THE ROLE OF PHENOTYPIC PLASTICITY
IN THE INVASIVENESS OF THREE TARAXACUM SPECIES

DISSERETATION

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By

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ABSTRACT

Biological invasion is a global phenomenon that has caused great damage to ecosystems as well as to the economy. Many factors have been found to be associated with and contributed to the success of invasive species. Phenotypic plasticity, the ability of a plant genotype to respond to different environmental conditions by producing different phenotypes, might play an important role in biological invasion, but more empirical studies are needed before a general pattern emerges that can be used in predicting the invasive potential of a species.

This dissertation describes studies that investigated the role of phenotypic plasticity in the success of invasive plants using three dandelion species (*Taraxacum*, Asteraceae) as model system. *Taraxacum officinale* is an aggressive weed, while *T. laevigatum* only has limited distribution in North America. *T. kok-saghyz* has been introduced as a potential crop, but its potential invasiveness is unknown. In three major experiments, I tested the hypothesis that the invasive *T. officinale* and non-invasive *T. laevigatum* will exhibit different phenotypic plasticity in germination, growth, and reproduction in various lab, greenhouse, and field environments. I also proposed that their responses in
stressful and favorable conditions could be used to assess the invasive potential of *T. kok-saghyz*.

The results revealed complicated responses of the three species in various environments. The invasive *T. officinale* showed higher germination in high alternating temperature, and accumulated more biomass than the non-invasive *T. laevigatum* in favorable greenhouse conditions. Surprisingly, *T. laevigatum* germinated better than *T. officinale* in other stressful environments (dark, low water potential, long aging period), and also exhibited higher fecundity in favorable greenhouse conditions. In field experiments, however, the performance of *T. officinale* was overwhelmingly better than *T. laevigatum*, which suffered very high mortality and failed to survive for more than two growing seasons. These results suggest that *T. officinale* might benefit from its ability to grow, reproduce, and survive in various environments, while *T. laevigatum* relies on seed reproduction to maintain its population. With the exception of germination, the responses of *T. kok-saghyz* were more like *T. officinale* than *T. laevigatum*, which suggested that this species has some potential to behave as a weed.

This work demonstrated the importance of comparative study between invasive and non-invasive species across different environments, and showed complicated mechanisms underlying invasion success.
Dedicated to my husband and daughter
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# TABLE OF CONTENTS

Abstract........................................................................................................................................ ii
Dedication....................................................................................................................................... iv
Acknowledgments....................................................................................................................... v
VITA................................................................................................................................................ vi
List of Tables ............................................................................................................................ ix
List of Figures ............................................................................................................................ xi

Chapters:

1. Background and literature review ......................................................................................... 1
   1.1 Introduction ..................................................................................................................... 1
   1.2 Factors contributing to plant invasion ................................................................. 2
   1.3 Prediction .................................................................................................................. 9
   1.4 Weeds and invasive plants ....................................................................................... 12
   1.5 Phenotypic plasticity .............................................................................................. 13
   1.6 Review of *Taraxacum* species ............................................................................. 17
   1.7 Objectives and hypothesis ...................................................................................... 21

2. Germination patterns in different environments ................................................................. 29
   2.1 Introduction .............................................................................................................. 29
   2.2 Materials and Methods .......................................................................................... 32
   2.3 Results .................................................................................................................... 38
   2.4 Discussion .............................................................................................................. 41
   2.5 Conclusion ............................................................................................................. 50

3. Growth and reproduction in different greenhouse environments ..................................... 58
   3.1 Introduction ............................................................................................................. 58
   3.2 Materials and Methods .......................................................................................... 61
LIST OF TABLES

