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Does a Trend in Declining Stem Density of *Lepidium latifolium* Indicate a Phosphorus Limitation? A Case Study

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Lepidium latifolium (perennial pepperweed) is a weedy alien crucifer that has invaded wetlands throughout the western United States. We monitored *L. latifolium* invasion of an *Elytrigia elongata* (tall wheatgrass) community at the Honey Lake Wildlife Refuge in northeastern California. In 1993, a 40-m^2 plot was delineated, at which time only two single plants of *L. latifolium* were present. Beginning in 1994, *L. latifolium* stem density was measured yearly until 2011. From 1994 through 2000, the density of *L. latifolium* increased to greater than 120 stems m^{-2}. At its height of stem density and stature between 1998 and 2000, it appeared that *E. elongata* had been extirpated. From 2001 through 2006, stem density and plant stature of *L. latifolium* declined, but there were still areas of the plot where stem density exceeded 60 stems m^{-2}. From 2007 through 2009, stem density decreased considerably and averaged less than 30 stems m^{-2} and a healthy recovery of *E. elongata* occurred. In the years 2010 and especially 2011, stem density increased, but individual plants were small in stature. Soil bicarbonate-extractable phosphorus data suggest that phosphorus availability may be crucial to the invasiveness of *L. latifolium*. Long-term biogeochemical cycling by *L. latifolium* may reduce soil phosphorus availability in deeper soil horizons and enrich availability in the soil surface, which alters the competitive relationship between *L. latifolium* and *E. elongata*.
Nomenclature: Perennial pepperweed. *Lepidium latifolium* L.; tall wheatgrass, *Elytrigia elongata* Host (Nevski).
Key words: Invasive plants, perennial pepperweed, soil nutrient availability, tall wheatgrass.

The exotic Brassicaceae species *Lepidium latifolium* L. (perennial pepperweed, tall whitetop), a native to southeastern Europe and Asia, has become widely distributed in wetland and riparian habitats, causing concern among wildlife managers, alfalfa growers, and native hay producers (Renz and Blank 2004; Young et al. 1998). Plants on average are 0.4 to 1.0 m (1.3 to 3.3 ft) tall, with a multitude of stems forming dense thickets. Plants are clonal and have extensive underground budding rootstocks that radiate in all directions from newly established plants. In two growing seasons, an established plant can grow into a small colony up to several meters in diameter. After 5 yr, infestations of *L. latifolium* can become near monocultures. Roots of *L. latifolium* are coarse, widely spaced, and often extend greater than 3 m into the soil. Maximal growth potential of *L. latifolium* occurs in a narrow range of soil water potentials, ranging from −20 to −400 kPa (Blank et al. 2002). Its general adaptation to wet soils may be partially due to its sparse root architecture. With widely spaced roots, access to necessary nutrients such as phosphorus is greatly enhanced by high soil water content (Barber 1995). Indeed, greenhouse studies have shown that, as the nutrient-supplying capacity of the soil declines, plants with greater rooting density can outcompete *L. latifolium* (Blank et al. 2002). High levels of phosphorus in tissue coupled with a large biomass indicate that *L. latifolium* bio-cycles substantial levels of phosphorus from deeper in the soil profile, where it is typically more available due to higher water content, to the soil surface (Blank and Young 2002). At some point, depletion of phosphorus deeper in the soil profile and its enrichment near the soil surface may alter the competitive relationships between *L. latifolium* and more fibrous-rooted plants capable of obtaining phosphorus from drier surface soils. As it became clear that *L. latifolium* density was declining, we tested the hypothesis that soil phosphorus availability, particularly in deeper soil horizons, is crucial to the competitive ability of *L. latifolium*.

