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RESEARCH PAPER

Nodding behavior observed in Japanese stiltgrass, *Microstegium vimineum* , seedlings from time-lapse observations

Winnie Zhao and Eric D. Brenner

Department of Biology, Pace University, New York, New York, USA

ABSTRACT

Invasive species are the second main cause of biodiversity loss because of their exceptional ability to supplant native species by creating major upheavals in ecosystems. Inexpensive and prevalent time-lapse photography provides an exciting opportunity to better understand the aggressive behavior of invasive species including how they invade and conquer new territory. One of the most pervasive invasive species in the Eastern United States is Japanese stiltgrass, *Microstegium vimineum* (Trin.) A. Campus, which originated from Southeast Asia. Previous research has examined the conditions that enable Japanese stiltgrass to become invasive, but nothing is known regarding root and shoot behavior. Here time-lapse was used to examine Japanese stiltgrass seedlings, early in their development, as a first step to observe its behavior. Our results demonstrate that Japanese stiltgrass shoots appear to drop or collapse and then resurrect back to an upright stature – sometimes the same plant exhibits this behavior multiple times. We have shown, in addition, that emergent stilt root growth rate increases with increased root length. This and similar kinds of analyses may provide insight into how Japanese stiltgrass thrives aggressively in a non-native environment with the goal of developing better methods of controlling this noxious weed.

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Introduction

Plants appear placid in real time but when viewed using time-lapse photography plants display complex growth patterns including sophisticated movements.[1,2] One key priority of these movements is to occupy space – to enter the necessary real estate with enough light to conduct photosynthesis for survival as well as territorial expansion with further growth. Understanding how plants compete for space is particularly important given that the second major cause of biodiversity loss is due to invasive species, because they are often more adept at survival in their new habitat then endemic species. For instance, some invasive species exploit new territory by germinating earlier than native species and eventually shade over them – essentially starving their victims of sunlight[3] or through allelopathy by releasing phytotoxins to which they are immune.[4] Examination of entire landscapes using remote time-lapse photography has documented large-scale loss of native species habitat due to the encroachment of invasive species.[5] However, besides these kinds of panoramic views of plant habitat change, to date, there is little time-lapse documentation of the behavior of an invasive plant species in order to reveal their strategies for conquest.

Invasive species result in a cost of about $120 billion dollars in environmental related losses in the United States every year,[6] or even more in today's ecosystems; there are approximately 50,000 non-native species that now reside in the United States that were introduced for various needs.[7] Decline in biodiversity causes ecosystems to become less resilient to natural and man-made disturbances, which in turn makes native habitats more vulnerable to invasion from other opportunistic species.[8] A decrease in biodiversity typically leads to a decrease in the functions and services found in ecosystems.[9],Globally, about 80% of native species are endangered or at risk of becoming extinct due to habitat loss from invasive species.[7] This leads to a state where ecosystems come under intense stress due to the rapid reduction of native species diversity profile.[10]

One detrimental invasive plant species is Japanese stiltgrass (Poaceae) (Figure 1), which is ranked as one of the most difficult to manage in the wild.[11] This pernicious invasive weed causes significant damage to temperate Northeast Forests, where it infiltrates the understory by preventing recruitment among a variety of native plant species of ecologically essential trees including boxelder, maple, tulip tree, and American sycamore.[12]

Japanese stiltgrass is also referred to as Chinese packing-grass, Eulalia, Nepalese browntop, or Ashiboso.[13] It originated from Southeast Asia and can be found locally in the following countries: Korea, China, Japan, Nepal, Pakistan, and India.[14] Japanese stiltgrass was most likely introduced into the United States as packing material, to protect the porcelain shipped from China into the United States.[15] The very first record of Japanese stiltgrass in the United States is from 1919 in Tennessee.[16] Today, Japanese stiltgrass can be found in 24 states, mostly on the eastern side of the Mississippi River (Figure 2) and its range is continuing to grow[17] due to the life cycle of Japanese stiltgrass[18] with its versatile growth capabilities amongst various environmental conditions.[19]

