

Pathway from Ornamentals to Invasive Plants:

**A Case Study of *Impatiens capensis* and *Impatiens
glandulifera***

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ABSTRACT

The introduction of invasive species by humans is an enormous problem that causes widespread environmental and economic harm. In order to address this, extensive research has been done to understand more about the processes of biological invasion. I examined the process by which ornamental plants become invasive by conducting two experiments with *Impatiens capensis* and *Impatiens glandulifera*. Both species are aggressive annuals that have been introduced as ornamentals into habitats outside their native range and are model species for studying this process. Experiment 1 looks at the possibility of artificial selection for dry dormant seeds done by horticulturalists on *I. capensis* in the United States. Experiment 2 assesses one of the dispersal mechanisms of introduced ornamentals by comparing the ability of United States populations of *I. capensis* and *I. glandulifera* seeds to float in water and to tolerate water conditions at varying levels of salinity. There are insufficient data from Experiment 1 to determine whether or not there is evidence of artificial selection on *I. capensis* seeds for dry dormancy. On the other hand, data from Experiment 2 demonstrate that *I. capensis* seeds tend to float longer in water than *I. glandulifera* seeds and that their floating ability is affected by salinity to a greater extent than *I. glandulifera* seeds. *Impatiens capensis* seeds also tend to germinate more frequently than *I. glandulifera* seeds after exposure to saltwater, and all these differences may lead to dissimilar dispersal patterns between the two species. From the results, predictions for future dispersal of invasive populations of *I. capensis* and *I. glandulifera* can be made, such as the potential for spread into drier regions and regions with more moderate winters than their native habitats. In addition, there is also the potential for spread between freshwater habitats via brackish waterways. In order to supplement predictions of dispersal and provide ideas for effective control of invasive populations, I did an additional literature review of overlaps between characteristics of ornamentals and invasive plants. I have compiled this information to assist policy makers in creating more effective regulations and management schemes that will prevent the introduction of invasive species and minimize their establishment and spread.

INTRODUCTION

In modern times, human actions have had a tremendous impact on the environment. One example of this impact is the introduction of exotic species into new habitats outside their native range. Humans introduce exotic species into new environments for a variety of reasons. Introduced species can serve as sources of food for humans and animals, as sources of medicine, and as ornamentals for aesthetic purposes (Mack and Erneberg 2002). Only a small proportion of introduced species end up negatively impacting recipient ecosystems (Williamson 1996). However, due to the high volume of introduced species overall, a significant number of exotic species establish in new environments and become invasive. In general, an *invasive species* can be defined as a non-native or exotic species that has established itself in an environment outside its native range and that is spreading. In addition, invasive species have the ability to cause serious harm to populations of native species and drastically alter ecosystem processes, both of which will be explained in further detail.

Invasive species are considered one of the leading global threats to biodiversity and ecosystem functions. Scientists have listed “biotic exchange,” or the successful establishment of invasive species, as one of the five major drivers of biodiversity change that will take place over the next century (Sala et al. 2000). The introduction of exotic species also plays a huge role in homogenizing global biota (Chapin et al. 1997). Within the United States, invasive species are the second leading cause of biodiversity loss (Enserink 1999). In some extreme cases, the introduction of certain invasive species have led to extinctions of native species (Williams and West 2000; Kolar and Lodge 2001). However, further research is still needed to determine the extent to which these particular invasive species have contributed to native species extinctions and whether or not invasive species in general – as opposed to specific invasive species – are major contributors to extinctions (Gurevitch and Padilla 2004). Invasive species have also caused changes in nutrient cycling, hydrology, and fire regimes (Levine et al. 2003). In addition, invasive species are responsible for huge financial losses. In the United States, \$137 billion is lost annually due to invasive species (Pimental et al. 1999; Kolar and Lodge 2001). These costs result from herbicide/pesticide use, crop loss, damage to the environment and human health, and enforcement of regulations (US Congress OTA 1993).

In the United States, over 2000 out of the 4542 known introduced species are plants (US Congress OTA 1993). Although there has been extensive research on how introduced plants

become invasive in general (Enserink 1999; Kolar and Lodge 2001; Sakai et al. 2001; Hierro et al. 2005), little is known regarding the process(es) by which an ornamental plant becomes invasive. There have been many documented cases of invasive plants that started off as seemingly harmless ornamental plants. For example, the majority of woody invaders in North America were originally introduced as ornamentals (Reichard and Hamilton 1997). In the United States, there are also a number of herbaceous ornamentals that became invasive. Current established invaders that were brought in as ornamentals include *Lonicera japonica* or Japanese honeysuckle, *Rosa multiflora* or multiflora rose, *Rhamnus carthartica* or European buckthorn, and many more (Mack and Erneberg 2002; Mehrhoff et al. 2003). Due to the significant number of invasions by ornamental exotics, this paper seeks to examine in more detail the process by which ornamental plants become invasive plants.

Invasion biology theory divides the process of biotic invasion into three stages: 1) introduction, 2) establishment, and 3) spread (Sakai et al. 2001). Exotic species can be introduced through direct human activities, as previously mentioned, or through indirect human activities, as in the case of seed contaminants that are brought along with deliberately introduced species (Mack and Erneberg 2002). Once species are introduced into a new environment, they can establish themselves in novel habitats through a number of hypothesized pathways, such as having the ability to utilize resources unused by native species and/or having the ability to evade natural predators in their new environment (Hierro et al. 2005). Propagule pressure or the repeated introduction of exotic plants has also been linked to greater invasive success (Hierro et al. 2005), and this is particularly important for ornamentals that are often introduced repeatedly. However, it is important to note that the ability of an exotic species to establish outside its native range is not limited to these major hypothesized pathways. Invasions can often be idiosyncratic, and reasons for invasion can vary depending on the species being introduced and the environment into which it is brought. After introduced species are established in a recipient community, they can continue to spread with the help of adaptations for dispersal (Sakai et al. 2001) or dispersal by humans.

In this paper, I will focus on the introduction and establishment stages of ornamental plants that become invasive by addressing the following questions:

- 1) Do efforts to domesticate plants as ornamentals alter seed dormancy or germination requirements in ways that could facilitate invasibility?
- 2) How can certain dispersal mechanisms allow us to predict where ornamentals will escape to and establish wild populations?

The first question examines the introduction phase of an invasive or potentially invasive ornamental. When horticulturalists domesticate native plants to become ornamentals, it is highly likely that they would deliberately or unintentionally select for certain traits that would allow native plants to be more desirable as ornamentals. Ornamental seeds are often dried before transport, so it is possible that there is selection for dry dormant seeds in species that do not naturally produce these types of seeds, such as *I. capensis* and *I. glandulifera*. In addition, horticulturalists may also select for seeds that have shorter dormancy periods. This type of selection allows seeds of ornamentals to be more easily transported and to germinate readily after they are planted in gardens.

In addition, the ability for seeds to tolerate dry conditions while remaining dormant could be seen as a form of stress tolerance. Although being stress-tolerant may not be the same as being invasive, the ability to tolerate ecologically stressed conditions in general could improve the capacity of an exotic species to invade. For instance, this tolerance can allow exotics to out-compete native populations in terms of their ability to respond to disturbances, limiting resources, and enemies. Selection for seed desiccation-tolerance and shorter seed dormancy periods could potentially allow ornamental seeds to establish in habitats that are drier than and climatically different from their native habitats. They may also be able to better tolerate disturbances such as droughts or long-term climate changes in their recipient habitats.

To examine whether or not there has been selection on ornamentals to alter seed dormancy and germination requirements, in Experiment 1, I tested whether seeds from native populations or ornamental populations of *I. capensis* have the greatest proportion of germinators under stressful conditions. The stresses that I imposed were desiccation, lack of stratification

during the seed dormancy period, and shortened dormancy period. My hypothesis was that ornamental populations have a greater proportion of germinators under all stress treatments.

While the first question addresses mainly the introduction phase of biological invasion, the second question looks at the transition from the introduction phase to the establishment phase. This question examines the dispersal mechanisms of introduced exotic species, which allows ornamentals to escape from the controlled environments in which they have been placed and establish wild populations. Ornamentals provide minimal threat (if any) to ecosystems as long as they remain in controlled environments such as gardens. However, they can escape in great numbers and potentially establish wild populations in new environments via different dispersal mechanisms. Thus, understanding these mechanisms is important to predicting where ornamentals will end up and establish populations.

Humans can also indirectly affect seed dispersal ability. When selecting for desirable traits in ornamentals, horticulturalists may unintentionally select for other closely linked traits that could affect an ornamental's dispersal ability. One example is related to the selection for dry dormant seeds. Seed dormancy is largely regulated by the phytohormone abscisic acid, or ABA, which desiccates seeds before they become dormant. High levels of ABA can enable plants to tolerate both water stress and salt stress (Farnsworth 2000). Therefore, if horticulturalists select for dry dormant seeds, it is possible that they could unintentionally select for seeds that are also salt-tolerant.

The two species that I studied in an effort to answer the second question were *Impatiens capensis* and *Impatiens glandulifera*, which are both found along waterways and can be water-dispersed. Both species are found in freshwater habitats, but because waterways can vary in salt concentration, I was interested in investigating the potential for seeds to travel via saline waterways to novel freshwater habitats. In Experiment 2, I examined the effects of salinity on how long seeds from native populations of *I. capensis* and invasive populations of *I. glandulifera* in the United States can stay afloat in water and the effects of salinity on the percent germination of seeds. My hypothesis was that increased salinity may allow both native and invasive seeds to float longer in water. I also hypothesized that saltwater would decrease the percent germination of seeds from both populations since both species are typically found in freshwater habitats.

Both of these questions place an emphasis on the first two phases of biotic invasion rather than the final phase of invasion. By focusing on preventing invasions from occurring and

predicting future invasions, people can take precautionary measures rather than depend on corrective measures to ameliorate impacts after the introduced species have already established, are spreading, and are negatively impacting ecosystems. Studies have shown that it is easier to reduce the impacts of invasive species in earlier stages of invasion rather than later stages (Kolar and Lodge 2001; Byers et al. 2002). In addition, this focus on seeds could allow us to better understand how plants are introduced and established from an early life-history stage.

STUDY SPECIES

Both study species belong to the family Balsaminaceae and have similar life history traits. *Impatiens glandulifera* Royle, commonly known as the Himalayan Balsam or Policeman's Helmet, is a native of the Himalayas (Beerling and Perrins 1993). It was first introduced as an ornamental garden plant in 1839 in Britain, and it was first recorded in the wild in 1855 in Middlesex and Hertfordshire (Beerling and Perrins 1993; Preston et al. 2002). In the United States, it is possible that it was introduced as an ornamental in New England. Judging from the distinct clusters of *I. glandulifera* populations spread throughout the region (Mehrhoff et al. 2003), it is highly likely that there were multiple introductions focused around the eastern coast of Maine, the Berkshires in western Massachusetts, the eastern coast of Massachusetts, and central Connecticut (see FIGURE 1). Although it was reported to have escaped from cultivation in 1950 (Fernald 1950), the Invasive Plant Atlas of New England (IPANE) database has records of a sighting in 1883 in a garden in Norwich, Connecticut (Mehrhoff et al. 2003).