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Materials and Methods

Research was conducted at the Fleming Unit of the Honey Lake Wildlife Refuge in northeastern California (40°21′188″N, 120°18′148″W) in a 32-ha (80 acres) field

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Management Implications

Over an 18-yr period, we monitored stem density of the exotic invasive crucifer *Lepidium latifolium* in an area at the Honey Lake Wildlife Refuge in northeastern California. Following a near record flood event in January 1997, in some areas density and stature of *L. latifolium* dramatically increased to form a near monoculture and appeared to have extirpated the perennial grass *Elytrigia elongata* planted in 1987 as nesting habitat. From its peak in 1998 to 2000, stem density and stature of *L. latifolium* has declined considerably and allowed *E. elongata* to once again assume dominance in many areas. The decline in stem density is not due to herbicide use or any management decisions. Instead, our evidence suggests that lowered precipitation and declining availability of soil phosphorous has tipped the competitive balance between *L. latifolium* and *E. elongata*. More research is needed to determine the range of soil phosphorus availability over soil depths that might constrain the invasiveness of *L. latifolium*. Our data, however, suggest that expensive control strategies for *L. latifolium* can be targeted to soils with high native levels of phosphorus availability; invasibility in areas with low phosphorus availability may naturally decline over time as phosphorus is bio-cycled by the plant.

that had been planted to *Elytrigia elongata* Host (Nevski) (tall wheatgrass) in 1987 for waterfowl nesting habitat. Parent material is silt-to-clay–textured, saline, lacustrine sediments. The entire field is mapped as the Humboldt series, a fine, smectitic, calcareous, mesic, Fluvaquentic Endoaquolls. The topography is nearly level to very gently undulating and is interrupted by low swales associated with the distributary system of the Susan River. The area is occasionally flooded by spring snowmelt from the Sierra–Cascade mountains to the west via the Susan River. Prior to planting to *E. elongata*, native vegetation included black greasewood [*Sarcobatus vermiculatus* (Hook.) Torrey], inland saltgrass [*Distichlis spicata* (L.) E. Greene], basin wildrye (*Leymus cinereus* Schribner & Merr.), sedges (*Carex* spp.), and rushes (*Juncus* spp.). Invasion by *L. latifolium* began in the mid-1980s and by the early 1990s most stream channels of the Susan River, along with the sides of irrigation control ditches, were completely occupied by *L. latifolium*. In May of 1993, we marked out a 40-m^2 plot in the field to inventory the spread of *L. latifolium*. From 1994 through 2011, we used a 1-m^2 frame and counted stem density of *L. latifolium* every 4 m in a matrix covering the plot. At no time throughout the monitoring period were herbicides applied to the plot. Soil samples were taken in the years 1998 to 2000 and again in 2013. Eight randomly chosen areas were sampled in June 1998, September 1998, April 1999, and May 2000, which compared soils beneath *L. latifolium*–invaded areas with soil beneath noninvaded areas occupied by *E. elongata* (Blank and Young 2002). These collection sites were to the south, east, and north of our stem-density measuring plot. In 2013, soil samples were collected (four replicates) in areas once dominated by *L. latifolium*, but which through time, had returned to robust stands of *E. elongata*. These samples were collected from the western edge of our stem-monitoring plot away from the 1998 to 2000 sampling sites. We also collected soil samples (four replicates) from areas that remained invaded by *L. latifolium* from 1998 through 2013, located southeast of the stem-monitoring plot. For all collection times, soil was sampled at depths of 0 to 15, 15 to 30, 30 to 50, and 50 to 86 cm, (0 to 6, 6 to 12, 12 to 20, and 20 to 34 inches) homogenized, returned to the laboratory, and analyzed. We report on bicarbonate-extractable phosphorus (Olsen and Sommers 1982), a quantitative measure of plant-available phosphorus in alkaline soils.

The bicarbonate-extractable phosphorus data were grouped into four plant dominance categories for statistical analysis: (1) areas sampled between 1998 and 2000 that remained occupied by *E. elongata* as the invasion took place; (2) areas sampled between 1998 and 2000 that had been invaded by *L. latifolium*; (3) areas sampled in 2013 that had been invaded by *L. latifolium*, but then reverted to *E. elongata* dominance; and (4) areas continuously invaded by *L. latifolium* from 1998 through 2013. ANOVA was utilized with the fixed effects of plant dominance categories and soil depth (0 to 15, 15 to 30, 30 to 50, and 50 to 86 cm). Means separation used Tukey's honest significant difference test. Data were log transformed to normalize.