CONTACT Eric D. Brenner ebrenner@pace.edu Department of Biology, Pace University, 1 Pace Plaza, New York, New York 10038, USA

Once established, Japanese stiltgrass can alter the nutrient cycle in an ecosystem. Field studies and lab experiments examining growth of Japanese stiltgrass in various conditions have shown that it alters soil chemistry composition, including the available nitrogen and phosphorus levels in the soil, affecting arthropod diversity.[21] It has been demonstrated that Japanese stiltgrass invasion increases the intake of nitrogen in the environment and it also changes the carbon and nitrogen ratio in the soil as demonstrated by the fact that soil pH levels are higher in the presence of Japanese stiltgrass.[13] The increase in pH is correlated with an increase in the nitrification rate of Japanese stiltgrass patches because soil with low pH lowers nitrification rate.[22]

Japanese stiltgrass is known as a "super-generalist" because it can utilize the C_4 pathway to invade different environments with varying light availability in forest understories and grow successfully despite limited resource availability. As a C_4 plant, it is resilient in drier climates[12] and grows at a faster rate than native plants because it is more efficient at light-harvesting.[19] Moreover, Japanese stiltgrass is also tolerant of shade and can thus flourish even in low light conditions.[17] Japanese stiltgrass can grow up to two meter tall, depending on the light conditions and resource availability in the environment.[19]

Japanese stiltgrass seeds typically germinate from the beginning to the middle of spring with continuing growth until the middle of summer where the plant reaches its largest size, and in the late summer to fall it produces all of its seeds.[19] The specific germination time varies depending on environmental conditions, such as light availability, temperature, ground-litter, and moisture level.[19] As an annual grass, a single Japanese stiltgrass plant can produce 100 to 1000 seeds where the seeds remain viable in the soil for up to three years.[18] If the seeds are kept at low humidity, they can presumably last even longer. A viable seed bank remains in the soil over long periods making eradication difficult.[20] Prior research has been conducted on seed yield and the success rate of seed germination.[23] Leicht et al. (2005)

[18], performed a competition study comparing Japanese stiltgrass shoot height with other grass species in light vs. dark conditions. Japanese stiltgrass may grow upright or prostrate depending on what plants and other objects are nearby that can act as supports. As part of its invasive strategy, Japanese stiltgrass produces lateral tillers, or side shoots, that emerge from the stem at nodes, which greatly expands its stature as the plant matures in order to successfully invade new territory.[24] Tillering and shoot branching can lead to what appears to be a suffocating mesh of roots and shoots (Figure 1). Previous work has shown that invasive species potentially have superior root foraging properties compared to native species.[25] Hence measuring the rate of root growth could be an important characteristic to observe in Japanese stiltgrass.

To date there is no information regarding how the dynamics of Japanese stiltgrass behavior might enable it to out compete competitors and conquer new terrain for roots or shoots. Using time-lapse photography, we report two unexplored dynamic qualities of Japanese stiltgrass: root growth rate and shoot movements – the latter offering the unexpected observation that young plants rise and fall, seeming to pivot up and down over time.

Figure 1. A tangled mesh of Japanese stiltgrass plants. Plants grown in adjacent pots have entered each other's space. Shoots and roots have become intertwined.

Materials and methods

Seed source

Japanese stiltgrass seeds were collected in 2017 in a garden bed on the south side of City Hall Park, located in Lower Manhattan, New York. Analysis was conducted on seedlings from second generation seeds collected from the original batch that were grown in the lab.

Plant cultivation

Plants were cultivated in 2.5-inch pots with Miracle-Gro Seed Starting Potting Mix soil. A clear cover was placed over the flat to let the seeds germinate at high humidity. When most of the plants germinated, about four to seven days after the seeds were planted, the cover was removed. Once the plants were about twoweeks old, fertilizer was added to the water using Miracle-Gro All Purpose Plant Food that included micronutrients according to Brenner 2017[1]. The plants were grown for approximately four to eight weeks before the recordings were made. Plants were grown in either 24-hour light or 16-hour light/8 -hour dark (note there was some light leakage into the room during the dark cycle).