Impatiens glandulifera is highly invasive in the British isles (Beerling and Perrins 1993), and it is becoming increasingly invasive in the northeastern United States (Mehrhoff et al. 2003). In Britain, it has naturalized in communities ranging from riparian environments to woodlands (Beerling and Perrins 1993). One study has shown that *I. glandulifera* produces more nectar than native plants; thus, it receives more visits from European bumblebees (Levine et al. 2003), perhaps making the species more competitive for pollinators than native plants. In the United States, *I. glandulifera* is found in early successional forests, floodplain forests, roadsides, wet meadows, yards and gardens (Mehrhoff et al. 2003). Relatively few associated herbaceous plant species are found in stands of *I. glandulifera* in Britain (Beerling and Perrins 1993) and from personal observations, there are very few associated species in stands in New England as well. Little information is available to explain this unexpectedly low species richness. However, the

expansion of populations of *I. glandulifera* has been shown to positively correlate with the anthropogenic destruction of natural river bank communities (Beerling and Perrins 1993). From personal observations, the *I. glandulifera* stands surveyed in Berkshire County in Massachusetts were often located close to roadsides or sites of human development, so one possibility could be that *I. glandulifera* tends to establish populations in habitats that have already undergone disturbances that reduced the species diversity.

Impatiens capensis Meerburg, commonly known as the Spotted Jewelweed or Touch-Me-Not, is native to North America (Magee and Ahles 1999). It is widespread in the Pacific Northwest and in the eastern half of the United States from Maine to Florida (USDA, NRCS 2004). The first introduction to Britain was probably in the early nineteenth century, and it was first recorded in the wild in Surrey in 1822 (Preston et al. 2002). The current Norfolk population in Britain came from a second introduction in the tributary of Bure near Aylsham in 1927 (Preston et al. 2002). It has now naturalized in Britain in woody, wet, and shady habitats. Compared to *I. glandulifera* and a close relative that has naturalized in Britain, *Impatiens parviflora*, *I. capensis* is the least invasive (Perrins et al. 1993). As a result, its potential invasiveness in Britain remains controversial even though it has established and is spreading. Nonetheless, it is important to remember that a common feature of invasions is the lag time between initial colonization and aggressive invasive spread (Sakai et al. 2001). Thus, *I. capensis* has the potential to become an even greater threat in the near future.

Seed Dormancy

Besides unfavorable environmental conditions, properties of a seed can also inhibit germination (Baskin and Baskin 1998). Many temperate *Impatiens* species require a period of cold stratification in order to break seed dormancy, and *I. glandulifera* and *I. capensis* are no exception. Since seed production for both species occurs from mid-summer to early fall (Leck 1979; Mumford 1988), the chilling requirement before dormancy is broken ensures that most seeds will germinate after winter has passed and when conditions are more favorable for seedling establishment in early spring.

Some freshly harvested and imbibed *I. glandulifera* seeds are capable of germinating after 45 to 89 days of stratification at 4°C, but in order to achieve greater germination success, more than 89 days of stratification is required (Mumford 1988). When seeds are stored in high

temperatures (i.e. 20°C), they synthesize factors that maintain the state of dormancy (Mumford 1988). However, in previously cold-stratified seeds, exposure to high temperatures will result in germination rather than dormancy (Mumford 1988). In Mumford's study (1988), seed dryness was only examined in relation to storage temperature; dry seeds that were stored at 4°C required a shorter stratification period than dry seeds that were stored at higher temperatures.

Favorable conditions for storage of dormant *I. capensis* seeds are similar to those of *I. glandulifera* seeds. According to previous studies of *I. capensis*, at least four months or about 120 days of stratification at 5°C is required to break seed dormancy (Leck 1979). *Impatiens capensis* seeds also cannot tolerate desiccation and must be imbibed while they are stratified (Leck 1979).

Although neither *I. capensis* nor *I. glandulifera* is known for producing persistent seed banks, an experiment has shown that under some circumstances, *I. glandulifera* seeds can persist in seed banks for at least 18 months (Beerling and Perrins 1993). This could further increase the chances of *I. glandulifera* seeds germinating in favorable conditions. In general, variation in the depth of dormancy and sensitivity to dormancy-breaking conditions can increase the chances of producing seeds that will be viable in a range of environments (Bradford 2005). As a result, this variation can potentially be useful in invading new environments.

Seed Dispersal

Both species are capable of short-distance dispersal by explosive dehiscence of their seed capsules: *I. glandulifera* seeds are capable of traveling up to 5 m (Beerling and Perrins 1993), while *I. capensis* seeds are capable of traveling at least 2.2 m (Schmitt et al. 1985). In addition, seeds of both species can be dispersed by small rodents (Beerling and Perrins 1993), which may allow seeds to move short distances upriver. Long-distance dispersal can occur by water currents and by deliberate or unintentional spread by humans (Antlfinger 1989; Beerling and Perrins 1993). Studies of spatial correlations have shown that populations of *I. glandulifera* are significantly associated with riparian systems (Collingham et al. 2000), and *I. capensis* seeds are capable of floating (Parker and Leck 1985). These findings are consistent with observations that waterways act as a secondary method of seed dispersal in both species (Perrins et al. 1993). Since both species have been observed in habitats close to the coast, there is a chance that they are capable of dispersing between freshwater habitats via brackish waterways. By exploring

which factors affect the ability of seeds to float and the percent germination of seeds at varying levels of salinity, predictions can be made regarding the types of habitats to which they can be dispersed and how well they can establish in those new habitats.

METHODS

Collection Sites

Seedlings of native populations of *I. capensis* were collected from various sites in southern New England in the spring of 2003 and brought back to the Brown University Plant Environmental Center's greenhouse. Seeds from self-fertilized cleistogamous flowers were then harvested to establish laboratory lines. For my experiments, native populations of *I. capensis* seeds came from laboratory-reared descendants of plants collected from four different sites in April 2003: 1) "AJS," sun populations collected from the forest ecosystem in the Alton Jones campus of the University of Rhode Island in West Greenwich, Rhode Island; 2) "LWI," sun populations collected from Lincoln Woods State Park in Lincoln, Rhode Island; 3) "TW" and "TS," wood and sun populations, respectively, collected from the Touissett Marsh Wildlife Refuge of the Rhode Island Audubon Society in Warren, Rhode Island; and 4) "WW," wood populations collected from Weetamoo Woods in Tiverton, Rhode Island. The native populations were divided up into two groups. Plants from "sun" populations grow in areas with open canopy while plants from "wood" populations grow under predominantly red maple canopies that are the result of secondary growth.

Ornamental populations of *I. capensis* seeds were ordered from two different online seed companies. "Internet 1" are seeds from Easyliving Wildflowers (<http://www.easywildflowers.com>), which were collected from a wild population in Douglas County of south central Missouri (Clinton 2004a) in September 2004 (Clinton 2004b). "Internet 2" are seeds from Mikamoki Seeds (<http://mikamoki.safeshopper.com>), which were collected from their garden in Hocking County of Logan, Ohio late in the summer of 2004 and stored at room temperature (Mikamoki Seeds 2004).

Seeds from invasive populations of *I. glandulifera* were collected from three populations that were roughly 1 km inland of the western coast of Penobscot Bay of Maine in September 2004: 1) "Camden," which were collected from the town of Camden; 2) "Rockland," which were

collected from the town of Rockland; 3) “Thomas,” which were collected from the town of South Thomaston.

Experiment 1: Seed Dry Dormancy

For this experiment, native *I. capensis* seeds were harvested from laboratory-reared native lines of TW and WW in the greenhouse of Brown’s Plant Environmental Center and then stored dry at 4°C for up to one month (the native lines AJS, LWI, and TS were not used in this particular experiment). Ornamental *I. capensis* seeds from Internet 1 and Internet 2 were harvested by the companies, air-dried, and stored at room temperature before they were shipped. Upon arrival after shipping, the seeds were stored dry at 4°C for up to one month. Seeds from invasive populations of *I. glandulifera* from Thomas and Rockland were also used, but due to their extremely low percent germination in this experiment, I will focus mainly on the seeds from native and ornamental populations of *I. capensis*.

Seeds were subjected to 8 different treatments in a fully crossed randomized design in order to simulate the different environmental conditions to which dormant seeds could be exposed. The environmental variables were the length of treatment (2.5 months and 4 months), moisture during storage (dry and wet), and temperature during storage (room temperature or 25°C, and 4°C). Based on previous literature, the 4-months, wet, and 4°C treatment was considered the control treatment since *I. capensis* seeds require at least 120 days of stratification and *I. glandulifera* seeds require at least 89 days of stratification for greater germination success (Leck 1979; Mumford 1988).

The rest of the treatments subjected the seeds to stress conditions that were different from the optimal conditions within their native range. The 2.5-month treatments allowed us to determine how well seeds could tolerate reduced seed dormancy periods, which are environmental conditions that seeds could be exposed to in areas with more moderate climates such as England. The dry treatments allowed us to determine how well seeds could tolerate desiccation, which would simulate conditions that ornamental seeds could be subjected to while being stored or transported. Finally, the 25°C treatments allowed us to determine how well seeds could germinate without stratification, which could imitate the conditions of being stored or transported in a warmer climate. In addition to the control treatment (4-month, wet, 4°C), the other stress treatments were as follows: a) 4-month, wet, 25°C; b) 4-month, dry, 4°C; c) 4-month,

dry, 25°C; d) 2.5-month, wet, 4°C; e) 2.5-month, dry, 4°C; f) 2 months, wet, 25°C followed by 0.5 months, wet, 4°C; and g) 2 months, dry, 25°C followed by 0.5 months, wet, 4°C.¹

For TW and WW, 72 seeds from each population were placed into each treatment, which was a total of 72 x 8 or 576 seeds per native population. For Internet 1 and Internet 2, 36 seeds from each population were placed into each treatment, which was a total of 36 x 8 or 288 seeds per ornamental population. All seeds were placed in separate microtiter trays for each treatment, and distilled water was added to the microtiter trays of the seeds in the wet treatments. The trays were then loosely sealed in Ziploc bags. The microtiter trays of seeds in the 25°C treatments were kept in cardboard boxes in a drawer in the laboratory where the average temperature in the laboratory was around 25°C. The microtiter trays of seeds in the 4°C treatments were kept in a cardboard box in the laboratory refrigerator, which was set at 4°C. Wet seeds were checked once a month to insure that there was sufficient water and air available for the seeds. All seeds were also checked periodically and scored for moldiness; seeds that were moldy were discarded.

After the stress treatments, surviving seeds from all treatments were randomized and planted in 25.5 cm x 52 cm plug trays with 8 rows by 15 columns of wells. Each well was filled with “Metromix 360 with ScottsCoir,” an artificial soil medium from Scotts-Sierra Horticultural Products in Maryville, OH, USA. Initially, all plug trays were to be placed in growth chambers set at 18°C with 12-hour days with 8 fluorescent light bulbs and five 60W bulbs. Relative humidity in the growth chambers ranged from 34 to 36%. The trays were bottom watered every other day and scored for germination (and in some cases, moldiness).

