EFFECTS OF TEMPERATURE AND LIGHT ON CHINESE TALLOW (*SAPIUM SEBIFERUM*) AND TEXAS SUGARBERRY (*CELTIS LAEVIGATA*) SEED GERMINATION

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Abstract.—Experiments were performed to assess germination requirements of seeds of Chinese tallow (*Sapium sebiferum* (L.) Roxb.) and Texas sugarberry (*Celtis laevigata* Willd.). *Sapium* and *Celtis* seeds were exposed to different combinations of light and temperature. It was predicted that *Sapium* would germinate under a variety of environmental conditions, but *Sapium* seeds germinated predominantly in fluctuating temperature conditions. *Celtis* seeds also germinated readily in such conditions but had less restrictive germination requirements. Since *Celtis* appears to be better adapted to a variety of germination conditions, a broader range of environmental germination tolerances does not explain *Sapium's* greater establishment success as an alien invader. Nevertheless, seeds requiring oscillating temperatures to germinate are most commonly found in canopy gaps or open areas suggesting that *Sapium* invasions may be especially problematic in disturbed habitats.

Chinese tallow tree (*Sapium sebiferum*) is an invasive deciduous tree species in ecosystems throughout the southeastern United States. Originally from Asia, it has extended its distribution considerably throughout the southeastern United States since its introduction in 1772 (Bruce et al. 1997; Barrilleaux & Grace 2000). *Sapium* displaces many plant species and drastically alters community structure by transforming native grasslands and other habitats into monospecific woodlands (Harcombe et al. 1993; Bruce et al. 1995; Grace 1998). The objective of this study was to assess the effects of light and temperature on seed germination of *Sapium* and an ecologically similar native, Texas sugarberry (*Celtis laevigata*). *Celtis* and *Sapium* are both small deciduous, fast growing trees that are insect pollinated and have bird dispersed seeds (Van Auken & Lohstroh 1990; Jubinsky & Anderson 1996; Renne et al. 2000). In the absence of proper management regimes, *Celtis* may also invade grassland ecosystems (Van Auken & Bush 1990; Harcombe et al. 1993).

Understanding what factors control *Sapium* germination is necessary for understanding the success of this invasive species and may provide insights for managing its growth at early developmental stages. Studying germination of *Celtis* in conjunction with *Sapium* provides a model for comparison with an ecologically similar native species. Germination requirements for *Sapium* seeds were predicted to be governed less by environmental conditions than *Celtis* seeds and these differences were expected to partially explain the success of *Sapium* as an alien invader.

MATERIALS AND METHODS

Sapium sebiferum and *Celtis laevigata* seeds were collected from several uncultivated trees at the University of Houston Coastal Center in Galveston County, Texas in December 1999. Seeds were stored in the dark at room temperature for two months. In February 2000, seeds were planted in subdivided germination trays lined with a thin layer of peat moss and then filled with a mixture of 2/3 commercial top soil and 1/3 humus. Seeds of each species were randomly assigned to a temperature treatment (hot, cold and cycling) and a light treatment (light, dark and cycling) in a full-factorial design. Within each treatment, pairs of *Sapium* and *Celtis* seeds were randomly assigned to one of 240 cells (2 cm by 2 cm by 5 cm deep) in germination trays. The trays were kept in a temperature controlled room without windows for the duration of the experiment.

Seeds in the hot treatment were warmed with a germination mat that maintained the soil at a constant 32°C. Seeds in the cold treatment were kept constant at 16°C. Seeds in the cycling temperature treatment were subjected to 16 h of 32°C and 8 h of 16°C daily. Seeds assigned to the light treatment received 24 h of continuous light supplied by commercially available wide-spectrum plant grow lights suspended 20 cm above the tray surface (average PAR = 50 μmol/m^2/sec). The cool fluorescent bulbs in the cold room emitted a negligible amount of heat that was unlikely to influence soil temperatures. Seeds in the dark treatment were kept dark 24 h per day. Although the dark treatments were isolated by opaque barriers, they were periodically exposed to low levels of diffuse light. Seeds assigned to the light cycle received 16 h of light and 8 h of dark per day. The temperature and light cycles were synchronous. All treatments were lightly watered and checked for germination daily. Newly germinated seeds were removed from their cells. The experiment was conducted for 175 days, but no seeds germinated after 120 days.

Separate Kruskal-Wallis nonparametric tests (i.e. nonparametric *ANOVAs*) were used to examine the effects of temperature treatment and light treatment on *Celtis* and *Sapium* germination (Statview 5.0, SAS Institute). Each cell was treated as an experimental unit and it was assigned a value of "yes" if a seedling germinated and a value of "no" if no seedling germinated in the cell.