Plant growth and movement recordings

Recordings were made using the time lapse recording app, *Lapse It* – version 2.52 , on generation 6 iPod Touches to capture the growth and movements of the plants. The recording set up and the settings used on *Lapse It* is similar to the ones used in Brenner 2017 [1], where an iPod facing its subject is used to create a time-lapse movie. The time interval equaled one image taken every fiveminutes over a period of two to three days. During the recording process, the focal point was centered either on the roots of Japanese stiltgrass or a wider view encompassing multiple Japanese stiltgrass plants. A ruler with a black background and white increment marks was placed in the focal plane to calibrate the scale.

There were a total of 19 time-lapse videos . Five videos for roots were shot over two to three days when the plants were from six to eight weeks old. Videos for root analysis zoomed in on the emerging tillers to enable measurements of root growth rate. Wide-shot videos examining the continuous movement of the entire plant stature were initiated when the plants reached approximately four weeks old to seven weeks old, . The wide-shot videos consist of seven videos of Japanese stiltgrass in 16-hour light/8-hour dark and seven in 24-hour light conditions. .

To calculate the rate of above-ground root growth (tillers), root lengths were measured and growth of root length was calculated. During root growth, each node can produce 2 or more aerial roots (Figure 3)). One root emerges first and then the second one follows shortly after. The root growth rate was determined using the equation: length/(frame/min x time length in the video).[26] The data was compiled from a series of five videos taken of Japanese stiltgrass in 2019, from October 21st through the beginning of November. The measurements were taken from 16 different roots growing in these five videos, where some of the measured roots emerged from the same plant at different nodes. Root length was measured using the distance from the emergence point to the apex of the root.

Table 1. Two-sample t-test assuming equal variance on data from Figure 4.

Best-Fit Regression Line	y = 0.0152x + 0.1744
Slope (mm/(mm/hour))	0.0152
Standard Error of the Slope (mm/(mm/hour))	0.0288
t value	8.5128
P-value	2.4524 x 10–10
95% Confidence Interval (mm/(mm/hour))	0.2423 to 0.3627

After the videos were analyzed, data were collected on aerial root length and were presented in a graph to show a comparison between root length and the rate of root growth. The data were used to create a scatter plot, as shown in Figure 4. From this data a two-sample t-test was then performed for statistical analysis, assuming equal variance, is shown below in Table 1.

Annotated videos

Two annotated videos (see representative still shots in Figure 5, left and right panel) that were created using the *Lapse It* time-lapse movie of young Japanese stiltgrass To annotate the videos, they were placed into the app, *SnapMotion*, to extract the individual frames from the time-lapse in order to do the annotations (. Boxes were placed on select individual plants to highlight their movement during their growth and to distinguish them from the other plants for viewing, Figure 5. Different colored boxes were arbitrarily chosen to annotate plant movement. For the photo of the movie on the right, Time-lapse 2, more than one plant has been annotated with boxes that follow their movement. The plants with a red box appeared to show more dramatic, rapid movement during the recorded time period, the plants with the blue box were