Results

In 1993, before we began our stem density counts, *L. latifolium* was largely confined to an irrigation ditch to the west of our plot. Three small colonies occupied the western side of the plot in 1994 and expanded from those points in 1995 through 1996 (Figure 1). The greatest growth of *L. latifolium* occurred between 1998 and 2000, at which time plant density exceeded 120 stems m^{-2} and individual plants were nearly 2 m tall (Figure 2). The stem density graph also visually demonstrates that in the 40-m^2 plot, some parts never became invaded by *L. latifolium* throughout the study period. This finding is also true in surrounding areas we had visually monitored. In 1998, Blank and Young (2002) quantified nutrient fluxes in live biomass at the end of the growing season in *L. latifolium* stands and nearby noninvaded *E. elongata* stands. Nitrogen, phosphorus, sulfur, calcium, and potassium were measured in *L. latifolium* (N = 3,090 mg m^{-2} (0.010 ounces $feet^{-2}$), P = 632 mg m^{-2}, S = 1,564 mg m^{-2}, Ca = 4,608 mg m^{-2}, K = 3,760 mg m^{-2}) and *E. elongata* (N = 950 mg m^{-2}, P = 181 mg m^{-2}, S = 236 mg m^{-2}, Ca = 476 mg m^{-2}, K = 572 mg m^{-2}). In the years of greatest *L. latifolium* density and height, *E. elongata* appeared to have died, with no new green shoots produced. In 2000, *L. latifolium* density increased somewhat, but plants were not

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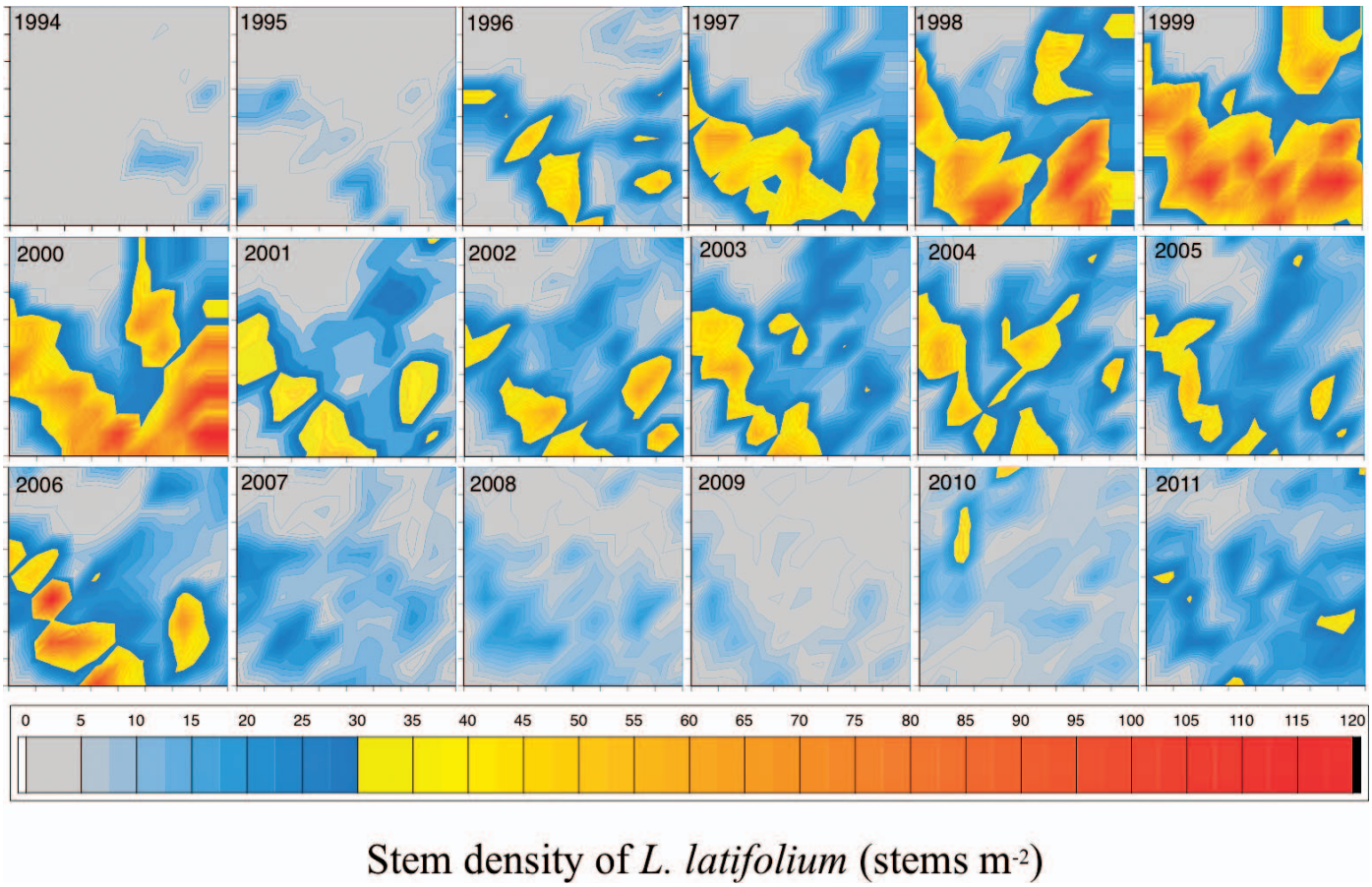