<table>
<thead>
<tr>
<th>Table</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>1.1</td>
<td>Some of the simple biological and ecological traits related to invasiveness. a Relational type between biological traits and invasiveness. (+) positive; (-) negative; (NS) not significant; (*) non-directional significant relationship. ............................................................... 23</td>
</tr>
<tr>
<td>1.2</td>
<td>Selected synthetic biological and ecological traits related to invasiveness. a Relational type between biological traits and invasiveness. (+) positive; (-) negative; (NS) not significant; (*) non-directional significant relationship. ............................................................... 24</td>
</tr>
<tr>
<td>1.3</td>
<td>Ideal weed characteristics (from Baker 1974) ...................................................... 24</td>
</tr>
<tr>
<td>1.4</td>
<td>Characteristics used to distinguish TOF and TLA (Hitchcock et al. 1955) ..................................................................................................................... 25</td>
</tr>
<tr>
<td>2.1</td>
<td>Description of sample collection .......................................................................... 52</td>
</tr>
<tr>
<td>2.2</td>
<td>Description of models used in the analysis. Gen – genotype; Temp – temperature; Spp – species; GLZ – generalized linear model; Mixed – Mixed model; “</td>
</tr>
<tr>
<td>2.3</td>
<td>ANOVA tables for all germination experiments ...................................................... 54</td>
</tr>
<tr>
<td>3.1</td>
<td>ANOVA of 2-species (TOF and TLA) analysis for the first run. Bold P values are significant at 0.05 level................................................................. 91</td>
</tr>
<tr>
<td>3.2</td>
<td>ANOVA of 3-species (TOF, TLA, and TKS) analysis for the first run. Bold P values are significant at 0.05 level ................................................................. 93</td>
</tr>
<tr>
<td>3.3</td>
<td>ANOVA of 2-species (TOF and TLA) analysis for the second run. Bold P values are significant at 0.05 level................................................................. 95</td>
</tr>
</tbody>
</table>
3.4 ANOVA of 3-species (TOF, TLA, and TKS) analysis for the second run. Bold $P$ values are significant at 0.05 level .................................................... 97

4.1 Survival count in each census. Data of 2006 October and 2007 May was aggregated into only two groups (short grass and no grass) because fertility and tall grass treatments were not applied before these two censuses. Individuals in tall grass treatment were not censused after 2008 April because sample size was too small. ......................... 132
# LIST OF FIGURES

<table>
<thead>
<tr>
<th>Figures</th>
<th>page</th>
</tr>
</thead>
<tbody>
<tr>
<td>1.1 Reaction norms of four types of genotype-environment interaction scenarios: a) environmental effect only, b) genotypic effect only, c) genotype by environment interaction, but no genotypic or environmental effect, and d) environmental, genotypic, and environment by genotype interaction (see text for detail).</td>
<td>26</td>
</tr>
<tr>
<td>1.2 Three possible fitness plasticity responses of invasive (black line) and non-invasive (gray line) species across an environmental gradient. a) Jack-of-all-trades, b) Master-of-some, and c) Jack-and-master. Reprint from Richards et al. (2006).</td>
<td>27</td>
</tr>
<tr>
<td>1.3 Distribution of TOF and TLA in North American, and some of the states in United States. OH: Ohio; MI: Michigan; IN: Indiana; PA: Pennsylvania; KY: Kentucky; WV: West Virginia. Maps came from USDA Plants Database (USDA and NRCS 2008).</td>
<td>28</td>
</tr>
<tr>
<td>2.1 X-ray image of seeds after cleaning. Most seeds were filled with embryos. Picture shown is TOF seeds.</td>
<td>55</td>
</tr>
<tr>
<td>2.2 Germination percentage (least square mean ± SE) in alternating Low (5°C/15°C), Mid (15°C/25°C), and High (25°C/35°C) temperature regimes. (a) All 27 genotypes of the three species (each species was analyzed separately). (b) Average across nine genotypes for each species (genotype as random effect). (c) Seed mixture of nine genotypes for each species. TOF: solid line; TLA: dotted line; TKS: dashed line.</td>
<td>56</td>
</tr>
<tr>
<td>2.3 Germination percentage (least square mean ± SE) of the three species in various constant temperatures and light or dark conditions.</td>
<td>57</td>
</tr>
</tbody>
</table>
Germination percentage (least square mean ± SE) of the three species in: (a) various water potentials, and (b) various accelerating aging period. TOF (solid line and filled circle), TLA (dotted line and open triangle), and TKS (dashed line and filled square) ........................................ 57

Hypothetical phenotypic responses of an invasive species (solid line) and a non-invasive (dashed line) species in a) fitness component, and b) morphological or physiological component. A successful invasive species would be expected to maintain higher and more stable fitness over stressful to favorable environments, and this would likely be achieved by more plastic morphological or physiological changes. .......................................................................................................................... 99

Photon spectral irradiance in full light (solid line) and green shade (dashed line). R:FR ratio (655-665/725-735nm) is 1.170 in full light and 0.556 in green shade..................................................................................... 100

Relationship between: a) measurement of TDR (%) and absolute amount of water (ml) added in a standard pot filled with completely dry grow mix, and b) water potential (MPa) and TDR measurement. .................................................................................................................................................. 100