However, while seeds from the 2.5-month treatments were in the growth chambers, there was a malfunction and the temperature in one of the growth chambers increased to 30°C. Twenty-five days after the seeds from the 2.5-month treatments were placed in the growth chambers, they were all moved to the greenhouse. For the rest of the experiment, the seeds from the 2.5-month treatments were in the greenhouse where they were bottom-watered every other day and scored for germination and moldiness. Seeds from the 4-month treatment also had to be placed in the greenhouse instead of the growth chambers after they completed the stress treatment since the growth chambers could not be set to a condition that was optimal for

¹ Treatments f and g have only 2 months of the stress treatment followed by 0.5 months in wet and 4°C conditions since a preliminary trial of the experiment showed that the combined stress of a shortened dormancy period and the lack of stratification was too severe and resulted in 0% germination for all populations. For simplicity and because the total length of Treatments f and g before planting is 2.5 months, Treatments f and g are referred to as “2.5-month treatments” along with Treatments d and e.

germination. The seeds from the 4-month treatment were also bottom-watered every other day and scored for germination and moldiness. Day length at the greenhouse varied slightly depending on the time of sunrise, but the average is 16 hours. Overhead high pressure sodium lights, which served as supplemental light sources, switched on around the afternoon until 8 pm. Relative humidity in the greenhouse was an average of 46.7%, and the average daily temperature ranged from 16.4°C to 21.0°C.

Experiment 2: Seed Water Dispersal Ability

Native populations of *I. capensis* harvested from the laboratory lines AJS, LWI, and TS and invasive populations of *I. glandulifera* from Camden, Rockland, and Thomas were used in this experiment (N = 480 seeds, with 80 seeds per population). All seeds were air-dried, weighed, and then placed in 1.5 ml plastic microcentrifuge tubes. 1 ml of distilled water was added to the tubes, along with different concentrations of NaCl (0 ppt, 10 ppt, 20 ppt, and 30 ppt), which were meant to simulate the salinities of different water bodies through which either species could be dispersed. Freshwater habitats have close to 0 ppt salinity while the approximate salinity in marine estuaries is around 10 to 20 ppt. The average salinity of ocean water is 35 ppt, although waters closer to the coast may be around 30 ppt (Bhatt 1983). Each treatment was applied to 20 seeds from each of the six populations, for a total of 120 seeds per treatment. Seeds that immediately sank to the bottom of the microcentrifuge tubes as soon as water and salt (if any) were added were recorded. All tubes were placed in cardboard boxes and stored in the refrigerator at 4°C. Seeds were checked once a week to see whether or not they were floating. After the *I. glandulifera* seeds had been in the microcentrifuge tubes for 4 months and the *I. capensis* seeds had been there for 3 months,² all seeds (both floating seeds and seeds that sank) were moved to microtiter trays filled with distilled water. One month later, they were planted in 8-by-15 plug trays filled with “Metromix 360 with ScottsCoir” and placed in the greenhouse. Seeds were also bottom-watered periodically and scored for germination and mold.

² *Impatiens capensis* seeds spent a shorter amount of time in the microcentrifuge tubes due to time constraints of the experiment.

Statistical Analyses

All statistical analyses were done using SAS Version 8.0, 1999. The LOGISTIC procedure was used to run a logistic regression to compare the percent germination among the different dormancy treatments in Experiment 1. It was also used to compare the percent germination of seeds in the control treatment between native and ornamental populations of *I. capensis* (Internet 1 and 2 seeds compared to TW and WW seeds). The FREQ procedure was used to compare the germination rate between all populations by looking at two variables: 1) the percent of seeds that germinated by Day 10 and 2) the percent of seeds that germinated after Day 10. Due to the malfunction in the growth chambers and consequent exposure to different conditions during germination of the 2.5-month stress treatment seeds, most of the analysis was focused on seeds from the 4-month treatments.

For Experiment 2, a Type III analysis of covariance (ANCOVA) was used within the GLM procedure with the number of days it took for a seed to sink as the dependent variable. (Seeds that sank but later floated were omitted from this analysis.) This test was used to examine the relationship between the days it takes for seeds from both populations to sink and salinity, weight of seed, species, and populations nested within species. All tests were run after the values for days to sink and seed weights were transformed so that the variables were normally distributed. This was done by taking each individual value within one variable (days to sink or seed weight), subtracting it by the mean of the values within the variable (average number of days to sink or average seed weight, respectively), and dividing the difference by the standard deviation of the values within the variable (standard deviation of the number of days to sink or standard deviation of the seed weight, respectively). In addition, post hoc comparisons in ANOVA (the Least Square Means comparison) were used to determine which species has seeds that take a greater number of days to sink. In order to examine the differences between seeds from invasive populations of *I. glandulifera* and native populations of *I. capensis* in more detail, I also looked for correlations between the days it takes a seed from each individual species to sink and two variables, salinity and weight. A two-sample t-test assuming unequal variances was used to determine whether or not the seed weights of *I. glandulifera* and *I. capensis* differed significantly. The germination data from Experiment 2 were also analyzed using logistic regression, and the values for percent germination were transformed like days to sink and seed weight so that the variables were normally distributed before analysis. This was used to

determine what factors (such as salinity, weight of seed, and days it took for the seed to sink) affected the percent germination of the seeds.

RESULTS

Experiment 1: Seed Dry Dormancy

Percent germination in stress treatments. Overall, the percent germination for all populations (N=1717 seeds) was highest in the control treatment, and this was significantly higher than any of the other treatments (see FIGURE 2). The percent germination of native and ornamental populations of *I. capensis* did not differ significantly among the stress treatments, which were all treatments excluding the control treatment (see FIGURE 2). The 2.5-month and 4-month treatments were analyzed separately using the LOGISTIC procedure. However, the number of germinators in stressed conditions was so small (and even zero in some cases) that none of the results were statistically significant even when results of the control treatment were excluded from the analysis.

Percent germination in control treatment. Native and ornamental populations of *I. capensis* differed in percent germination within control conditions (the 4-month, wet, 4°C treatment; N=214 seeds). Using the LOGISTIC procedure, I found that there was a significant difference in percent germination in control conditions between native and ornamental populations ($P < 0.0001$), with native populations germinating at higher percentages.

Germination rate in control treatment. Using the FREQ procedure, I compared the percent of seeds that had germinated by Day 10 (out of all the seeds that germinated) and the percent of seeds that germinated after Day 10 (out of all the seeds that germinated) between the different populations. Day 10 was selected since it was around the middle of the period of seed germination. Populations differed in the percent of seeds that germinated before Day 10 and seeds that germinated after ($P = 0.0002$ for both variables). Roughly 90% of the Internet 1, Internet 2 and TW seeds that germinated in the experiment had germinated by Day 10 while 67% of all the WW seeds that germinated in the experiment had germinated by Day 10.

When germination rate was defined as the change in percent germination over time (measured in days after seeds were planted) Internet 1, Internet 2 and TW had similar

germination rates: their germination rate was greatest in the first 4 to 6 days after they were planted, followed by a marked decrease in germination rate after Day 6 (see FIGURE 3). On the other hand, the germination rate of WW was lower than that of the other three populations (see FIGURE 3). However, since its germination rate remained relatively constant and did not decrease until 16 days after the seeds were planted, the total percent germination of WW was the highest out of all populations. In a sense, the germination rate of TW was more similar to the germination rates of the ornamental populations than to WW. This difference in germination rates between TW and WW could indicate the variation within native populations that are found within close proximity and in similar habitats. When doing further comparisons between native and non-native populations of *I. capensis*, it would be important to keep in mind that native populations can be very heterogeneous.

Experiment 2: Seed Water Dispersal Ability

Overall factors that affected floating ability. Floating ability was affected only by salinity and differed between the species (see TABLE 1). Within *I. capensis* seeds (N=234 seeds), floating ability was affected by both salinity and weight (see TABLE 2). Within *I. glandulifera* seeds (N=238 seeds), there were no statistically significant relationships. In terms of the post hoc results, the Least Square Means difference between *I. capensis* and *I. glandulifera* was 140.3 days ($P < 0.0001$), and *I. capensis* took longer to sink than *I. glandulifera*.

Effects of salinity and species on the floating ability of all seeds. After isolating factors that affected the days for a seed to sink, I examined some of the relationships in greater detail. The relationship between floating ability, species, and salinity was examined in a log plot of the percent of *I. capensis* and *I. glandulifera* seeds floating in different salt treatments over time, which was measured in days (see FIGURE 4). However, since very few *I. capensis* seeds in the 0 ppt salt treatment and the 10 ppt salt treatment actually sank, the R^2 values for the best-fit lines were small. As a result, these R^2 values suggest that a logarithmic function might not be the best model for those two treatments (see FIGURE 4). Overall, a greater proportion of *I. capensis* seeds than *I. glandulifera* seeds remained floating across all treatments. The floating ability of *I. glandulifera* seeds was also less sensitive to changes in salinity than the floating ability of *I. capensis* seeds. Most *I. glandulifera* seeds simply sank within the first 40 days regardless of

their salt treatment, while *I. capensis* seeds sank more gradually, which is consistent with the post hoc results.

Effects of salinity and weight on the floating ability of I. capensis seeds. Within *I. capensis*, a greater proportion of seeds remained floating in water with lower concentrations of salt: 79% remained floating in water with 0 ppt salt and 83% remained floating in water with 10 ppt salt while 70% remained floating in water with 20 ppt salt and 35% remained floating in water with 30 ppt salt (see FIGURE 4). Similar to *I. glandulifera*, when I examined only the *I. capensis* seeds that sank, the majority of them sank within the first 40 days as well. In terms of the relationship between days to sink and weight among *I. capensis* seeds, although the GLM procedure showed that there was a significant correlation, I was unable to determine the exact nature of the correlation since none of the regression lines fitted had meaningful R^2 values.

Factors that affected percent germination of I. capensis. Only one *I. glandulifera* seed germinated; thus, all the analyses of germination were done using data from *I. capensis* seeds. From the results of logistic regression (see TABLE 3), salinity, weight, and days to sink affected the percent germination of *I. capensis*. I found that the percent germination decreased as salinity increased (see FIGURE 5). However, there was not a steady decline in percent germination as salinity increased. Instead, it appears that percent germination decreased sharply after reaching a critical threshold of salinity. Moreover, the majority of germinators across all salt treatments were seeds that never sank (see FIGURE 6). Some of the seeds that sank in the first few days also had a higher percent germination than seeds that sank later (see FIGURE 6). Further discussions on the effect of weight on the percent germination of *I. capensis* seeds are in the APPENDIX section.

DISCUSSION

The results of the two experiments conducted provide information that can help predict the future dispersal of *I. capensis* and *I. glandulifera*. By understanding how *I. capensis* seeds responded to the different dormancy treatments in Experiment 1 and by examining the differences in the floating ability of *I. capensis* and *I. glandulifera* in Experiment 2, I can make predictions on where they can establish and how readily they can escape from controlled

environments. This can be useful in preventing invasions from happening at an early stage when plant populations are easier to control.