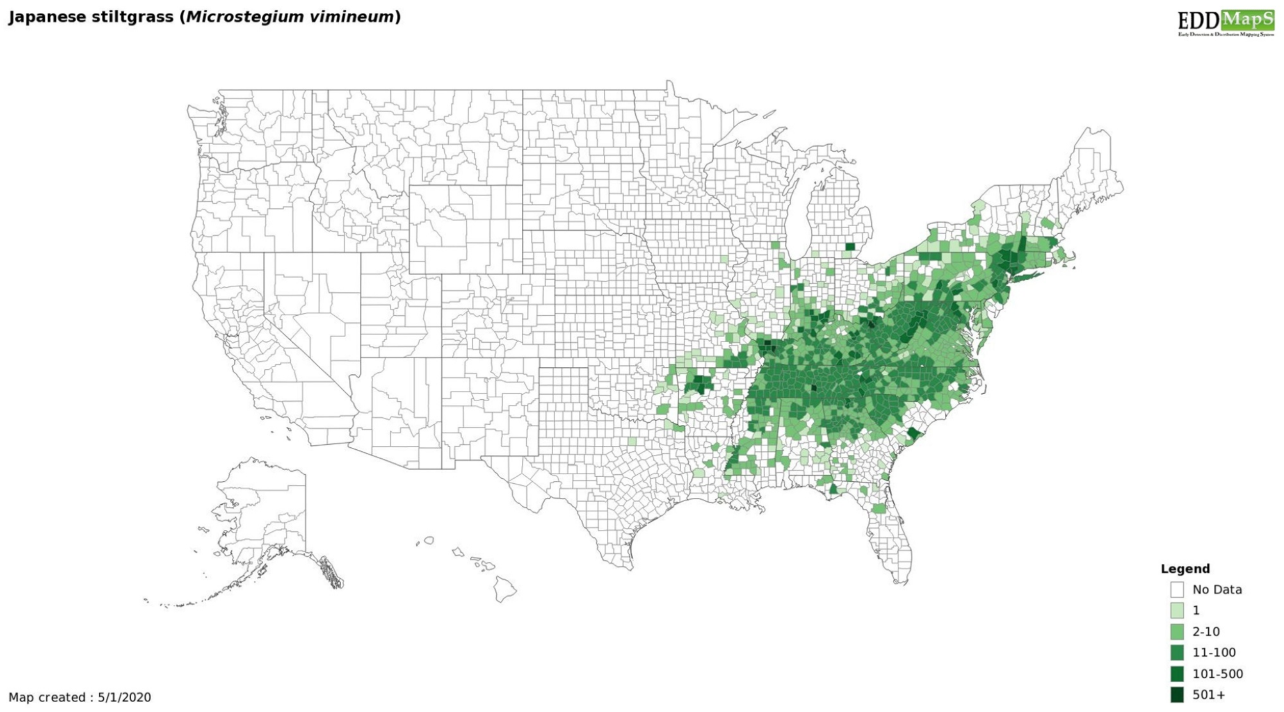

Figure 2. Japanese stiltgrass geographical distribution. This map generated from EDDMaps[20] shows the distribution of Japanese stiltgrass, where it has invaded eastern regions of the United States and is spreading continuously westward.

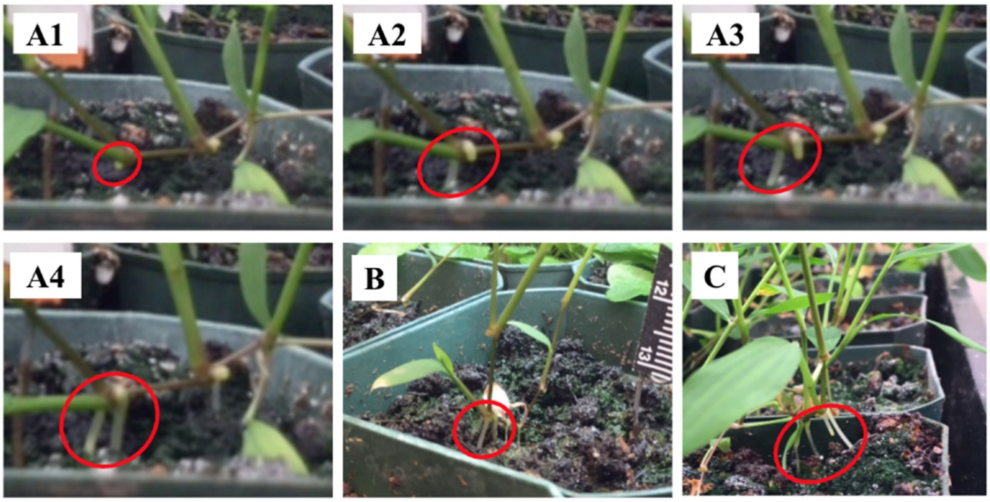

Figure 3. The emergence of aerial roots from a node on Japanese stiltgrass. Panel A1-A4 comprises two emerging roots on the same stem. Panel B and Panel C are single images of two separate root emergent events.