Coefficient of variation (CV) and least square mean of morphological traits of the three species in the first run. TOF: *Taraxacum officinale*; TLA: *T. laevigatum*; TKS: *T. kok-saghyz*. a – c: CV for height, diameter, and leaf shape index. Error bar shows 1 standard error. Different letters on the bars indicates means are different at 0.05 significant level as indicated by Tuckey’s HSD test. No letters were added if no significant differences were found among the three species. d – f: Means across all treatment combinations (dry (D) vs. wet (W) soil, low (L) vs. high (H) fertility, and green shade (G) vs. full light (F)) for height, diameter, and leaf shape index for TOF (solid line and filled circle), TLA (dotted line and open triangle), and TKS (dashed line and filled square).............................. 101

Coefficient of variation (CV) and least square mean of allocation traits of the three species in the first run. TOF: *Taraxacum officinale*; TLA: *T. laevigatum*; TKS: *T. kok-saghyz*. a – d: CV for investment in leaf, investment in root, shoot : root ratio (SRR), and investment in reproduction. Error bar shows 1 standard error. Different letters on the bars indicates means are different at 0.05 significant level as indicated by Tuckey’s HSD test. No letters were added if no significant differences were found among the three species. e – h: means across all treatment combinations (dry (D) vs. wet (W) soil, low (L) vs. high (H) fertility, and green shade (G) vs. full light (F))
for investment in leaf, investment in root, SRR, and investment in reproduction for TOF (solid line and filled circle), TLA (dotted line and open triangle), and TKS (dashed line and filled square). i – k: species means in dry and wet soil for investment in leaf, investment in root, and SRR. l, m: species means in DL, DH, WL, and WH for investment in reproduction and investment in root............................................. 102

3.6 Coefficient of variation (CV) and least square mean of reproduction traits of the three species in the first run. TOF: *Taraxacum officinale*; TLA: *T. laevigatum*; TKS: *T. kok-saghyz*. a – d: CV for investment in seed, total seed, seed biomass, and seed weight. Error bar shows 1 standard error. Different letters on the bars indicates means are different at 0.05 significant level as indicated by Tuckey’s HSD test. No letters were added if no significant differences were found among the three species. e – h: means across all treatment combinations (dry (D) vs. wet (W) soil, low (L) vs. high (H) fertility, and green shade (G) vs. full light (F)) for investment in seed, total seed, seed biomass, and seed weight for TOF (solid line and filled circle), TLA (dotted line and open triangle), and TKS (dashed line and filled square). i – k: species means in DL, DH, WL, and WH investment in seed, total seed, and seed biomass. l: species means in low and high fertility for seed weight. m: species mean in LG, LF, HG, and HF for investment in seed. n: relative total seed across all environment (see assessment of phenotypic plasticity). ............................................. 104

3.7 Coefficient of variation (CV) and least square mean of biomass of the three species in the first run. TOF: *Taraxacum officinale*; TLA: *T. laevigatum*; TKS: *T. kok-saghyz*. a – d: CV for investment in total biomass, leaf biomass, root biomass, and reproduction biomass. Error bar shows 1 standard error. Different letters on the bars indicates means are different at 0.05 significant level as indicated by Tuckey’s HSD test. No letters were added if no significant differences were found among the three species. e – h: means across all treatment combinations (dry (D) vs. wet (W) soil, low (L) vs. high (H) fertility, and green shade (G) vs. full light (F)) for total biomass, leaf biomass, root biomass, and reproduction biomass for TOF (solid line and filled circle), TLA (dotted line and open triangle), and TKS (dashed line and filled square). i, j: species means in low and high fertility for total biomass and leaf biomass. k, l: species mean in dry and wet soil for root biomass and reproduction biomass. m: relative total biomass across all environment (see assessment of phenotypic plasticity). n: species mean in DL, DH, WL, and WH for root biomass............................................... 106
3.8 Least square means and coefficient of variation (CV) of morphology traits of the three species in first run (a, b), and second run (c – f). TOF: Taraxacum officinale (solid line and filled circle); TLA: T. laevigatum (dotted line and open triangle); TKS: T. kok-saghyz (dashed line and filled square). Environment: dry (D) vs. wet (W) soil, low (L) vs. high (H) fertility. a, b: species means of first run (full light only) in DL, DH, WL, and WH for height and diameter. c, d: species means of second run in DL, DH, WL, and WH for height and diameter. e, f: CV of second run for height and diameter. Error bar shows 1 standard error. No significant differences were found among the three species. ............................................... 108