Very few seeds from native or ornamental populations of *I. capensis* were able to germinate after exposure to the stresses imposed in Experiment 1. Therefore, it was difficult to compare the relative ability of native and ornamental populations to tolerate dryness, lack of stratification, and shortened dormancy period. While it is possible that *I. capensis* simply does not respond to selection by horticulturalists, it is also probable that *I. capensis* is not a species that is selected for greater dry dormancy by these particular online seed companies or perhaps by horticulturalists in general. Nonetheless, it is important to consider that horticulturalists may select for other traits besides seed dry dormancy that could improve the ability of a plant to invade. Perhaps these traits are expressed at later life-history stages, including higher reproductive output or adult stress-tolerance.

The percent germination of ornamental seeds in the control treatment, which may be an indication of their viability, was also lower than that of native seeds. One possible explanation for this may be the fact that ornamental seeds were already exposed to some of the stresses tested by the experiment. Before even starting the experiment, the seeds were already exposed to desiccation and lack of stratification during their storage, shipping, and transport. The result of these additional stresses on ornamental seeds before the treatments in the experiment began may have led to lower germination in the control treatments and possibly lower than normal observed germination in the stress treatments. Another alternative could be that the ornamental seeds had not completed their stratification requirement and were still dormant.

Although the overall number of seeds from all populations that can tolerate the stress treatments is small, the fact that a few seeds were able to tolerate desiccation, lack of stratification, and a shortened dormancy period means that they still have the potential to spread into habitats with environmental conditions that are very different from their native range. This selection bottleneck may enable them to produce offspring that can tolerate the same stresses and establish new colonies or nascent foci that aid in invasive spread (Moody and Mack 1988). Seeds that can tolerate dryness may be able to move farther inland and away from streams or disperse more effectively from stream to stream separated by dry habitats. A greater proportion of them may also remain viable after they have been dried and shipped. Seeds that can germinate without stratification may be able to establish in warmer climates at lower latitudes.

Seeds that can germinate after a shortened dormancy period also may be able to establish in areas of the world with shorter, more moderate winters; such conditions might become more prevalent under global climate change (Sala et al. 2000). More specifically, increased average temperatures could allow *I. capensis* and *I. glandulifera* to spread to northern latitudes as winters become warm enough to reach the optimal temperature for stratification. In fact, native populations of *I. capensis* found in the southern region of the United States where winters are more moderate suggest that some native populations of *I. capensis* can already thrive in milder climates. Thus, a rise in average global temperature could allow these populations to shift their range and potentially invade new habitats.

Floating ability is an important quality in *I. capensis* and *I. glandulifera* since they are often found in riparian habitats, and water dispersal is one mechanism that allows them to spread and establish new populations. By testing the floating ability of seeds from native populations of *I. capensis* and invasive populations of *I. glandulifera*, I found that a greater proportion of seeds remain floating in water with lower concentrations of salt. This contradicts my initial hypothesis that seeds will float longer in higher salinity. At the same time, increasing salinity decreases the percent germination in *I. capensis* seeds. As a result, salinity appears to be a powerful stress: not only do more seeds sink in water with higher concentrations of salt, fewer seeds germinate as well. In fact, since the majority of the seeds that sank never germinate, sinking could be an indication of the loss of viability.

Similar to the case of stress tolerance, however, the fact that a small percent of seeds were still able to germinate even after being immersed in 20 and 30 ppt saltwater means that they have the potential to spread into environments that are very different from their native habitats and could potentially produce offspring that can tolerate dispersal in brackish waters. More specifically, it could allow them to travel between freshwater habitats connected by salty waterways, such as two tributaries separated by a tidal estuary. For example, the Norfolk Broads of Britain, near the site of the second introduction of *I. capensis*, is a large, low-lying wetland that is often inundated by tidal waters. Since populations of *I. capensis* can be found along the many tributaries that are connected to the Broads, salt-tolerant seeds may be able to travel great distances along tributaries, even ones that are separated by the wetland.

Another important factor to consider is that although *I. glandulifera* seeds do not float in water as long as *I. capensis* seeds, 40 days can still be enough time for *I. glandulifera* seeds to

disperse to new habitats and to establish new populations. This is especially significant since *I. glandulifera* can produce an average of 500 to 800 seeds per medium-sized plant, with greater fecundity at lower densities than high densities (Beerling and Perrins 1993). Even though the percent germination is slight, a small proportion of 500 to 800 *I. glandulifera* seeds that do survive in new habitats can grow into many adults, which can create a considerable presence in a few generations.

A higher proportion of *I. capensis* seeds are capable of floating indefinitely and, on average, they also take more days to sink than *I. glandulifera* seeds. However, *I. glandulifera* tends to be found along fast-moving rivers and streams while *I. capensis* is found along slower-moving canals (Beerling and Perrins 1993). Thus, although *I. glandulifera* seeds sink much faster, seeds from both species may be capable of traveling equally far from their source populations.

While these results provide a considerable amount of information that can be used to make predictions on future dispersal, they also highlight a number of limitations to the spread of *I. capensis* and *I. glandulifera*. As previously mentioned, studies have found *I. capensis* to be a less successful invader compared to other invasive species of *Impatiens*; thus, its impact in communities where it has to compete with other invasive species of *Impatiens* may be limited. In addition, *I. glandulifera* may also experience some limitations to invasive spread. Results from the floating seeds experiment indicate that *I. glandulifera* seeds sink quickly. Therefore, their capacity for invasive spread may be limited to habitats that are along fast-moving rivers since most of their seeds would sink to the bottom of slow-moving streams or canals. One study has shown that *I. glandulifera* plants are also sensitive to drought (Beerling and Perrins 1993). This could imply that while *I. capensis* seeds have the capacity to move inland or away from streams and rivers to dryer habitats, *I. glandulifera* seeds and/or plants are more restricted to habitats with a significant amount of moisture. In addition, *I. glandulifera* does not spread to areas where soil pH is below 3.5 (Beerling and Perrins 1993). This information could be particularly relevant to New England, where soils are often very acidic. For example, the Berkshires of western Massachusetts have some of the least acidic soils in New England and this may explain why many populations of *I. glandulifera* are found in that area. Based on all this information, one could rank habitats by the likelihood of invasion by *I. capensis* and *I. glandulifera* seeds and better predict where future populations may appear.

Literature Review: Overlaps Between Characteristics of Ornamentals and Invasives

The experiments mentioned above were conducted in order to examine two possible pathways by which ornamentals can become invasive. While this recognizes the potential negative impacts of introducing ornamentals in general, not every introduced ornamental becomes invasive. Instead, there may be particular types of ornamentals that are more likely to invade. From a regulatory standpoint, it would be difficult to completely restrict all exotic ornamentals from the market. However, scientists can make a case against introducing specific exotic ornamentals that have a high potential for invading, based on the extensive work done on previous invasions. By surveying literature dedicated to identifying qualities associated with invasiveness and literature concerning ornamental plants that have become invasive, I hope to better understand which types of ornamentals pose a greater risk of being invasive and how to prevent these ornamentals from establishing and invading.

There are numerous qualities linked to invasiveness and causes of invasion can be varied, but there are some consistent qualities found in invasive species that were once ornamentals. Studies have found that species that have a history of invasion in one region of the world can have a greater chance of invading if they are introduced into a new region (Reichard and Hamilton 1997; Kolar and Lodge 2001). This is especially important for ornamentals since they are often introduced repeatedly to different parts of the world. This case applies to *I. glandulifera*, which was introduced as an ornamental and is now invasive in England (Beerling and Perrins 1993; Perrins et al. 1993), parts of central Europe (Pysek and Prach 1993), and coastal areas as well as areas around the Great Lakes in the United States (USDA 2004). In a more extreme case, *Eichhornia crassipes* or the common water hyacinth, was originally a native of Brazil and was introduced to numerous regions of the world as an ornamental; now, it is an invasive species throughout most of Central and South America, Australia, China, India, Japan, Thailand, and South Africa (Penfound and Earle 1948). It was first introduced into ponds and gardens as a decorative plant in the United States in 1884 (Penfound and Earle 1948). Since then, it has been listed in many states as a noxious weed or pest (USDA 2004), and it is responsible for millions of dollars of economic loss annually by obstructing navigation, impeding drainage, and destroying wildlife resources (Penfound and Earle 1948). As a result, significant environmental and economic costs can be avoided if countries – or even states and provinces within countries –

ban the import of plants that are known invaders in other parts of the world, especially areas with similar environmental conditions to the region in which the plant is being imported.

Plants belonging to a family or genus with species that are already invasive in the region where the plant is being introduced have a high probability of becoming invasive as well. Closely related plants (i.e. congeners or plants within the same taxonomic genus) may be more likely than distant relatives to share traits that enable them to establish novel populations and invade. For example, *I. parviflora*, *I. capensis*, and *I. glandulifera* were all introduced to England as ornamental garden plants (Preston et al. 2002). Now, *I. glandulifera* is a well-established invader while *I. parviflora* and *I. capensis* are also invasive but to a lesser extent (Perrins et al. 1993). Another example of this phenomenon is known in members of the genus *Lonicera*. Species such as *L. maackii* or Amur honeysuckle, *L. morrowii* or Morrow's honeysuckle, and *L. japonica* or Japanese honeysuckle, which were originally introduced as ornamentals, are now invasive in various regions of the United States (Huchinson and Vankat 1997). Judging from these examples, taking steps to limit or prevent the introduction of species within families and genera with invasive species may be a necessary precaution.

Another commonly cited characteristic of invasive plants is the evolution of invasiveness or the ability of introduced plants to undergo rapid genetic changes that improve their ability to establish and invade new habitats (Clements et al. 2004; Hierro et al. 2005). Studies have shown that even with low genetic variation, introduced plants can adapt to a range of habitats due to phenotypic plasticity (Novak et al. 1991; Williams et al. 1995; Clements et al. 2004). *Impatiens capensis* exhibits considerable phenotypic plasticity in terms of its response to density (Donohue et al. 2001; Schmitt et al. 2003) and shade (Schmitt et al. 2003), which can allow it to establish in environments that vary widely in terms of density and light availability. *Lonicera japonica* is another invasive species that exhibits phenotypic plasticity for leaf phenology, plant architecture, and response to herbivory (Schierenbeck 2004). This allows it to establish in a heterogeneous variety of habitats. It also recovers from herbivory more rapidly than native species (Schierenbeck et al. 1994). Although one study has highlighted limitations on using plasticity to explain invasions (Lee 2002), such flexibility could interact with other mechanisms to improve the ability for a plant to invade. As a result, ornamental plants that exhibit phenotypic plasticity should be examined more closely for other characteristics associated with invasiveness before they are allowed to be introduced into a new environment.

By identifying overlaps between characteristics of ornamentals and invasives, one can better determine which ornamental plants and/or what type of ornamental plants should be discouraged or banned from sale or propagation. Although not all plants with these characteristics establish and negatively impact native species and habitats, the risk of environmental and economic losses from ornamental invaders is great and the long-term health of native ecosystems and species should take precedence over short-term economic benefits from importing or selling potential invasive ornamentals. While this is not an exhaustive review of all the overlaps between characteristics of ornamental plants and invasive plants, it provides a preliminary overview of possible areas to look into in order to better understand the pathway between an ornamental and an invasive. Furthermore, many of these characteristics are found in other types of introduced plants so this information can be used to assess the potential invasiveness of non-ornamental exotics as well.

