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Influences of life history, environmental gradients, and disturbance on riparian tree regeneration in Western Oregon

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ABSTRACT

In two related field studies: (1) a multiscale riparian forest inventory and (2) a comparative study of natural forest gap and nongap environments, we explored regeneration patterns of native riparian trees in relation to large- and small-scale ecological drivers in four western Oregon watersheds spanning a climatic gradient from dry to wet. Twenty-three tree species were classified by life history traits into five functional groups that differed in shade and drought tolerance; distribution and abundance of tree regeneration were analyzed by group. For most groups, seedling abundance varied substantially across the large scale climate gradient. In particular, drought tolerant species decreased sharply in abundance from the drier to wetter watersheds. Overall seedling frequency and diversity also decreased from the driest to wettest watersheds, while nurse log use increased. Regeneration of most, but not all, species was greater in gaps.

Principal conclusions are that life history information was useful for categorizing species and quite predictive of regeneration behavior overall, yet for many species contextual factors such as climate, forest structure, and adjoining species were also very important. Species appeared to regenerate opportunistically wherever local conditions fell within their environmental tolerances and competitive abilities. Management or restoration of riparian forests, therefore, requires knowledge of site conditions, the life history of the riparian trees present, and in particular an understanding of the species' environmental tolerances, disturbance responses, and competitive abilities relative to one another.

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1. Introduction

Riparian forests are among the most dynamic and complex ecosystems in nature and add disproportionately to landscape diversity where they occur (Naiman et al., 1993; Acker et al., 2003; Sabo et al., 2005). The patterns and dynamics of riparian forest establishment (hereafter regeneration) can be as varied as the geomorphic and biological complexity they contain. Consequently, a complete understanding of riparian forest regeneration requires a quantitative understanding of the tree species present, as well as the functional variation in the riparian environment.

The regeneration environment in any riparian forest encompasses variation caused by environmental gradients and a variety of disturbances (Sakai et al., 1999; Acker et al., 2003). Near stream margins, frequent flooding favors species with adaptations to fluvial disturbance such as rapid juvenile growth, flexible stems, and tolerance of seasonally saturated soils. On higher floodplain terraces, interplant competition is a strong influence on composition. At upland edges of the riparian zone, seasonal drought and fire disturbances are potentially important (Russell and McBride, 2001). Gap-creating disturbances also influence tree regeneration. The presence of unique substrates, such as nurse logs, is likely important for some Pacific Northwest trees (e.g., *Tsuga heterophylla* (Raf.) Sarg., *Picea sitchensis* (Bong) Carr.) (Pabst and Spies, 1999). At larger scales, gradients associated with climate, topography, and geography will interact with local scale factors to affect the regeneration environment on a given stream (Hupp, 1986; Tabacchi et al., 1996; Montgomery, 1999; Pabst and Spies, 1999).

Although local stand chronosequences have provided exemplary models of riparian forest development (Hawk and Zobel, 1974; Van Pelt et al., 2006), such intensive studies have so far been localized. Recent work by Pabst and Spies (1998, 1999) and Sarr and Hibbs (2007a,b) have demonstrated that riparian vegetation composition, diversity, and structure vary substantially across sites in geographically complex regions such as western Oregon. For long-lived tree species, as are many of the conifers occurring in riparian forests of the Pacific Northwest, the distribution of adult trees may not be a strong predictor of conditions for current regeneration. Rather, regeneration is likely favored by an opportunistic

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interaction between seed availability and near-ground regeneration environment.

The many types of variation in the regeneration environment are likely to affect species individualistically based on their ecological tolerances and their relative competitive abilities in different settings. A functional understanding of species response to the regeneration environment, therefore, requires a means to link species life history traits with environmental conditions. Seed size and tolerances of shade, drought, heat, and flooding are attributes that often differentiate establishment of species along environmental or successional gradients (Huston and Smith, 1987). Where several species share life history traits, they likely will show similar functional responses to their environment (e.g., regenerate in similar environments). Models of forest dynamics have often used functional group classifications to simplify the interpretation of plant species responses to environmental variation and disturbance (Grubb, 1977; Grime, 1977; Whitmore, 1989; Veblen, 1992). Veblen (1992), for example, recognized continuous, gapphase, and catastrophic "regeneration modes" to describe species adaptations to regenerate in closed forest conditions, and small and large disturbed areas, respectively, along disturbance gradients. Whitmore's (1989) stringent model suggested only two types of forest trees, pioneers (gap-dependent) and climax (non gapdependent) species. Yet other models have integrated resource gradients as another avenue for species specialization in heterogeneous environments (Grime, 1977). Grime (1977) lists competitive, ruderal, and stress tolerator strategies to describe plant specializations for dominance at resource rich sites, exploitation of disturbance at resource rich sites, and tolerance of resource poor sites, respectively. This paper describes an exploration of the influences of life history, environmental gradients, and gap disturbance on riparian forest regeneration in western Oregon.