Figure 1. Each consecutive year's panel shows stem density of *Lepidium latifolium* in the same 40-m^2 plot at the Honey Lake Wildlife Refuge, from 1994 through 2011.

as robust as they had previously been. Density of *L. latifolium* declined considerably from 2001 through 2009, and it was rare that an individual plant exceeded 0.5 m in stature. Moreover, during these years there was an increase in the robustness of *E. elongata*. The years 2010 to 2011 saw a slight increase in *L. latifolium* stem density, but not in plant stature. The recovery of *E. elongata* has been remarkable (Figure 2).

The study area averages 22 cm of annual precipitation and during the monitoring period it ranged from 12.5 to 44 cm (Figure 3). During the period of study, the Susan River reached its second highest recorded flood level on January 2, 1997 (NOAA 2014), and the study area was completely underwater for several months. Years with above average snowfall in the catchment of the Susan River included 1995, 1996, 1998, and 2005 (PRISM Climate Group 2004).

Bicarbonate-extractable phosphorus was significantly ($P \leq 0.05$) affected by plant dominance category and soil depth (Figure 4). Pooled over soil depth, soil beneath areas continuously occupied by *L. latifolium* from 1994 through 2013 (Figure 4D) had significantly greater bicarbonate-extractable phosphorus than all other plant dominance categories (Figures 4A–C). Moreover, areas that never became invaded by *L. latifolium* (Figure 4A) had significantly less bicarbonate-extractable phosphorus than all other plant dominance categories. Pooled over plant dominance categories, the surface 15 cm of soil had significantly greater bicarbonate-extractable phosphorus (mean = 1.09 mmol kg^{-1}) than depth increments of 15 to 30 cm (mean = 0.85 mmol kg^{-1}), 30 to 50 cm (mean = 0.52 mmol kg^{-1}) or 50 to 82 cm (mean = 0.27 mmol kg^{-1}).

Discussion

The research plot, within the Honey Lake Wildlife Refuge, resides near the end of the distributary system of the Susan River. The extensive flooding event in 1997 (5.28-m crest at Susanville, CA; NOAA) may have been partially responsible for the large increase in *L. latifolium* stem density. The seed capsule, or silicle, floats in water making seed dispersal very efficient during flooding events (Francis and Warwick 2007). Once a plant becomes

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Figure 2. Top photo taken in June of 1999 at the Honey Lake Wildlife Refuge at the height of *Lepidium latifolium* stem density and biomass, which appeared to have extirpated *Elytrigia elongata* planted as nesting habitat. Contrast the top photo with the bottom photo taken in May of 2013. The refuge had mowed a portion of the field to rehabilitate nesting habitat, but the dry plant material in the unmown portion are seed heads of last year's growth of *E. elongata*. In about 15 years, *Lepidium latifolium* has gone from the dominant plant to near extinction and *E. elongata* has been revitalized.

established, spread is mainly through creeping rootstock (Young et al. 1998). Plant stature and stem density of *L. latifolium* was greatest in the years of 1998 through 2000 following the flood. Since 2000, *L. latifolium* stature and stem density have declined considerably. This decline in stem density may be partially explained by a series of less than normal precipitation years beginning in 1999 (Figure 3). On-site precipitation is but a component of the hydrologic budget; runoff from the Susan River is very important and was quite variable following the 1997 flooding. Above average crests at Susanville since 1997 included 4.23 m in 2005 and 2.81 m in 2004 (NOAA).