3.9 Least square means and coefficient of variation (CV) of allocation traits of the three species in first run (a – d), and second run (e – n). TOF: Taraxacum officinale (solid line and filled circle); TLA: T. laevigatum (dotted line and open triangle); TKS: T. kok-saghyz (dashed line and filled square). Environment: dry (D) vs. wet (W) soil, low (L) vs. high (H) fertility. a – d: species means of first run (full light only) in DL, DH, WL, and WH for investment in leaf, investment in root, SRR, and investment in reproduction. e – h: species means of second run in DL, DH, WL, and WH for investment in leaf, investment in root, SRR, and investment in reproduction. i – l: CV of second run for investment in leaf, investment in root, SRR, and investment in reproduction. Error bar shows 1 standard error. No significant differences were found among the three species. m, n: species means of second run for investment in root and investment in reproduction in dry and wet soil environments. ................................................................................................ 109

3.10 Least square means and coefficient of variation (CV) of reproduction traits of the three species in first run (a – d), and second run (e – p). TOF: Taraxacum officinale (solid line and filled circle); TLA: T. laevigatum (dotted line and open triangle); TKS: T. kok-saghyz (dashed line and filled square). Environment: dry (D) vs. wet (W) soil, low (L) vs. high (H) fertility. a – d: species means of first run (full light only) in DL, DH, WL, and WH for investment in seed, total seed, seed biomass, and seed weight. e – h: species means of second run in DL, DH, WL, and WH for investment in seed, total seed, seed biomass, and seed weight. i – l: CV of second run for investment in seed, total seed, seed biomass, and seed weight. Error bar shows 1 standard error. No significant differences were found among the three species. m: species means of second run for investment in seed in low and high fertility environments. p, n, o:
species means of second run for investment in seed, seed biomass, and seed weight in dry and wet soil environments. .................................................. 111

3.11 Least square means and coefficient of variation (CV) of biomass traits of the three species in first run (a – d), and second run (e – l). TOF: *Taraxacum officinale* (solid line and filled circle); TLA: *T. laevigatum* (dotted line and open triangle); TKS: *T. kok-saghyz* (dashed line and filled square). Environment: dry (D) vs. wet (W) soil, low (L) vs. high (H) fertility. a – d: species means of first run (full light only) in DL, DH, WL, and WH for total biomass, leaf biomass, root biomass, and reproduction biomass. e – h: species means of second run in DL, DH, WL, and WH for total biomass, leaf biomass, root biomass, and reproduction biomass. i – l: CV of second run for total biomass, leaf biomass, root biomass, and reproduction biomass. Error bar shows 1 standard error. No significant differences were found among the three species. ........................................ 113

3.12 Matured seed head count of the three dandelions species in the first run (a), and second run. TOF: *Taraxacum officinale* (solid line and filled circle); TLA: *T. laevigatum* (dotted line and open triangle); TKS: *T. kok-saghyz* (dashed line and filled square). Data were summed for each week and averaged across all treatments from the first collection date. Error bars represent 1 standard error.................................. 114

4.1 Experiment design and layout. Each 1.5 m × 1.5 m plot received one of the 6 environmental treatments and contained 9 plants, 3 from each species (as indicated by different symbols). On replicate (block) measured 7.5 m × 5.0 m, and included 6 small plots as described above. The entire experiment had 12 replicates with 3 × 4 layouts in field. .................................................................................................................... 134

4.2 Over winter survival rate of a) 2006-2007 and b) 2007-2008: TOF (grey), TLA (white), and TKS (hatched). Short/No refers the status of surrounding vegetation. High/Low refers the fertility level. 2006-2007 data was aggregated into only two groups (short grass and no grass) because fertility and tall grass treatments were not applied until 2007 spring. TLA and individuals in tall grass treatment were not censused in 2007 - 2008 because sample size was too small....................................................................................................... 135

4.3 Seasonal survival of year a) 2006, b) 2007, and c) 2008: TOF (grey), TLA (white), and TKS (hatched). Tall/Short/No refers the status of surrounding vegetation. High/Low refers the fertility level. 2006 data was aggregated into only two groups (short grass and no grass) because fertility and tall grass treatments were not applied until
2007 spring. TLA and individuals in tall grass treatment were not censused in 2008 because sample size was too small................................. 136

4.4 Total seed head count (mean + 1 standard error) of three dandelion species in different habitats in a) 2007 and b) 2008: TOF (grey), TLA (white), and TKS (hatched). Tall/Short/No refers the status of surrounding vegetation. High/Low refers the fertility level. Data of tall grass habitat and TLA in 2008 was not measured. Insert shows seed head counts of tall grass and short grass in a different scale.......................... 137