Policy Issues Regarding the Introduction and Establishment of Invasive Species

Current laws and regulations regarding the introduction and establishment of invasive species range from international agreements to local statutes and bills within different countries. While some international treaties such as the United Nations Environmental Program's Convention on Biological Diversity recognize the threat that is posed by invasive species, organizations such as the World Trade Organization ignore this and continue to encourage the free movement of goods, even invasive and potentially invasive species (Le Maitre et al. 2004). It appears that implementation of treaties that aim to prevent the negative impacts of invasive species is problematic in the international community due to the high volume of international treaties and their occasionally conflicting goals.

In terms of local statutes and bills, for the purposes of this paper, I will focus mostly on those within United States, particularly New England. In the past, the United States government has created a number of acts that limit the shipment of certain alien plant and animal species into the country. In 1996, the National Invasive Species Act was created, but its scope was not significantly different from the Non-indigenous Aquatic Nuisance Prevention and Control Act of 1990, which mostly deals with the control of aquatic invasive species and their introduction through ballast waters (USDA 2004). The Plant Protection Act of 2000 mainly deals with preventing the introduction of noxious weeds that harm agricultural crops (USDA 2004).

Although federal, state and local governments have set out many regulations and programs that restrict new invaders and manage and eradicate established ones, many of these regulations and programs are fragmented among dozens of agencies at the national level, and hundreds at the state and county level (Schmitz and Simberloff 2001).

Local governments vary greatly in terms of their policies concerning invasive species since there is no federal legislation that explicitly states what action should be taken specifically to prevent the introduction of invasive species (i.e. by importing, transporting, propagating, or selling invasive species) and how these measures can be enforced. In New England, only one state recognizes *I. glandulifera* as an invasive and has legislation to prevent its spread. The State of Connecticut's House Bill 547 "An Act Concerning Fines for Banned Invasive Plants" specifically lists *I. glandulifera* as one of the plant species that no person may "import, move, sell, purchase, possess, cultivate, or distribute," or else s/he may be fined no more than \$100 (State of Connecticut 2004). Maine and New Hampshire both have statutes that prohibit the sale, transportation and propagation of a list of invasive species but do not recognize *I. glandulifera* as one of them (Mehrhoff et al. 2003). Thus, it is possible that *I. glandulifera* is still not seen as a threat compared to other more visible invaders like *Ailanthus altissima* (tree of heaven) or *Polygonum cuspidatum* (Japanese knotweed), which are all banned in Maine and New Hampshire. In Vermont, there is legislation that encourages the control of invasive populations, but it does not address ways to prevent introductions of invasive species (Mehrhoff et al. 2003). Rhode Island legislation does not explicitly touch upon deliberate introductions of invasive species but tries to prevent the accidental introduction of potentially invasive species through ship ballast water (Mehrhoff et al. 2003). Finally, in Massachusetts, there is no legislation that deals specifically with invasive plants (Mehrhoff, Silander et al. 2003; USDA 2004). However, the Massachusetts Invasive Plant Advisory Group, which was formed by the Ad Hoc Native Plant Advisory Committee in 1999 and is recognized as part of the Massachusetts Council on Invasive Species, works with various organizations (including horticulturalists) to identify invasive plants and strategies for managing the spread of invasives (MIPAG 2005a; MIPAG 2005b).

From reviewing laws and regulations that aim to prevent the introduction and establishment of invasive species, it seems that international treaties on free trade must recognize the importance of using the precautionary principle in certain situations, such as the trade of

invasive and potentially invasive organisms, and exercise more caution over which products can be openly traded. In terms of United States federal regulations, their scope should be expanded to address a broader definition of invasive species and not just aquatic invasive species and noxious weeds. Individual governmental agencies should also continue to work on coordinating their efforts to regulate and more effectively control invasive and potentially invasive species (Schmitz and Simberloff 2001).

Laws and regulations in some New England states are moving in the right direction. Since invasions are a transboundary problem and require the cooperation of neighboring states however, it is essential to get even more states, not only those within New England, involved. For example, many of the populations of *I. glandulifera* surveyed in Massachusetts were found along the Housatonic River, which flows through both Massachusetts and Connecticut. Even though Connecticut has strict laws preventing the introduction of *I. glandulifera*, Massachusetts has no legislation preventing the introduction of this species or any other invasive plants. Because *I. glandulifera* seeds are capable of water dispersal, there is a chance that they can spread downstream from Massachusetts to Connecticut. This demonstrates that there must be a coordinated effort between states in order to effectively prevent the introduction, establishment, and spread of invasive species.

Overall, laws and regulations should offer more specific guidelines on how one can prevent the introduction and establish of invasive species. The creation of these policies can be greatly supported by continued research on the process of invasion. For example, with more information regarding traits associated with invasiveness and susceptibility to invasion, more stringent screening processes for imported organisms could be set up at various borders to prevent invasive species from being introduced in the first place. One method that has been suggested is to set up a screening process for imported plants, with importers bearing the cost of screening (Reichard and Hamilton 1997). In return, if the species being imported passes the screening and has a low invasive potential, the importer could have exclusive rights to control and distribute cultivars of that species for a given period of time (Reichard and Hamilton 1997). A separate fund should be available for the control of species that become invasive even after the screening process so importers would not have to bear these costs and be discouraged from complying with screening regulations (Reichard and Hamilton 1997). Through similar economic

incentives, policymakers have the potential to effectively control the introduction and establishment of invasive species on a much broader scale.

In addition to having laws and regulations in place to prevent the introduction and establishment of invasive species, it is essential that governments and organizations educate the public on the negative impacts of invasive species and promote the use and sale of native species whenever possible. Certain nurseries and retail outlets still sell invasive ornamentals, and landscape designers have been known to use invasive species for decorative purposes. These are problems that deserve attention, and it is important for scientists, policymakers and buyers and sellers of ornamentals to continue to work together and limit the deliberate introduction of harmful invasive species. Currently, there is little published scientific evidence for the harmfulness of specific invasive ornamentals, which could be why nurseries, retail outlets and landscape designers are hesitant to stop selling or using those species. This highlights the importance of continued research on the actual impacts of invasives. While not all exotics are invasive or potentially invasive, in general, the merits of selling and using only native plants whenever possible should be more highly promoted among all those who participate in the sale and use of ornamentals. By getting as many individuals as possible involved in issues regarding invasive species, there is a better chance of preventing the harmful effects of introduction, establishment and spread of invasions.

FURTHER RESEARCH

In this paper, I have examined the introduction and establishment phases of invasive plants that were introduced as ornamentals by studying seed dry dormancy and water dispersal in native and ornamental populations of *I. capensis* and invasive populations of *I. glandulifera* in the United States. Due to unexpected challenges during the seed dry dormancy experiment, however, I feel that more research should be done to determine the role of horticultural selection on stress tolerance. Determining the viability of seeds would also be helpful in future comparisons of stress tolerance.

One possible outgrowth of the experiments mentioned above could be to collect the germinators from different treatments and compare and contrast stress tolerance, along with other traits, at later stages of life from seedlings to full-grown adults. Comparing the entire life-history of populations of *I. capensis* and *I. glandulifera* plants, not only their seeds, could

provide valuable information on how invasive populations behave (Clements et al. 2004) and consequently, how they can be controlled. For example, poor weed biocontrol can be attributed to the lack of information regarding which life-history stages are demographically important (Hierro et al. 2005), so a more complete picture of plant life cycles could improve the effectiveness of controlling invasive populations.

Hierro et al. (2005) emphasized the importance of comparing populations of exotics in both their introduced and native ranges so future research should be conducted by observing both native populations of *I. capensis* in the United States and invasive populations in England as well as both native populations of *I. glandulifera* in the Himalayas and invasive populations in both England and the United States. Populations can exhibit different traits in their native and introduced habitats (Hierro et al. 2005). Thus, by examining the differences in the traits of populations in their native habitat and populations in their introduced habitat, scientists can determine the underlying mechanisms of invasion, which can aid in assessing their impact and potentially minimize the harm caused by these invasions. One example is a comparative study that examined demographic differences in populations of *Echium plantagineum* in its native and recipient habitats (Grigulis et al. 2001). From this study, it was suggested that the seedling establishment rates of *E. plantagineum* may be linked to invasive success (Grigulis et al. 2001). Using this type of information, scientists and policy makers can know which characteristics and traits to focus on in order to more efficiently control invasive populations.

The research in this paper has focused mainly on characteristics of ornamentals that enable them to invade new environments. However, the likelihood of invasion depends on the habitat that is being invaded as well. Research has shown that areas with lowered biological diversity and/or areas that have undergone disturbances are much more susceptible to invasion than stable environments with greater species richness (Chapin et al. 2000; Hierro et al. 2005). Many ornamentals are introduced into gardens, which can be thought of as a disturbed area in some ways since they are constantly being used and modified by humans. In addition, the environments outside gardens to which ornamentals could potentially escape are often roadsides, suburban woodlots, and other disturbed areas as well. These environments frequently have low species richness so there may more niches or unused resources readily available for exotics to appropriate (Chapin et al. 2000). Therefore, further studies could look into patterns in

environments where horticultural plants are introduced, where they escape to, and where they eventually become invasive.

For as long as humans have been migrating across the globe, they have brought along species from their native environments and introduced them into new habitats. Although most of these species are relatively harmless, some do become invasive and drastically change native habitats and species composition and abundance. The environmental and economic losses caused by these species are great, and it is important for policy makers to find effective ways of combating the introduction, establishment, and spread of invasive species. By taking greater responsibility for the role that humans play in invasion biology, more can be done to solve this problem.

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APPENDIX

In Experiment 2, the seed water dispersal ability experiment, I noticed a number of correlations with weight, which did not directly relate to the questions I was trying to answer but are worth further examination in future research. On average, *I. glandulifera* seeds are much heavier than *I. capensis* seeds ($p < 0.0001$, t critical one-tail = 1.6494). The mean weight of *I. glandulifera* seeds is 15.4 ± 0.020 mg while the mean weight of *I. capensis* is 8.02 ± 0.0041 mg. As previously mentioned, results from the GLM procedure indicate that the number of days it takes for an *I. capensis* seed to sink is affected by seed weight but the nature of this correlation is unknown (see FIGURE 7). There was also a correlation between seed weight and the percent germination of *I. capensis* seeds. The percent germination was at its maximum for seeds that are close to the mean weight of *I. capensis* seeds (see FIGURE 8). In terms of the two-way interaction between salt concentration and weight (see FIGURE 9), germination was greater at lower salt concentrations such as 0 ppt and 10 ppt across all weights, except for seeds that weighed less than 0.004 g. While I am uncertain if these correlations are meaningful to my experiment, they may lead to interesting questions in general studies of the seed biology of *I. capensis*.

TABLES

TABLE 1: Relationship between days for a seed to sink and various factors. Statistically significant results appear in bold.