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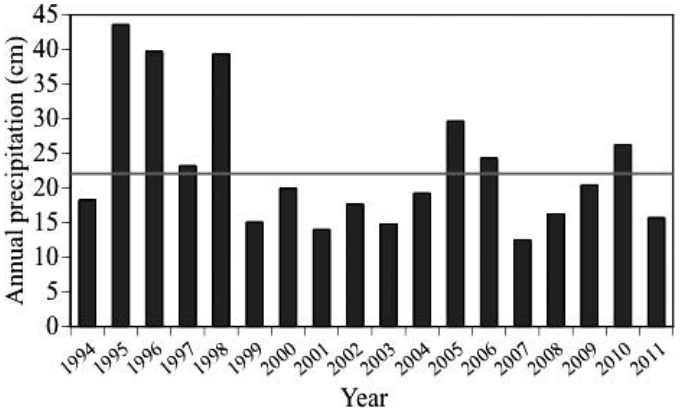


Figure 3. Annual precipitation, for the years 1994 through 2011, at the study site using PRISM Climate Group data. Horizontal line denotes average precipitation.

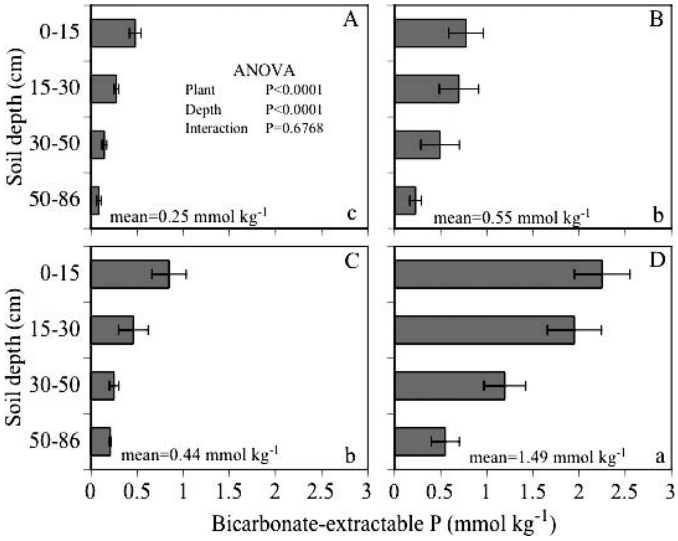


Figure 4. Bicarbonate-extractable phosphorus, as affected by plant dominance categories and soil depth. (A) ANOVA values presented; soil phosphorus availability beneath *Elytrigia elongate*–occupied areas, sampled between 1998 and 2000, which never became invaded by *Lepidium latifolium*. (B) Soil phosphorus availability beneath areas once occupied by *E. elongata*, which became invaded by *L. latifolium* before 1996, and were sampled between 1998 and 2000. (C) Soil phosphorus availability, sampled in 2013, in areas once invaded by *L. latifolium*, which later reverted to *E. elongata* dominance. (D) Soil phosphorus availability, sampled in 2013, beneath areas that have remained invaded by *L. latifolium* from 1994 through 2013 based on site monitoring. Standard error bars presented. Different lowercase letters shown in the lower right portion of the panel denote significant ($P < 0.05$) main effect differences due to plant dominances. In each panel, the means pooled over soil depth are presented.

Stem density increased in 2006, following above normal precipitation in 2005 and 2006, suggesting growth of *L. latifolium* may have been partly water-limited; however, stem density throughout the plot and plant stature never approached that of the years 1998 to 2000 (Figure 1).