Table 1. Separate Kruskal-Wallis nonparametric tests for dependence of the probability of a seed germinating in a cell for (a) *Sapium sebiferum* and (b) *Celtis laevigata* in response to temperature treatments (continuous cold, temperature-cycle, continuous heat) and light treatments (continuous dark, light/dark-cycle, continuous light).

Species	Factor	*df*	adjusted H	*P*-value
(a) *Sapium*	Temperature	2	83.7	<0.0001
	Light	2	8.2	<0.05
(b) *Celtis*	Temperature	2	375.2	<0.0001
	Light	2	36.0	<0.0001

RESULTS

A significantly higher proportion of *Sapium* seeds germinated in the temperature-cycle treatment (Table 1, Figure 1a). Germination in the hot treatment and the cold treatment were extremely low. Within the temperature-cycle treatment, more *Sapium* seeds germinated in constant light and constant dark treatments than the light-cycle treatment (Figure 1a). Likewise, a significantly higher proportion of *Celtis* seeds germinated in the temperature-cycle treatment (Table 1, Figure 1b). Germination of *Celtis* in constant temperature treatments was lower than the temperature-cycle treatment, but some constant temperature and light combinations had moderate levels of germination (Figure 1b). Within temperature treatments, *Celtis* germination tended to be higher as light levels increased. *Sapium* germination was lower than *Celtis* germination in all treatment combinations (Figure 1).

DISCUSSION

Germination requirements for *Celtis* and *Sapium* appear to be primarily affected by fluctuating temperatures. For both species, germination in the temperature-cycle treatment far exceeded the combined germination total in continual cold and continual heat treatments. Light treatments also had a significant, albeit less prominent, effect on germination. *Celtis* seeds appeared to have less restrictive germination requirements than *Sapium* seeds. This contrasted with predictions that *Sapium's* success as an invader may be partially due to a greater breadth of acceptable germination conditions than similar native woody species.

Many plant species use temperature fluctuations to monitor seasonal changes and assess growing conditions (Fenner 1985; Baskin & Baskin 1989). Additionally, soil and canopy vegetation can insulate seeds against daily temperature fluctuations under natural conditions. Adequate temperature fluctuations likely indicate appropriate burial depth and microhabitat conditions for successful establishment and new seedling growth (Fenner 1985; Baskin & Baskin 1989). For these reasons,