Source	DF	Mean Square	F Value	Pr > F
Salt	1	3.86907748	4.09	0.0436
Weight	1	2.58849644	2.74	0.0986
Species	1	13.02977330	13.79	0.0002
Pop'n (Species)	4	0.55158146	0.58	0.6747
Salt * Weight	1	3.25377821	3.44	0.0642
Salt * Species	1	20.62102375	21.82	< .0001
Weight * Species	1	1.51068208	1.60	0.2068

TABLE 2: Relationship between days for a seed to sink and various factors for *I. capensis*. Statistically significant results appear in bold.

Source	DF	Mean Square	F Value	Pr > F
Salt	1	23.44690052	26.66	<.0001
Weight	1	6.58643566	7.49	0.0067
Pop'n	2	5.06981895	2.88	0.0581
Salt * Weight	1	0.56859933	0.65	0.4222
Salt * Pop'n	2	4.53508189	2.58	0.0782
Weight * Pop'n	2	6.69154184	3.80	0.0238
Salt * Weight * Pop'n	2	1.22543620	0.70	0.4994

TABLE 3: Relationship between germination and various factors for *I. capensis*. Statistically significant results appear in bold.

Parameter	DF	Estimate	Error	Chi-Square	Pr > ChiSq
Salt	1	-0.3338	0.0575	33.7376	<.0001
Weight	1	1.7455	0.8412	4.3059	0.0380
Days	1	1.5507	0.7664	4.0944	0.0430
Salt * Days	1	-0.0234	0.3880	0.3791	0.5381
Salt * Weight	1	-0.1106	0.0432	6.5536	0.0105

FIGURES

FIGURE 1: Distribution of *Impatiens glandulifera* in New England

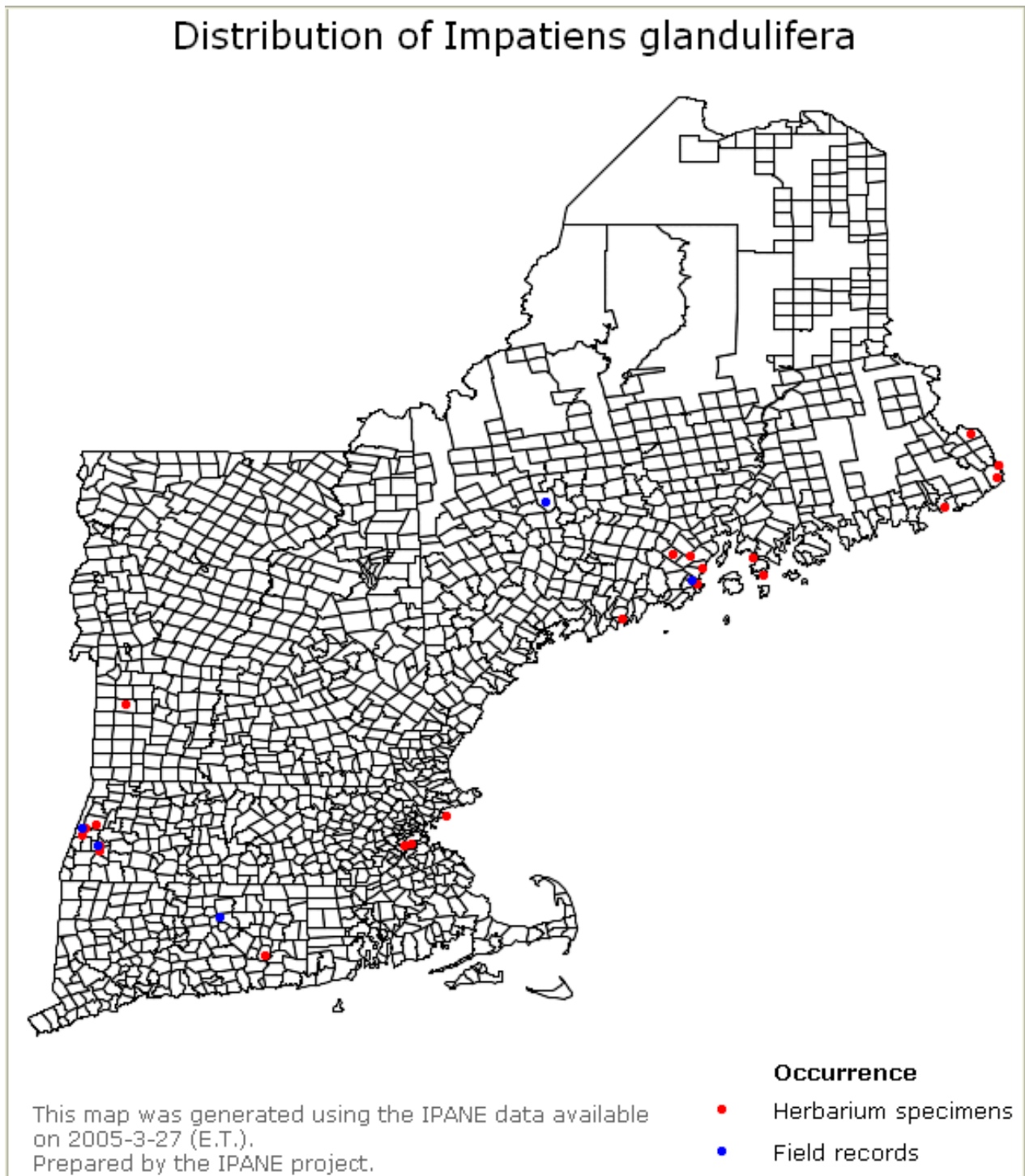


FIGURE 2: Percent germination for all populations in different treatments. The numbers above the bars indicate the percent germination.

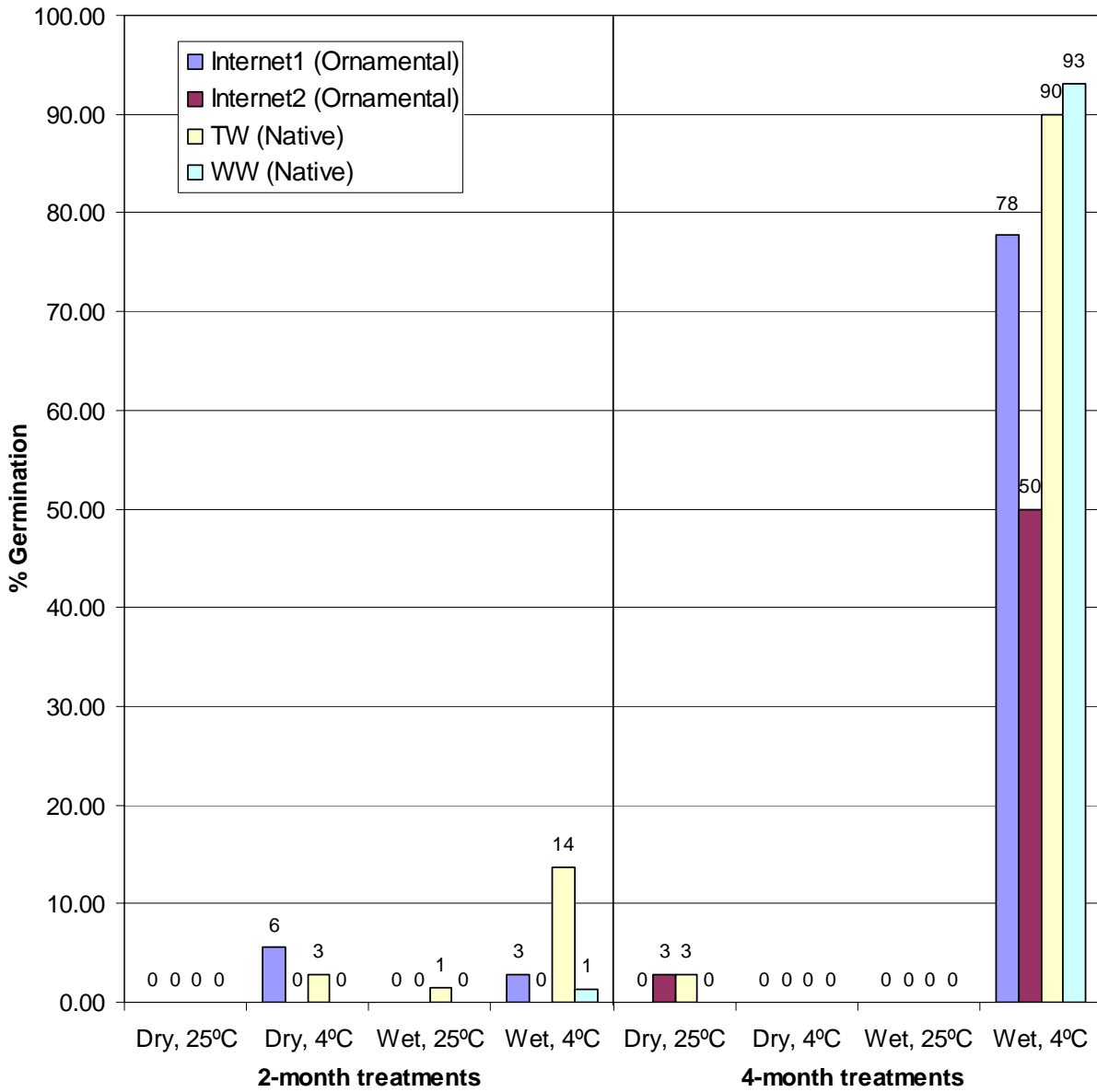


FIGURE 3: Germination of different populations in control conditions (4-month, wet, 4°C)

