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Influence of environmental factors on germination and emergence of *Pueraria lobata*

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Laboratory and greenhouse studies were conducted to determine the effect of several environmental factors on seed germination and seedling emergence of the invasive weed *Pueraria lobata* (kudzu). Germination occurred over a range of alternating temperatures from 15/6 to 35/25 C. Seed germinated equally well in alternating light/darkness and continuous darkness. At all temperature regimes, percentage germination was much greater for hand-scarified seed (95 to 100%) than for non-scarified seed (7 to 17%), indicating that *P. lobata* seed possesses physical dormancy. Germination exceeded 51% in solutions with pH 5 to 9. Maximum germination (99%) was observed in distilled water at pH 5.4. Germination was greatly reduced in solutions with osmotic potentials below -0.4 MPa (28% at -0.6 MPa, and 13% at -0.9 MPa); no germination was observed at -1.3 MPa. Percentage emergence was greater than 45% at burial depths in soil of 0.5 to 10 cm, with maximal emergence (72 to 85%) at depths of 0.5 to 4 cm. Seed sown on the soil surface had low seedling emergence ($< 13\%$). No seedlings emerged when seed was exposed to flooding for 7 d or more. *Pueraria lobata* seed is capable of germinating in a variety of climatic and edaphic conditions, but flooding may severely limit establishment of stands by seed.

Nomenclature: *Pueraria lobata* (Willd.) Ohwi PUELO, kudzu.

Key words: Light, temperature, scarification, pH, osmotic stress, planting depth, simulated flooding, weed biology, PUELO.

Pueraria lobata is a weedy perennial vine that has invaded many states in the southeastern U.S. Native to Japan, this leguminous vine was introduced into the U.S. in 1876 (O'Brien and Skelton 1946) and was first reported in Orange County, North Carolina, in 1934. By the mid-1970s, it had spread to at least 62 of 100 counties in the state (Patterson 1976). Today, its range extends from the Atlantic coast in the Southeast, north to Maryland and West Virginia, and west to Texas. Initially, *P. lobata* was used as an ornamental and as a forage crop (O'Brien and Skelton 1946). It grows well in low fertility soil, fixes nitrogen, and, once established, rapidly develops a deep, extensive root system. Soon after its introduction in the southeastern U.S., it was used to improve soil fertility and reduce soil erosion (O'Brien and Skelton 1946). Unfortunately, *P. lobata* is extremely difficult to control or eradicate. Most control measures, including mowing, burning, and herbicides, have had limited success because of the ability of its large root system to produce new shoots following these treatments (Tanner et al. 1979). In 1970, *P. lobata* was listed as a common weed in the South (Boyd Edwards 1982). Today, it grows prolifically along roadsides and ditchbanks throughout much of the southeastern U.S. and threatens to competitively replace native vegetation (Tanner et al. 1979).

Although *P. lobata* has received considerable attention for its uses as an agricultural resource (e.g., for fiber use in textiles and as a source of starch for yeast and ethanol fermentation), most of this research has focused on the vegetative phase of the species' life cycle (Tanner et al. 1979). Little is known about the plant's breeding system, when (age) plants begin to produce flowers, or how many seasons they flower. Furthermore, the species is believed to spread primarily by

vegetative propagation, even though no studies have attempted to quantify annual seed production, seed dispersal, and the number of seed in the soil seedbank. Previous reports have noted that *P. lobata* seed has a hard seedcoat (i.e., impermeable to water), which, unless scarified, prevents germination (O'Brien and Skelton 1946; Tsugawa et al. 1979). In a brief note, Tabor (1949) reported seed that was permeable to water germinated and established best if soil moisture remained adequate, compared with dry conditions. He also suggested shallow planting was optimal for emergence but presented no data to support this claim. To date, no detailed study has specifically investigated the germination biology of this troublesome invasive weed.

The purpose of this research was to determine the effects of temperature, light, scarification, pH, and osmotic stress on *P. lobata* seed germination. Also, the effect of simulated flooding and depth of burial in soil on seedling emergence was assessed. Understanding how its seed responds to climatic and soil conditions may help to predict how *P. lobata* spreads to new areas and why it successfully has invaded such a large area of the southeastern U.S.