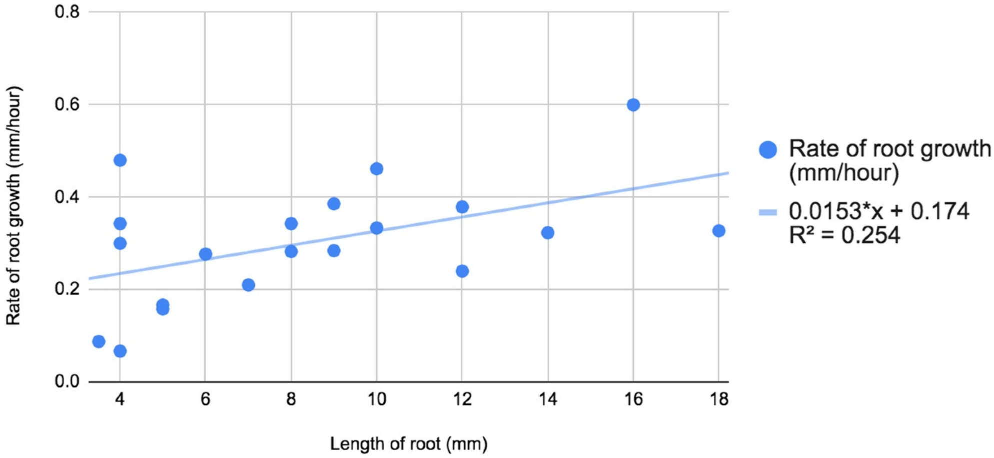

Figure 4. Graph of Japanese stiltgrass root length compared with rate of root growth. The graph above shows a positive correlation between increase in root length and the rate of root growth. It shows that as the Japanese stiltgrass root grows longer, it also grows faster.

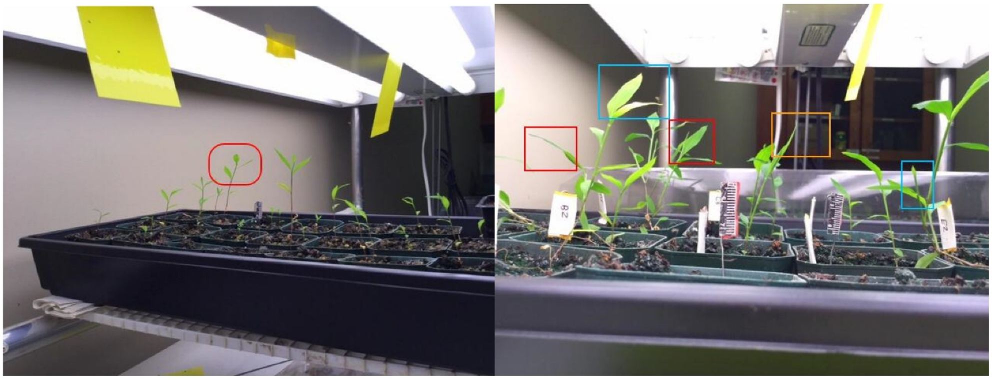

Figure 5. Japanese stiltgrass nodding behavior. Frames extracted from two different time-lapse videos that can be viewed here, Time-lapse 1 (left panel) and Time-lapse 2 (right panel) that have been annotated to help follow the movement of several Japanese stiltgrass plants showing dramatic up-and-down and side-to-side nodding behavior.

observed to show less movement, and the plant with an orange box showed a mix of fast and slow movement. After the boxes were placed, the annotated photos were placed into *QuickTime Player* and converted back to a video (Quicktime Player)[27]. The time-lapse videos in *Lapse It* were created with a rate of 20 frames per second. However after the reconversion of the video, the frame rate was a little faster at 24 frames per second due to the limited options available in *QuickTime Player*.