In the Pacific Northwest (USA), streamside forests occupy a central role in landscape conservation, containing a disproportionate share of landscape biological diversity and directly influencing the integrity of stream ecosystems, including anadromous fish and amphibian species (Gregory et al., 1991; Bury, 2008). Due to the rugged topography of the region, most riparian forests are embedded in steep, forested landscapes and directly influenced by upslope land uses. They provide an important buffering role between upland land uses and aquatic life and provide corridors for dispersal of riparian-dependent wildlife.

These often long-lived riparian forests contain an impressive diversity of tree species and environments (Minore and Weatherly, 1994; Tabacchi et al., 1996; Pabst and Spies, 1998, 1999; Dykaar and Wigington, 2000; Johnson et al., 2000; Hibbs and Bower, 2001). Riparian forests can take centuries to develop and contain some of the most massive trees in the world (Van Pelt et al., 2006). Given their critical role in regional conservation, there is a compelling need to understand their natural regenerative dynamics in space and time.

In this study, we explored relationships between environmental conditions and regeneration patterns for nearly two dozen native tree species that occur in mountain riparian forests across western Oregon. Our objectives were to: (1) analyze the regeneration behavior of a broad suite of native riparian trees and (2) report how regeneration behavior of native species responds to natural variation in the regeneration environment.

2. Methods

2.1. Identification of functional groups related to riparian tree regeneration

We reviewed literature pertinent to the regeneration requirements for 23 riparian trees found in western Oregon riparian forests to help classify them into functional groups with similar regeneration requirements. Our chief resource was the comprehensive work by Minore (1979) which developed environmental tolerance rankings by reviewing over 300 primary articles of field studies and silvicultural experiments comparing over 40 tree species native to the Pacific Northwest. To this we added insights from other regional field studies (Waring and Major, 1964; Waring, 1969; Zobel et al., 1976; Franklin and Dyrness, 1988; Burns and Honkala, 1990a,b; Minore and Weatherly, 1994; Pabst and Spies, 1999; USDA, 2002; and others). From this information base, we selected seed size and tolerance to shade, drought, heat, and flooding as traits potentially affecting species regeneration patterns. In addition, because heat tolerance is highly relevant to seedling survival (see Gray and Spies, 1997), and the species rankings in Minore (1979) did not include all our species, we included fire tolerance rankings (USDA, 2002) as a crude proxy for heat tolerance in our scoring.

For each of the five life history traits, we used the rankings from Minore (1979) and others, as needed, to score each species from 1 to 10 depending upon its tolerance relative to other species. For example, we scored *Taxus brevifolia* Nutt. and *T. heterophylla* a 10 for greatest shade tolerance, and *Populus trichocarpa* T. & G. 1 for least. These scores provided a set of semi-quantitative values with which to classify species' life history traits (Table 1). The resulting scores, therefore, are professional opinion, chiefly of Minore (1979), supplemented with our own interpretations of more recent literature.

We used Principle Components Analysis (PCA) and Hierarchical Cluster Analysis (HCA) in the multivariate analysis package PC-Ord 4 (McCune and Mefford, 1999) to ordinate the 23 tree species by the five life history traits and to guide the selection of functional groups (Fig. 2). We used the default settings of PCA and the variance/covariance centered option. Because drought, heat, and flood tolerance and seed size were all highly intercorrelated (r > 0.70), whereas shade tolerance was comparatively distinct, we upweighted shade tolerance by doubling the scores prior to conducting HCA. For HCA we used the Euclidean distance measure, with the Wards linkage method.

2.2. Field sampling

In 1999 and 2000, we sampled riparian vegetation in four watersheds chosen to span the steep climate gradient (warm, dry south to cool, wet north) across western Oregon: (1) the Applegate in the eastern Siskiyou Mountains; (2) the South Umpgua in the southern Cascades; (3) the McKenzie in the northern Cascades, and (4) the Alsea in the western Coast Range. The climatic moisture gradient is well expressed in summer (June-September) vapor pressure deficits (an index of atmospheric drought) calculated for the four watersheds from the temperature-based method of Running et al. (1987) (mean (±s.d.)=14.7 (±1.2), 14.0 (±0.9), 11.8 (±0.9), 8.6 (± 1.2) millibars, for the Applegate, South Umpqua, McKenzie, and Alsea watersheds, respectively). The study sites in the McKenzie watershed had fewer growing degree days (base 0°C, data derived from DAYMET model of Thornton et al., 1997) than the other three watersheds (mean (\pm s.d.)=3750 (\pm 263), 3672 (\pm 189), 3140 (± 237) , and 3961 (± 117) growing degree days, for the Applegate, South Umpqua, McKenzie, and Alsea watersheds, respectively). The high number of growing degree days in the Alsea watershed reflects a long growing season; it is the coolest and cloudiest of the watersheds in summer. More detailed climatic, geomorphic, and vegetative information for the sites is provided in Sarr and Hibbs (2007a).

We explored regeneration patterns in riparian forests of the four watersheds in two related field studies: (1) a broad riparian inventory of 64 1-ha riparian forest sites, 16 in each watershed; (2) a gap study using paired comparisons of regeneration in gaps and Download English Version:

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