We hypothesized that reduced soil phosphorus availability, particularly in deeper soil horizons due to biogeochemical cycling by *L. latifolium*, could be a major factor in declining stem density and stature of *L. latifolium*. The study site is arid and throughout much of the year, surface soils are very dry. A major, but periodic, additional source of water for the Honey Lake Wildlife Refuge is winter and spring runoff from the Sierra–Cascades to the west via the Susan River. These flooding events wet the soil profile throughout and contribute to elevated water tables. The surface soil, however, dries rapidly in this arid environment, resulting in a large gradient of water content with depth. Roots of *L. latifolium* are highly elongated, thick, with minimal branching, an efficient topology for accessing water and nutrient resources deep in the soil profile (Fitter 1991). Sparse root architecture and lack of mycorrhizal associations suggests the plant requires substrates with high nutrient-supplying capacity or high water content, or both, for optimal nutrient uptake of phosphorus (Ho et al. 2005). The two primary mechanisms of nutrient transport to roots are mass flow and diffusion (Barber 1995). Because of strong interactions with the soil matrix, phosphorus movement toward roots occurs dominantly by the process of diffusion, which is greatly affected by soil water content (Bhadoria et al. 1991; Mahtab et al. 1971). At low soil water content, phosphorus moves slowly and less efficiently to plant roots because the pathway is highly tortuous; the ortho-phosphorus moiety migrates through a thin layer of water around soil particles. Tortuosity is much less and diffusion is much greater at high soil water content (Barber 1995). This construct partially explains why *L. latifolium* is most invasive on soils with high water tables. Given its sparse rooting architecture, *L. latifolium* obtains phosphorus deep in the soil where higher water content allows efficient transport to the root. Biogeochemical cycling of phosphorus by *L. latifolium*, with high yearly fluxes, depletes deep soil reserves and enriches the soil surface, and over time may alter competitive interactions with *E. elongata*, which has much higher root densities in surface soil to acquire phosphorus in the drier soil. The very distribution of nutrients throughout a soil profile is largely a function of the elemental stoichiometry of plants (Jobbágy and Jackson 2004) and the literature contains many examples of how invasive species differentially affect biogeochemical cycling, relative to native plants, with lasting perturbations (Ehrenfeld 2003).

The bicarbonate-extractable phosphorus data set (Figure 4) partially supports our hypothesis that soil phosphorus availability may be crucial to the invasibility of *L. latifolium*. Firstly, areas that never became invaded by *L.*

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latifolium (Figure 4A), had significantly lower bicarbonate-extractable phosphorus, pooled over soil depth, than areas either invaded by *L. latifolium* (Figure 4B) or those same areas that converted to *E. elongata* dominance sometime after invasion by *L. latifolium* (Figure 4C). Secondly, areas that remained invaded by *L. latifolium* throughout the study period had the greatest levels of bicarbonate-extractable phosphorus. It is possible that such high levels of available phosphorus, in long-term invaded areas, preceded *L. latifolium* invasion, and suggests that in these areas, much more time must pass before sufficient biocycling can occur to reduce its competitive ability. Our phosphorus data set, however, does not provide conclusive evidence that biogeochemical cycling of phosphorus by *L. latifolium* is depleting deep reserves or has increased its availability in surface soil. In the study area, roots of *L. latifolium* extend over 3 m into the soil; yet in this study, phosphorus availability was quantified only to a depth of 86 cm. Given that deeper soil layers are more likely to have higher water content, it is possible that they could experience greater loss of phosphorus due to plant uptake. In a greenhouse study, after just two growth cycles, *L. latifolium* significantly reduced the bicarbonate-extractable phosphorus pool relative to unplanted controls (Blank and Young 2004). Moreover, soil phosphorus chemistry is exceedingly complex and researchers recognize several plant-available pools, which require specific extractants to quantify (Cross and Schlesinger 1995). Quantification of different pools of soil phosphorus may have been more sensitive to the effects of cycling of phosphorus by *L. latifolium*.

In summary, phosphorus is potentially a limiting nutrient in the invasion ecology of *L. latifolium*. Orthophosphorus, the dominant moiety of phosphorus in aqueous systems, is relatively immobile and diffusion-limited, and is preferentially retained in surface soil layers by strong covalent bonding to clay and other mineral surfaces (McBride 1994). Moreover, in surface layers, lower water content will greatly increase tortuosity and greatly limit phosphorus diffusion to roots. With increasingly aged stands, more phosphorus may be compartmentalized to the soil surface due to biogeochemical cycling with less available in the wetter underlying soil material where *L. latifolium* takes up most of its phosphorus. At some point, phosphorus will become limited in deeper soil horizons to *L. latifolium*, at which time other species adapted to seeking out nutrients more efficiently, such as *E. elongata*, will become competitive again. Given the previous construct, the time frame for *L. latifolium* to reduce deep phosphorus reserves sufficiently to limit its competitive ability will strongly depend on the initial size of phosphorus pools, the magnitude of biogeochemical cycling, and presence of desirable competitive plants.

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