to be more important than direct ones (Higashi and Patten, 1989; Patten, 1991, 1997, 1998, in preparation). Indirect ecological interactions do not lend themselves well to descriptive empirical or experimental approaches. Modeling is the only tool that can capture their essence (Patten and Auble, 1980). In modeling complex systems, the first step is to assemble relevant causes into a logical structure representing a conceptual model. An *envirogram* is a conceptual model that enables wide-ranging information about the environ-

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mental relations of organisms to be summarized (Andrewartha and Birch, 1984; James et al., 1997; Niven, 1975). Envirograms were originally used to good advantage in population ecology to explain complex animal systems' interactions with environment (Andrewartha and Birch, 1984; Niven, 1975). In this, the environment of an animal was organized into direct and indirect factors, called *centrum* and *web*, respectively (Andrewartha and Birch, 1984; Niven, 1980).

The original envirogram method can be modified to better reflect environmental system theory. This recognizes two environments of open-system entities—an incoming input environment and an outgoing output environment. The former is a direct and indirect stimulus environment and the latter a direct and indirect response environment. Realistic envirograms have multiple indirect factors regulating direct factors and also other indirect factors in webs. The direct factors comprise the envirogram *centrum*, and indirect factors comprise a *web*. The steps along this web beginning after the centrum will be designated web 1, web 2, . . ., etc. As indirect effects are frequently dominant over direct effects in ecosystems, envirogram webs frequently outweigh corresponding centrums in importance.

For this study the red spruce ecosystem in the Smoky Mountains (GSMNP) was considered an open system. The study provides a conceptual frame for understanding red spruce growth through an interdisciplinary synthesis of factors in envirograms (ARIRS), leading to a simulation model (ARIM) of annual radial growth.

2. Methods and materials

2.1. Study species and area, GSMNP

The distribution of red spruce (*Picea rubens* Sarg.) in the Great Smoky Mountains National Park (GSMNP), located in the southern Appalachian Mountains of Southeastern USA, is shown in Fig. 1. Red spruce is a long-lived (>300 years), shade tolerant, boreal species with a low reproduction rate and low genetic diversity (White and Cogbill, 1992). It is a major tree species in the high elevation coniferous forests of GSMNP (Busing, 2004), where elevations range from approximately 250 m to 2,025 m at Clingman's Dome (Madden et al., 2004; Welch et al., 2002). GSMNP soils are Inceptisols, with large organic matter content at the surface, and textures from silt to sandy loam (Creed et al., 2004; Madden et al., 2004). Climate is cool, temperate rainforest, with mean annual air temperature 8.5 °C and annual mean precipitation 230 cm (Creed et al., 2004; Webster et al., 2004). Red spruce ecosystems in GSMNP have short growing seasons (100–150 days), and are exposed to frequent cloud immersion and strong winds (Johnson et al., 1992).

2.2. Definition of study system

It is assumed that the *A*nnual *R*adial *I*ncrement of *R*ed *S*pruce (ARIRS) growth behaves as an open system. The system boundary is defined by the population instead of an individual tree. Annual variation in ARIRS is therefore the mean variation at the population level. The radial growth of a tree is net biomass accumulation. ARIRS used relative variation in annual radial increment, obtained by dividing each yearly average value by the corresponding long-term mean. ARIRS changes with annual variation of photosynthesis and respiration modulated by environment. If an annual radial increment is higher than the long-term average, this reflects an open system gaining biomass, and vice versa.

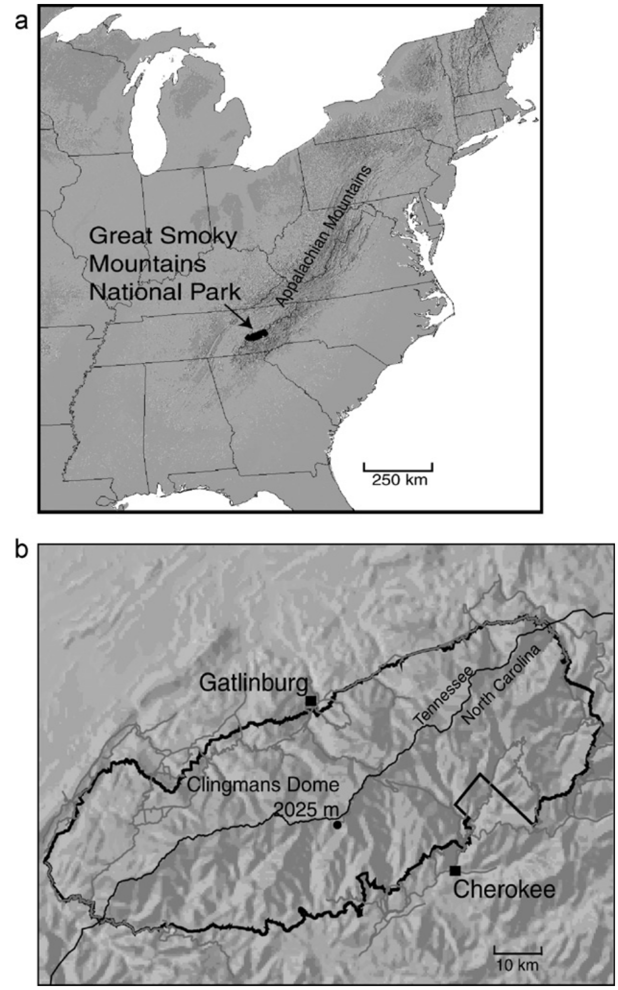

Fig. 1. (a) Shows location of GSMNP in the eastern United States and (b) boundary of GSMNP and elevation of Clingmans Dome. Source of maps is Madden et al. (2004).

2.3. Envirogram development

For the ARIRS envirograms factors that increase radial increment are taken as input environment and factors that decrease this are output environment. Both environments are divided into a centrum, representing direct influence, and multiple web positions, representing sequential levels of indirect influences. In addition, elements are categorized as internal or external. Internal elements include intrinsic biological characteristics (age and size effects), phenotypic plasticity, and density-dependent effects. Growth is influenced by tree age and size (Day et al., 2004; Mencuccini et al., 2007), but the annual radial increment focuses on adults to understand long-term relationships between ARIRS and environment. Age and size effects are therefore ignored in this study. External elements are biotic and abiotic factors such as herbivores, co-dominant species, and climate.

2.4. Data

Eagar and Adams (1992) and papers cited in Table A1 were primary sources used to develop the general characteristics of red spruce habitats and identify potential causes of growth decline and mortality. However, this information did not cover all aspects of the ARIRS envirogram. Basic information was also obtained from general physiology, climatology, plant genetics, and other ecological studies. Lambers et al. (1998), Geiger et al. (2003),