Materials and Methods

On January 30 and 31, 1999, *P. lobata* seed was collected from a site in Raleigh, NC. Seed was separated from fruits by hand and stored at room temperature (22 to 25 C) for 2 wk prior to use in germination and emergence experiments. Seed with visible indication of pathogen or insect damage was removed and not used in the experiments. Unless stated otherwise, individual treatments for all laboratory germination experiments consisted of three replications of

50 seeds placed on two sheets of filter paper¹ in 9-cm petri dishes. The filter paper was moistened initially with 4 ml of distilled water or test solution. If necessary, 1 to 5 ml of the appropriate solution was added to maintain adequate moisture. All dishes were placed in polyurethane bags² to slow desiccation. Germination studies were conducted in temperature- and light-controlled growth chambers. Dishes were arranged in a completely randomized design within each chamber. Alternating day/night temperatures were maintained for 12 h each. A 14-h daily photoperiod was maintained in each chamber, with the light period extending from 1 h before to 1 h after exposure to the daily high temperature. Fluorescent lamps produced a photosynthetic photon flux of 150 $\mu\text{mol m}^{-2} \text{s}^{-1}$. Dishes assigned to dark treatments were wrapped in two layers of aluminum foil and remained unopened until the final day of the experiment. Germination of seed exposed to light was monitored daily for a period of 21 d (no further germination was observed at either 28 or 35 d after the start of any experiment). A seed was considered germinated when the radicle protruded 1 mm from the seedcoat.

Effect of Temperature, Light, and Scarification

Seed was scarified manually with a scalpel by cutting a small hole in the seedcoat over the cotyledons. Scarified and nonscarified seed was placed in alternating light/darkness (as described above) or continuous darkness at 15/6, 20/10, 25/15, 30/20, and 35/25 C alternating temperature regimes. These temperature regimes were chosen to simulate the mean daily maximum and minimum temperatures for the months of *P. lobata's* growing season in central North Carolina.

Effect of pH

Buffered solutions with pH levels of 4, 5, and 6 were prepared using 0.1 M potassium hydrogen phthalate, while solutions with pH 7, 8, and 9 were prepared with 25 mM borax (Shaw et al. 1987). Buffer solutions were adjusted to the appropriate pH using 0.5 M NaOH or 1 N HCl. Scarified seed was placed in solution at 30/20 C (14 h light/10 h dark). Distilled water was used as a control.

Effect of Osmotic Stress

Solutions with osmotic potentials of 0, -0.3, -0.4, -0.6, -0.9, and -1.3 mPa were prepared by dissolving 0, 154, 191, 230, 297, or 350 g of polyethylene glycol³ (PEG) in 1 L of deionized water (Shaw et al. 1991). Scarified seed was placed in aqueous solutions of PEG at 30/20 C (14 h light/10 h dark).

Effect of Planting Depth

Twenty scarified seeds were planted in Norfolk loamy sand soil (85% sand, 9% silt, and 6% clay) in plastic cups (9.5-cm diam by 11-cm depth) at depths of 0, 0.5, 1, 2, 4, 6, or 10 cm below the soil surface. Each treatment was replicated four times. Cups were arranged in a randomized block design on greenhouse benches. All cups were surface irrigated daily to field capacity. Seedling emergence was recorded daily for 21 d. Greenhouse temperatures during this

and the following experiment were 33 ± 2 C during the day and 21 ± 2 C at night.

Effect of Simulated Flooding

Twenty scarified seeds were planted in Norfolk sandy loam soil in plastic cups at a depth of 1 cm. To simulate flooding, water was maintained approximately 2 cm above the soil surface for 0, 4, 7, 14, or 21 d after planting. After exposure to a given period of flooding, surface water was drained, and cups were watered as needed for the duration of the experiment to maintain adequate moisture. Cups were arranged in a randomized block design on greenhouse benches. Seedling emergence was recorded daily for 35 d.