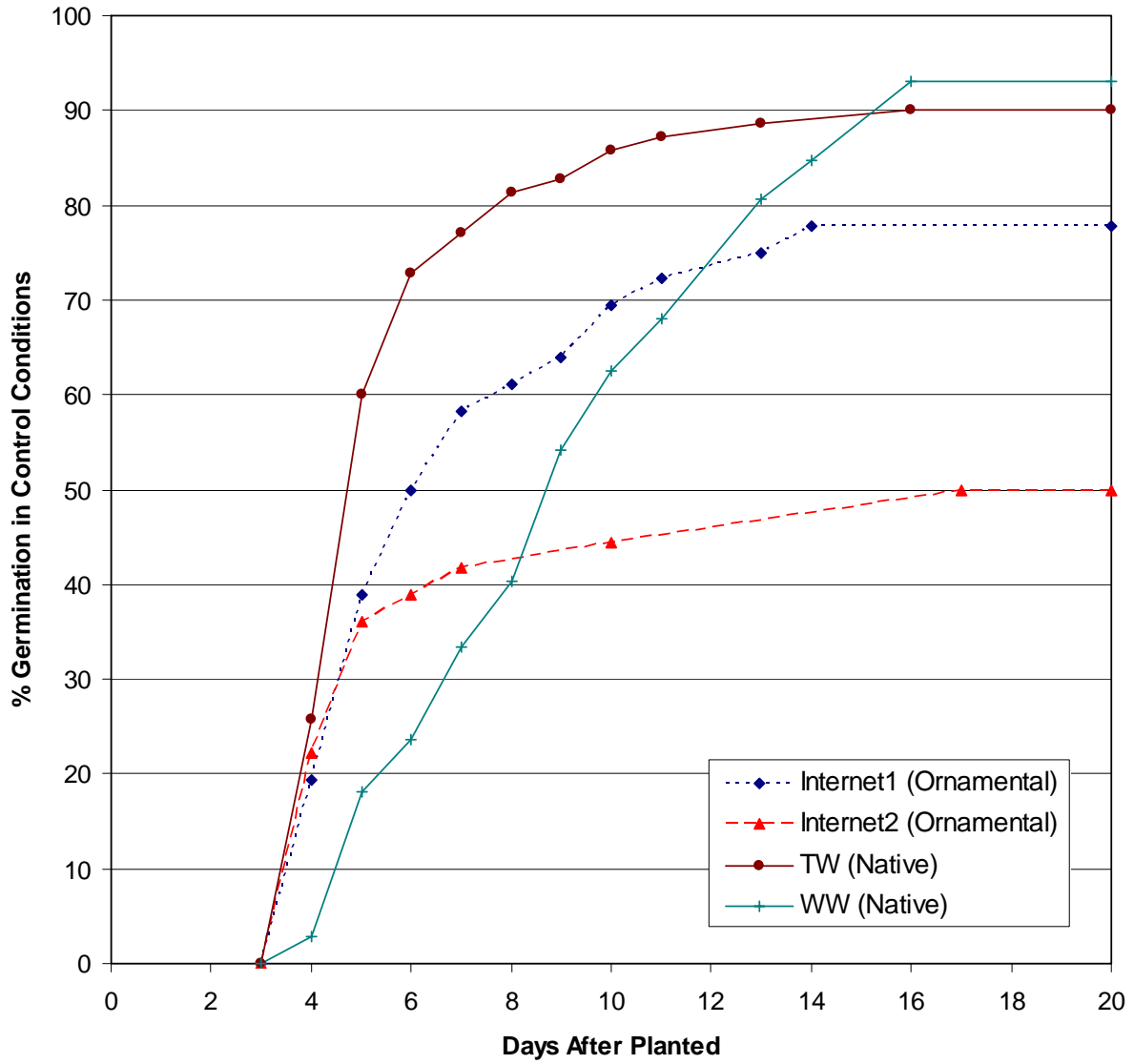


FIGURE 4: Log plot of the percent of floating *I. capensis* (C) and *I. glandulifera* (G) seeds in different salt treatments over time with best-fit logarithmic lines. Due to the poor fits for *I. capensis* seeds in the 0 ppt salt and the 10 ppt salt treatments, they are not shown on this log plot.

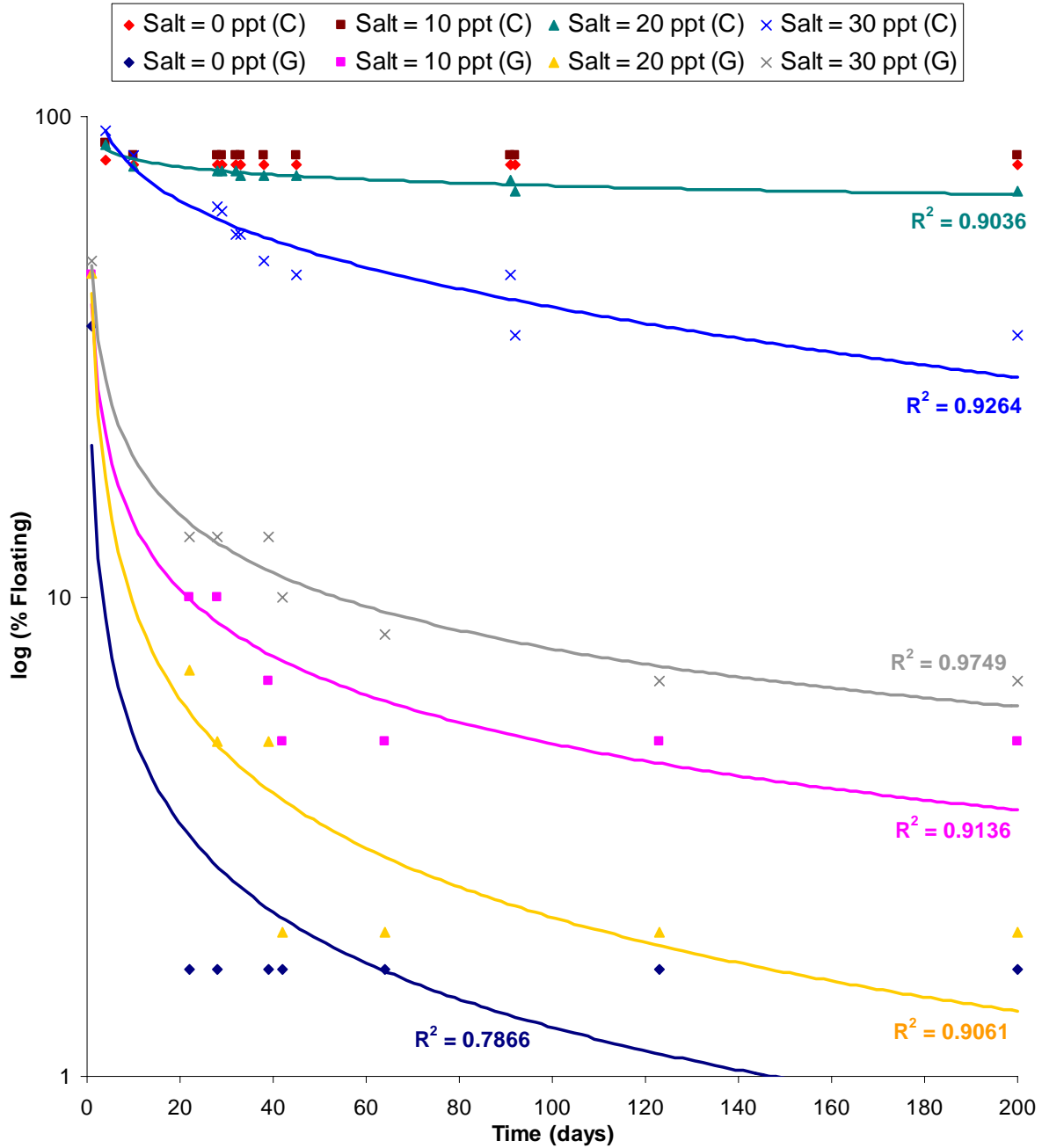


FIGURE 5: Percent germination of *I. capensis* at different salt concentrations.

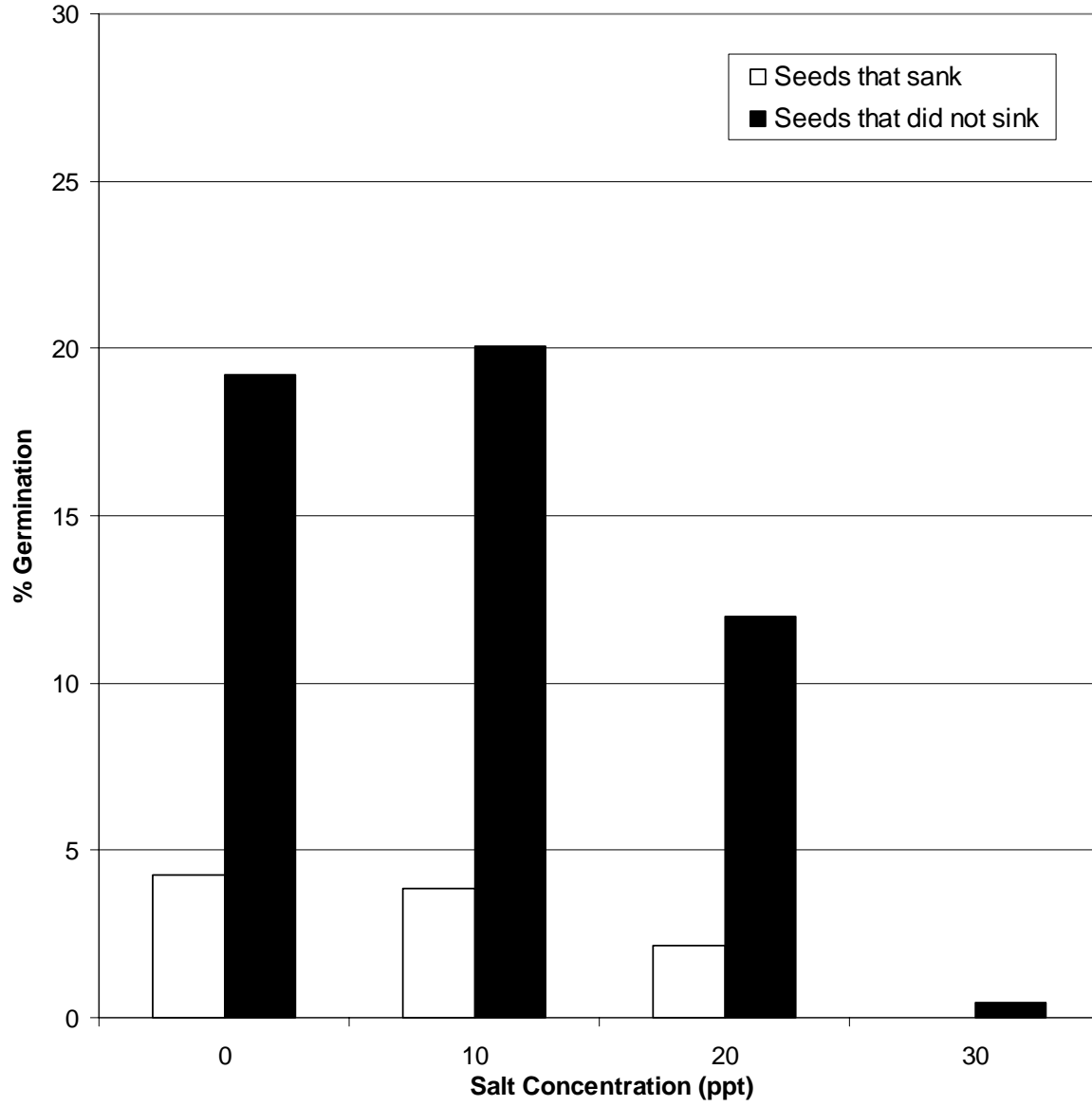


FIGURE 6: Percent germination of *I. capensis* seeds in different salt treatments and days to sink. Seeds that floated for 200 days did not sink during the experiment.