Results

General plant appearance

Our qualitative observations noted that when grown in 16-hour light and 8-hour dark, Japanese stiltgrass plants appeared healthier and greener, more robust than with 24-hours of light. In 24-hour light, the plants became chlorophytic and turned somewhat yellow with less robust growth (data available upon request).

Root growth rate

To determine the relationship between root length and the rate of root growth, a trend line was generated that yielded the equation in Figure 4. From the trend line, it appears that as Japanese stiltgrass root length increases, the rate of root growth also increases (at least prior to entry into the soil). To confirm this relationship, a two-sample t-Test was performed assuming equal variance for both samples where a positive correlation between root length and root growth was revealed. As shown in Table 1, the *p*-value, 2.4524 x 10–10, is less than 0.05, and therefore does not fall in the range of the 95% confidence interval, 0.2423 to 0.3627. Therefore, the null hypothesis that root length is not correlated with the rate of root growth is rejected. This analysis therefore shows that root length is correlated with how fast the root grows. The longer the root, the faster it grows at this early stage of development.

Japanese stiltgrass "nodding" behavior

It was observed from the time-lapse videos, during the growth of Japanese stiltgrass, that the shoots appear to drop over. In these videos, as the seedlings grew taller, the culm (stem) appears to drop down and then rises. . Certain individuals cycled up and down two or more times as if they were nodding. Plants grown in either 16-hour light or 24-hour continuous light both exhibited this behavior. 54% of plants grown in 16-hour light (12/22 plants) showed the falling and recovery response and 33% of plants in continuous light (5/15 plants) exhibited this behavior. One individual Japanese stiltgrass plant whose culm went up and down three times over its lifespan is shown in the first series of photos (Figure 6). This behavior was first observed when this specific plant reached approximately five cm in height. The plant then fell over again at a later stage of rapid development when new roots and leaves emerged from the main plant- the plant was seen falling a third time. It is possible that a higher percentage of plants exhibiting this behavior would be observed if the recordings persisted for a longer period.

Discussion

When viewing time-lapse recordings we often marvel at the intricate movement of plant shoots. However, besides carnivorous, herbivorous, and twining plants, we do not necessarily ascribe a function to this movement and consider it a consequence of growth or as an obvious tropistic (light, gravity etc.) event. In this regard, nothing is more enigmatic than the purpose of circumnutation (the back and forth swaying of organs) in plants.[28] It is possible that our observations of movement in Japanese stiltgrass seedlings reveal another manifestation of circumnutation. However, the movement we observed does not agree with the traditional ellipsoidal or zigzagging movement cycles of circumnutation. In this instance, Japanese stiltgrass seedlings appear to drop then regain an upright posture. This movement does not appear to be coordinated with the light cycle and occurs in a seemingly random fashion throughout the recording period of several days; this would suggest that diel fluctuation growth patterns, such as nyctinasty, which have a circadian basis,[29] are not a factor in these movements. Future experiments will repeat our analysis of Japanese stiltgrass growth in both light and dark conditions; the use of infra-red during the dark phase will further illuminate our perception of these plants movement. In addition, further studies could measure this movement in 3-D time-lapse to increase the accuracy of analysis.