Statistical Analysis

Two trials were conducted for all experiments. The data collected consisted of cumulative percentage germination or emergence. Prior to analysis, final percentage germination values were arcsine square-root transformed. The GLM procedure of SYSTAT (1997) was used to assess significant differences among trials and treatments. Since ANOVA revealed no significant trial by treatment interaction ($P > 0.05$), data for each trial were pooled for subsequent analyses. Factorial ANOVA was used to assess the effects of temperature, light, and scarification on percentage germination. One-way ANOVA was used to assess the effect of planting depth on percentage emergence. Significant differences among treatments were identified using Fisher's LSD test ($P < 0.05$). Nonlinear regression analysis was used to determine the effect of pH and osmotic stress on percentage germination.

Results and Discussion

Effect of Temperature, Light, and Scarification

Scarified *P. lobata* seed germinated $\geq 95\%$ across all temperature regimes, whereas germination for nonscarified seed was $\leq 17\%$. Such a broad temperature response would allow germination of *P. lobata* seed to occur from early spring to midautumn in North Carolina and the southeastern U.S. Several weed species have been shown to germinate over a wide range of temperatures (Akanda et al. 1996; Baird and Dickens 1991; MacDonald et al. 1992; Reddy and Singh 1992). Germination at a given temperature regime frequently differs when seed is exposed to light or dark, with percentage germination typically being greater in light than in darkness (see references cited above for examples). However, scarified seed of *Sida spinosa* L. (prickly sida) germinated to significantly higher percentages in darkness than in light at low alternating temperatures but not at high ones (Baskin and Baskin 1984). Exposure to light or darkness had no effect on germination percentages in *P. lobata* ($P = 0.693$). Hence, its seed does not require light for germination and should germinate when shaded by litter or a leaf canopy or following burial in soil. Scarification significantly increased *P. lobata* germination across all temperature regimes ($P < 0.001$). Germination of scarified seed was $> 95\%$ in both alternating light/darkness and continuous darkness at all temperature regimes, while nonscarified seed germination was 7 to 17%. The large increase in germination as a result

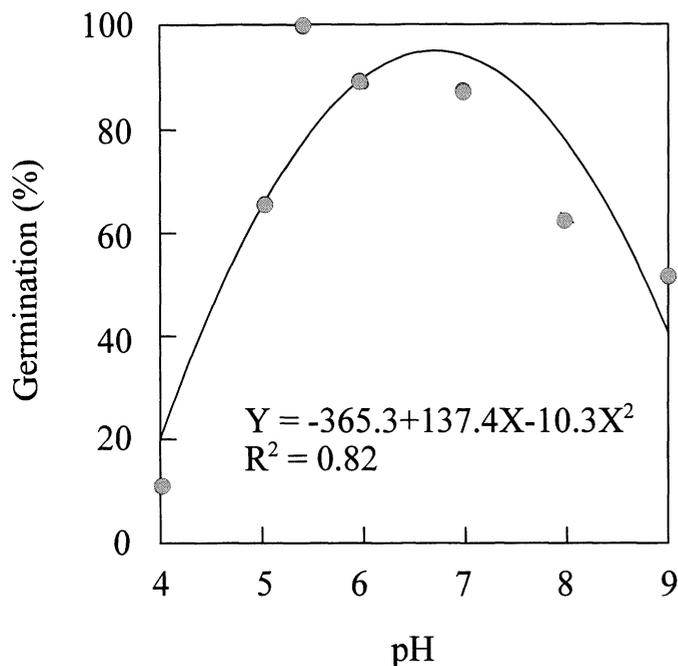


FIGURE 1. The relationship between pH and percentage germination of *Pueraria lobata*. Seed was incubated at 30/20 C (14 h light/10 h dark) for 21 d.

of hand scarification indicates that at the time of dispersal, *P. lobata* seed has a hard coat that is impervious to water. Impermeable seedcoats may ensure seed survival in the soil over several years through the presence of a persistent seedbank. Such physical dormancy is a common feature of seed of many species of legumes (Baskin and Baskin 1998; Everitt 1983; Nan 1992) and may explain why such persistent seedbanks have been found for a large number of species (65) in the Fabaceae (Baskin and Baskin 1998).