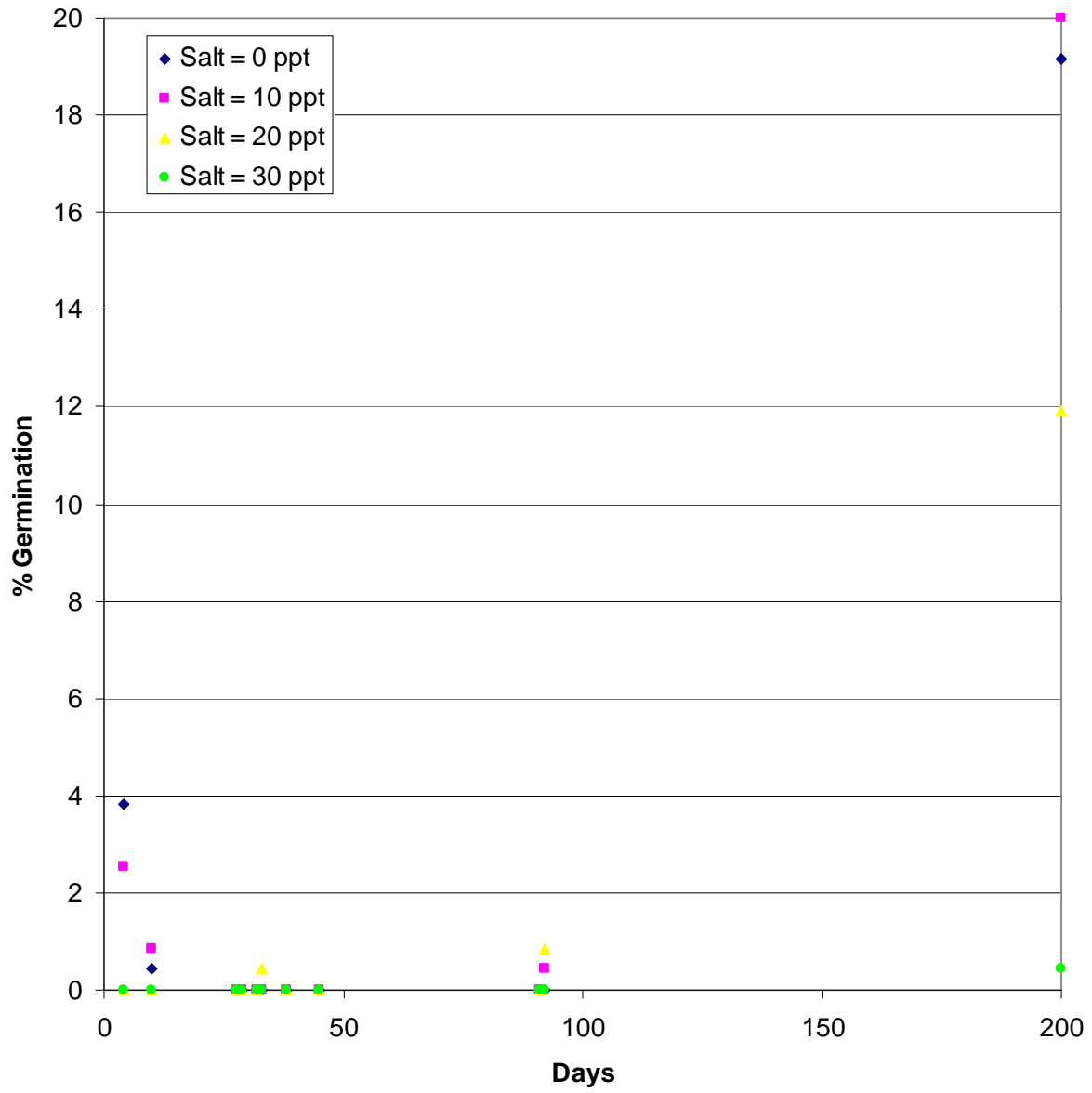


FIGURE 7: Days to sink for *I. capensis* seeds of different weights. Seeds that floated for 200 days did not sink during the experiment.

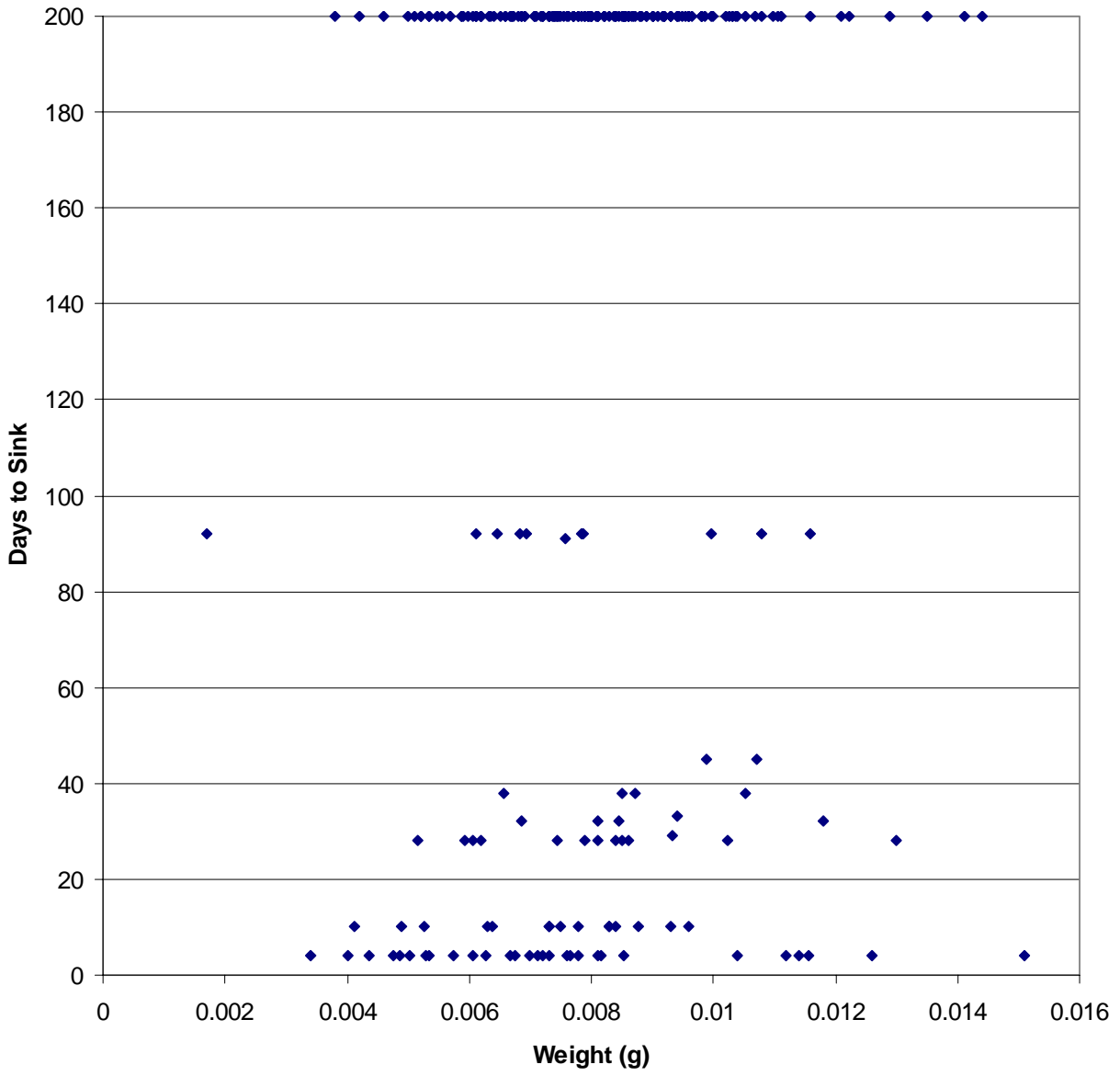


FIGURE 8: Histogram of percent germination of *I. capensis* seeds of different weights

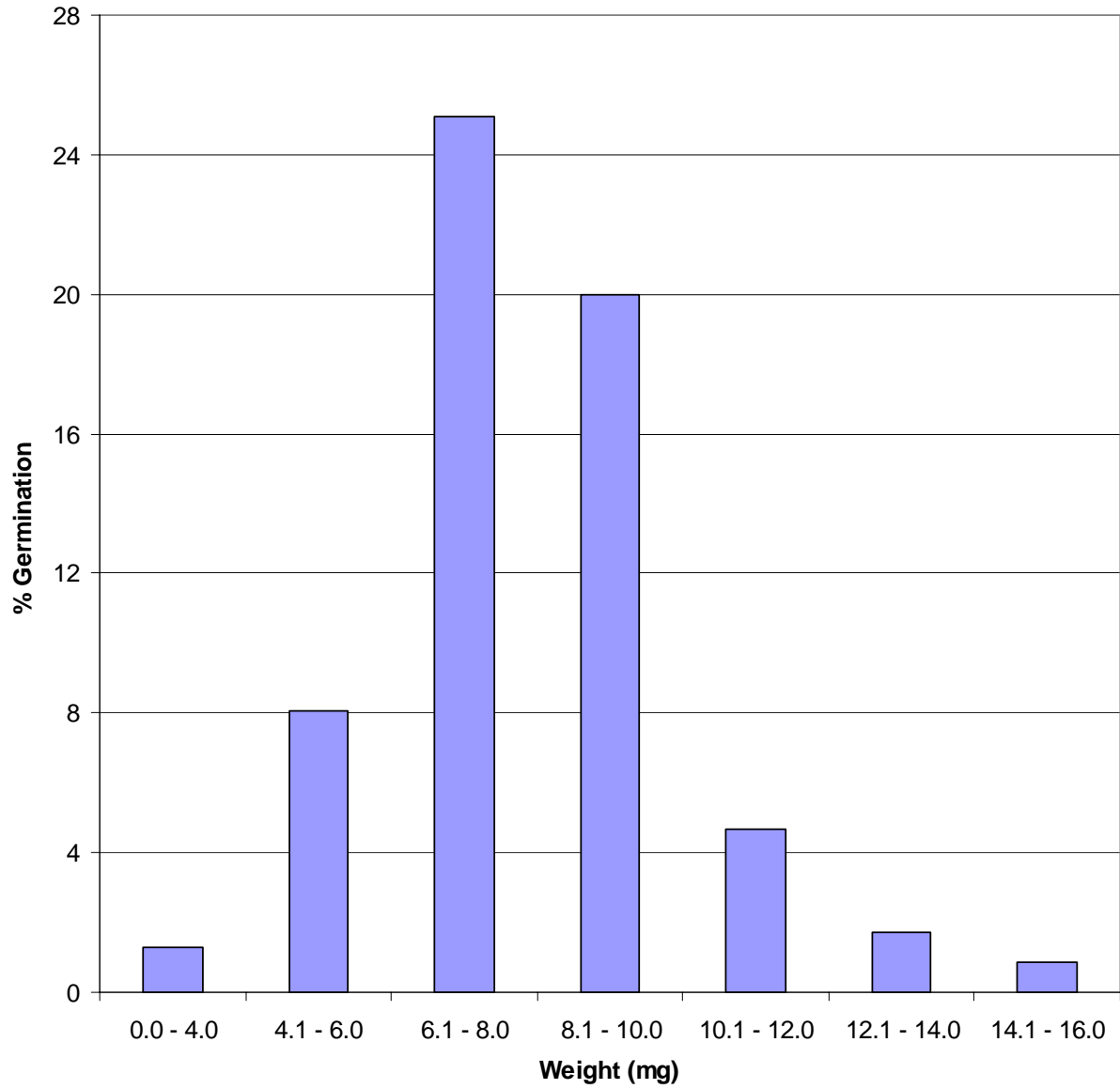


FIGURE 9: Histogram of percent germination of *I. capensis* seeds at different salt concentrations and weight.