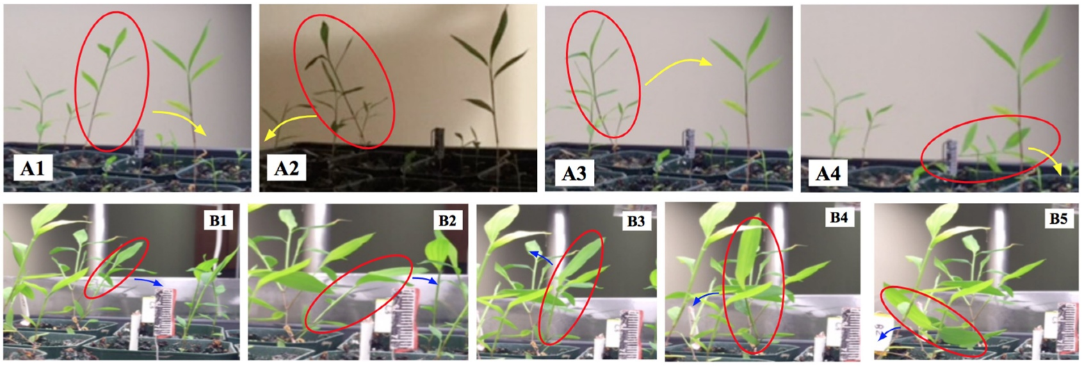

Figure 6. Japanese stiltgrass nodding behavior Above are screenshots from two instances of Japanese stiltgrass nodding behavior, taken from two separate instances.

The fact that we have observed this in a majority of plants suggests that, at least in artificial growth conditions, this is a consistent phenomenon. This movement behavior also occurred when Japanese stiltgrass plants were co-cultivated with up to three different species of plants (data not shown).

We do not know whether the mechanism behind this movement is caused by cell division, expansion, or contraction or some other event at the bending site. Future inquiries could examine whether other members of the Poaceae (the Grass Family), particularly creeping species, also exhibit this process. The Poaceae are a highly important agronomic crop. As a recently diverged evolutionary group with considerable genetic synteny,[30] most Poaceae exhibit a similar basic stem morphology of tillers that emerge from a culm.[31] Because of the agronomic importance of the Poaceae, considerable information is available regarding the development of the culm including meristem organization and the formation of derivatives.[32] However, the culm has not been studied as a mobile structural unit so it is not clear where the site of bending would be in Japanese stiltgrass during nodding behavior.

Although it is not known why this behavior is observed, one could speculate that the plant may move this way in order to sense its environment as an early step in development to determine its ideal placement – which could include detecting the presence of a competitor. One more interesting possibility could be that this movement is reminiscent of a form of nictation, similar to that found in parasitic nematodes that sense the presence of prey[33] or *Caenorhabditis elegans*, where nictation is presumed to be a behavior meant to find migrating hosts for transport to a new location.[34] There is precedent for such highly sophisticated and sensitive plant-to-plant detection systems. The plant parasitic plant *Striga* spp. can detect it's prey from volatile molecules released by its host[35] and even synchronize its flowering timing to match that of its prey.[36,37]

Alternatively, this movement could simply be a response to an internal process associated with growth and development that is not yet understood. Perhaps the growing plants become too top heavy and collapse under their own weight but then soon after resurrect an upright stature. These falling events could facilitate Japanese stiltgrass overlaying its competitors but not be connected to a complex sensing system. Future research could examine whether this movement is also exhibited at a more mature stage of development or in other species of the Poaceae, with emphasis on creeping grasses. It would be interesting to determine if this behavior is influenced by neighboring plants and to determine if thigmotropism influences this behavior. In a previous study, Japanese stiltgrass invades areas of greater plant diversity at a faster rate than an area with a monoculture or limited species diversity.[13]

As Japanese stiltgrass plants mature, they grow into a tangled meshwork of interwoven shoots and roots (Figure 1); this mesh-like growth is hypothesized to function as a mechanism which chokes out other species. This observation is supported by existing literature that Japanese stiltgrass grows in dense populations.[14] When grown in low light conditions, it also produces more tillers as a way to search for areas with richer nutrients.[19] Further studies, such as our examining the growth rate of Japanese stiltgrass roots is a first step toward this goal.

This is the first study of the movement behavior of Japanese stiltgrass using time-lapse observations. Considering its pernicious damage to native plant species and horticulture in America, understanding its behavior might help reveal vulnerabilities in its invasive tactics. These findings may encourage future studies to define invasive plant strategies using time-lapse photography as another weapon in the arsenal of land management to stop the spread of Japanese stiltgrass and other pernicious weeds whose modes of invasion are unknown.

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