Effect of pH

Pueraria lobata seed germinated over a wide range of pH, indicating that pH is not likely to be a limiting factor for germination in most soils. Germination was greatest in distilled water (pH 5.4) followed by buffer solutions with pH 6 or 7 (Figure 1). Germination was significantly lower in solutions above (pH 8 or 9) and below (pH 4 or 5) this pH range. Nevertheless, germination of 51% or greater occurred in treatments when pH ranged from 5 to 9. The lowest germination (11%) was at pH 4.

Effect of Osmotic Stress

As osmotic stress increased, *P. lobata* seed germination decreased (Figure 2). Only 28 and 13% of seed germinated at osmotic potentials of -0.6 and -0.9 MPa, respectively, whereas > 99% of seed germinated in deionized water where osmotic stress was 0 MPa. No germination occurred at an osmotic potential of -1.3 MPa. Several weedy species, such as *Cucurbita foetidissima* H.B.K. (buffalo gourd) (Horak and Sweat 1994), *Anthemis cotula* L. (mayweed chamomile) (Gealy et al. 1985), and *Solanum viarum* Dunal (tropical soda apple) (Akanda et al. 1996), can germinate relatively well at osmotic potentials as low as -0.8 , -1.0 , and -1.0 MPa, respectively, which indicates that they could ger-

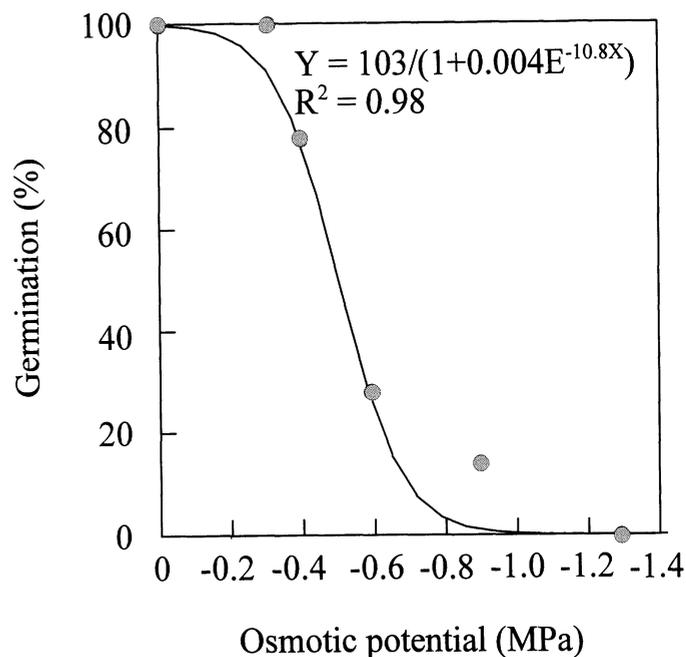


FIGURE 2. The relationship between osmotic potential and percentage germination of *Pueraria lobata*. Seed was incubated at 30/20 C (14 h light/10 h dark) for 21 d.

minate in arid conditions. However, like *Parkinsonia aculeata* L. (Mexican palo-verde) and *Acacia schaffneri* (Wats.) Herm. (Everitt 1983), germination of *P. lobata* seed progressively decreased at osmotic potentials of -0.4 MPa and below. *Pueraria lobata* seed seems to be best adapted to moist environments; hence, germination in the field may depend on adequate water availability.

Effect of Planting Depth

Pueraria lobata seedlings emerged from seed burial depths of 0 to 10 cm; however, percentage emergence decreased with increased depth of burial (Figure 3). Seed sown on the soil surface had low germination (< 13%). Greatly reduced seedling emergence for seed placed on the soil surface has been reported previously for many weeds (Balyan and Bhan 1986; Horak and Sweat 1994; Shaw et al. 1991; Singh and Achhireddy 1984). In each instance, seed of these species, like *P. lobata*, was sown on sandy or sandy loam soil. The poor hydraulic conductivity of sandy soils may explain the low seedling emergence for seed sown on the soil surface in these studies. For *P. lobata*, emergence (72 to 85%) was greatest at burial depths of 0.5 to 4 cm but decreased to 45% at 10 cm. In many species, seedling emergence decreased with increased depth of seed burial (Cussans et al. 1996; Qi and Upadhyaya 1993; Shaw et al. 1987; Vleeshouwers 1997). Emergence after burial in soil depends, in part, on seed size and light conditions. Larger seed with greater reserves can emerge from greater depths of burial (Baskin and Baskin 1998). Because light usually does not penetrate more than a few millimeters of soil, germination and emergence in species whose seed has a light requirement probably would be restricted to shallow depths. *Pueraria lobata* has relatively large seed (ranging from 8 to 19 mg) and does not have a light requirement for germination, so seedlings emerge well from greater depths.