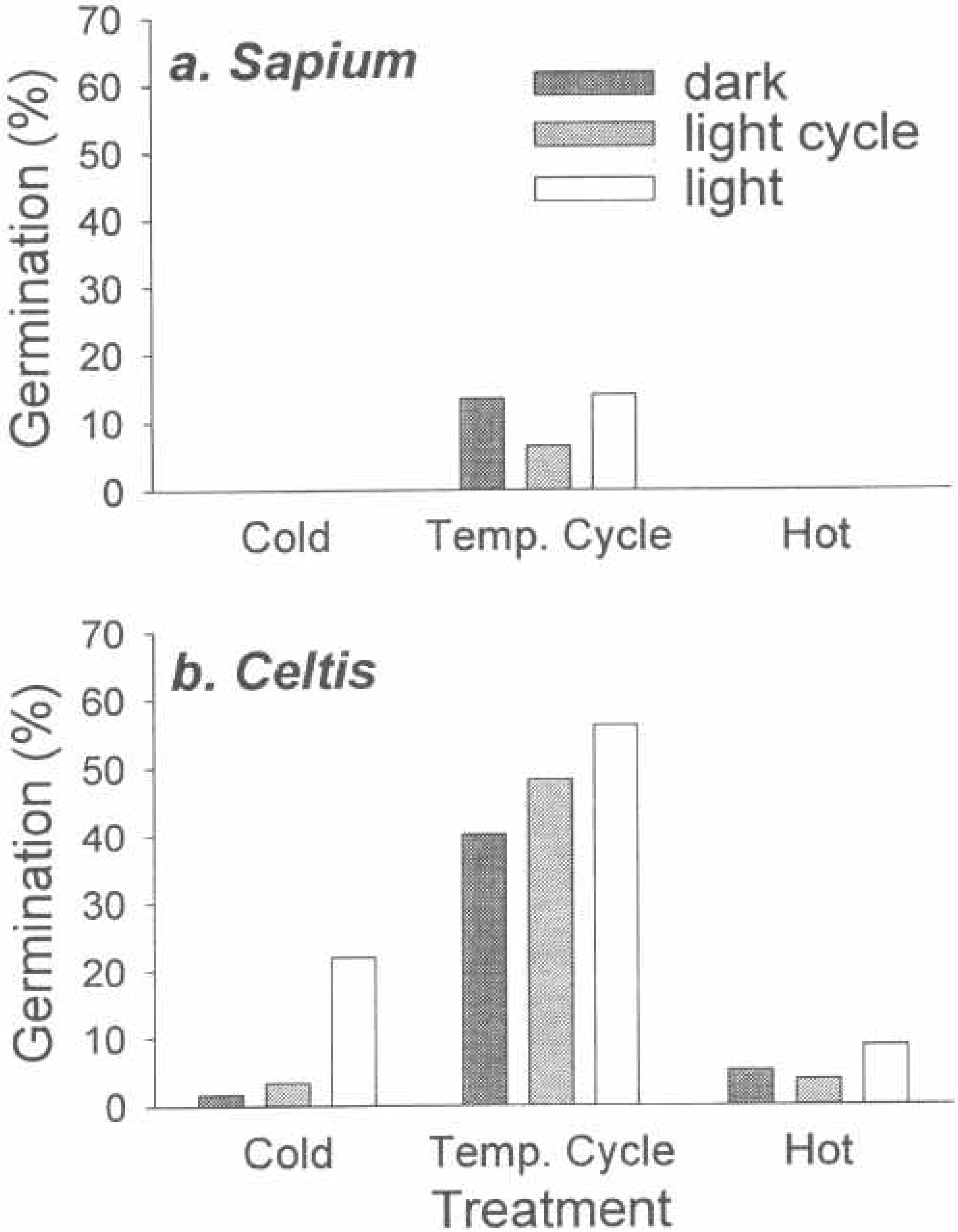

Figure 1. Percent germination of (a) *Sapium sebiferum* and (b) *Celtis laevigata* seeds subjected to factorial combinations of temperature and light treatments. Results show average seed germination percent for each treatment.

oscillating temperatures may be an important environmental cue for germination of *Celtis* and *Sapium* seeds.

While both *Celtis* and *Sapium* germination were highly dependent on temperature fluctuations, there were notable differences in germination responses between the two species. *Sapium* germination in constant heat and constant cold treatments was negligible, whereas *Celtis* seeds germinated with a comparatively greater frequency in constant temperature conditions. These results suggest *Celtis* has a greater total germination rate and is able to germinate across a broader range of environmental conditions than *Sapium*. This outcome was surprising based on the ability of *Sapium* seedlings to thrive in a variety of light and soil resource conditions (Jones & McLeod 1990; Rogers et al. 2000). The high occurrence of *Sapium* germination in the constant darkness/temperature-cycle treatment suggests it does not have a light requirement for germination. Conversely, *Celtis* germination always increased when exposed to continuous light, particularly in the constant cold treatment.

In a separate study of *Sapium* germination requirements, Conway et al. (2000) investigated whether germination depended on seed imbibition and cold stratification. This was tested by subjecting *Sapium* seeds to varying soaking and chilling regimes. Very low germination rates for *Sapium* seeds were found and no differences among soaking and chilling treatments were detected (Conway et al. 2000). The present study indicates that oscillating heat, rather than cold stratification, may be more important for releasing seed dormancy. It is likely that no combination of soaking and chilling will significantly effect germination without adequate temperature fluctuations. Similar to Conway et al. (2000), seeds in the present study that were watered and subjected to a continually cold environment did not germinate. In another study of *Sapium* germination, Cameron et al. (2000) found that *Sapium* seeds maximally germinated in a greenhouse during January and February. Since *Sapium* germination peaks between April and May in field conditions, it is possible that the earlier germination period observed was due to elevated greenhouse temperatures.

Sapium's success as an alien invader does not appear to be explained by having less restrictive germination requirements than similar native woody species. Nevertheless, it is likely that the conditions for releasing *Sapium* seed dormancy, temperature fluctuations, are commonplace in most natural environments. Combined with a high seed output (Scheld et al., 1984), seedling tolerance of varied environmental conditions and an apparent absence of insect herbivores (Jones & Sharitz 1989), *Sapium* invasion of multiple Gulf Coast habitats will remain problematic. This is particularly true of recently disturbed areas where the temperature fluctuations necessary for *Sapium* seed germination are more frequent (Fenner 1985; Baskin & Baskin 1989). Moreover, the role of long-term seed dormancy leading to the build-up of a persistent seed bank and the effect this has on *Sapium* invasion merits further study.

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