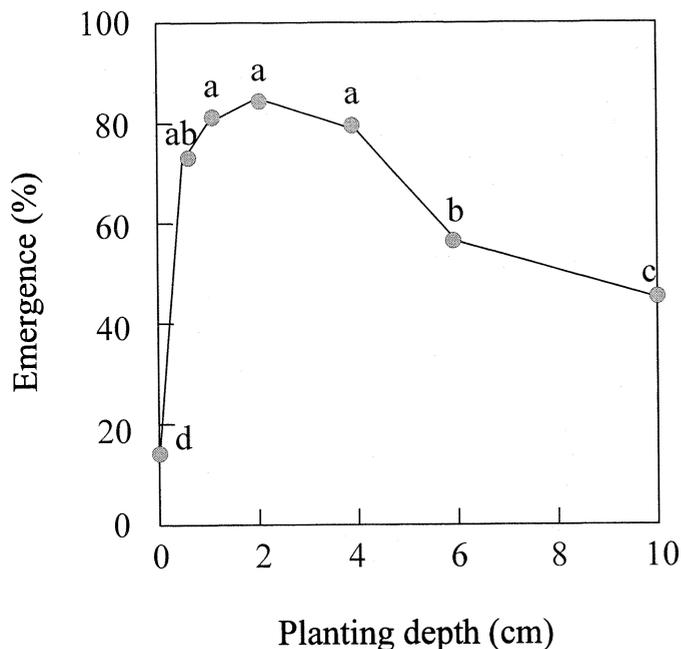


FIGURE 3. Effect of planting depth in soil on percentage emergence of *Pueraria lobata* 21 d after planting. Emergence percentages from planting depths followed by the same letter are not significantly different (Fisher's LSD, $P > 0.05$).

Effect of Simulated Flooding

A high percentage ($82 \pm 2.5\%$, mean \pm SE) of *P. lobata* seed emerged from a depth of 1 cm when not exposed to flooded conditions (control). In *Bidens pilosa* L. (hairy beggarticks), percentage emergence decreased significantly with increased duration of flooding of seed planted in soil. Unlike seed of *B. pilosa*, which had an emergence of 14% after 14 d of simulated flooded conditions, only one *P. lobata* seed out of a total of 320 germinated when exposed to flooded conditions 4 d or longer. Hence, although germination may be favored in moist soils, permeable *P. lobata* seed is unlikely to persist in areas prone to even short periods of flooding.

Germination of *P. lobata* seed occurred over a broad range of temperature, pH, osmotic stress, and depth of burial in soil, although apparent optima were observed for the latter three factors. Thus, seed of this species may be expected to germinate in a variety of soils with different levels of moisture and acidity. Because the seed possesses physical dormancy, a persistent seedbank may result once *P. lobata* becomes established at a site. Previous studies have reported poor germination and seedling establishment (O'Brien and Skelton 1946). Because seed in which physical dormancy has been broken can not tolerate even short periods of flooding, the presence of standing water may be a factor limiting the establishment of *P. lobata* stands from seed, particularly on poorly drained soils.

Sources of Materials

¹ Whatman #4 filter paper, Fisher Scientific, P.O. Atlanta, Box 4829, Norcross, GA 30091.

² Polyurethane bags, Tenneco Packaging Specialty Products Group, 1900 West Field Court, Lake Forest, IL 60045.

³ PEG 8000, Sigma Chemicals, P.O. Box 14508, St. Louis, MO 63178.

Acknowledgments

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