4.5 2007 seasonal seed head count (mean + 1 standard error) of three dandelion species in different habitats: TOF (solid line and filled circle), TLA (dotted line and open triangle), and TKS (dashed line and filled square). Tall/Short/No refers the status of surrounding vegetation. High/Low refers the fertility level................................................................. 138

4.6 2008 seasonal seed head count (mean + 1 standard error) of two dandelion species in different habitats: TOF (solid line and filled circle) and TKS (dashed line and filled square). Short/No refers the status of surrounding vegetation. High/Low refers the fertility level. ........................................................................................................ 139

4.7 Diameter (mean + 1 standard error) of three dandelion species in different habitats measured in a) 2007 May, and b) 2007 October: TOF (grey), TLA (white), and TKS (hatched). Tall/Short/No refers the status of surrounding vegetation. High/Low refers the fertility level.................................................................................. 140

4.8 Biomass (mean + 1 standard error) of three dandelions species in different habitats during 2007 growing season: TOF (grey), TLA (white), and TKS (hatched). Tall/Short/No refers the status of surrounding vegetation. High/Low refers the fertility level. Insert shows biomass of tall grass and short grass in a different scale......................... 141

4.9 Biomass (mean + 1 standard error) of two dandelions species in different habitats during 2008 growing season: TOF (grey), TKS (hatched). Short/No refers the status of surrounding vegetation. High/Low refers the fertility level. Insert shows biomass of short grass in a different scale...................................................................................... 142
CHAPTER 1

BACKGROUND AND LITERATURE REVIEW

1.1 Introduction

Biological invasion was defined by Mack (1996) as “the proliferation and persistence of a species in a new range such that it has detrimental consequences (abiotic or biotic, or both). This persistence is not dependent on deliberate human intervention.” Ever since the publication of Elton’s book – *The Ecology of Animal and Plant Invasions* (1958), biological invasion has become an important field of study. Invasive species have been recognized as the second most important cause of decreasing global biodiversity (Vitousek et al. 1997). In economic considerations, invasive species such as agricultural weeds and pest insects have cost great damage, and a huge amount of money is spent annually for their control (Pimentel et al. 2000).

Several generalizations have emerged to describe the invasion process, mechanisms, and factors that contribute to invasion success (Kolar and Lodge 2001, Sakai et al. 2001, Pyšek and Richardson 2007, Theoharides and Dukes 2007, Hayes and Barry 2008, Catford et al. 2009). In particular, many researchers have focused on identifying “invasive traits” that can be used to predict which species are likely to become invasive if introduced (Pheloung et al. 1999, Mack 2005, Caley and Kuhnert 2006).
The following review summarizes current knowledge of the factors contributing to successful biological invasions, and also the efforts to predict which species are likely to become invasive if introduced. The research conducted in this dissertation was based on this information, and aims to expand our knowledge of biological invasion.

1.2 Factors contributing to plant invasion

1.2.1 Introduction pattern

Propagules of non-native plants have been introduced into new geographic areas either accidentally or deliberately. For example, seeds of various species have been carried by migrating human populations and spread inadvertently to new habitats as contaminants in hay, animal feed, soil, shipping ballast, cargo, etc. The rate of accidental introduction decreased during the last century due to changes in migration patterns, production, shipping, and inspection practices (National Research Council 2002). However, most of the exotic plant species that have become established and spread into areas where they are not wanted were imported deliberately for agricultural, aesthetic, culinary, medicinal, cultural, or other practical purposes (Reichard and Hamilton 1997, Kolar and Lodge 2001, Mack and Lonsdale 2001). For example, sixty percent of the more than 600 naturalized taxa listed in a 1950’s botanic manual were deliberately introduced, and the true percentage was actually higher (Mack and Lonsdale 2001).

It has been suggested that common and widely distributed plant species were more likely to be introduced, because they were more familiar to people and better known for their benefit than rare species (Prinzing et al. 2002, Pyšek et al. 2004). Prinzing et al.
(2002) found non-native plants in two Argentine provinces were characterized by their frequent occurrences in native ranges of central Europe and regular human utilization. Pyšek et al. (2004) suggested that the location of the region of origin was also important: the probability of importation was higher if the distance between origin and destination area was short.

Initial population size, number of introduction attempts, and residence time are other factors contributing to success of invasion. Theoretically, newly arrived species are likely to go extinct due to demographic, environmental, and genetic stochasticity, but large numbers of individuals and multiple introductions can prevent such events because population size is more stable and genetic variation is higher in a larger initial population (National Research Council 2002). For invasive birds and biological-control insects, the survival probability of a species increases with the number of individuals released at one time (Williamson 1996, Williamson and Fitter 1996b). On the other hand, multiple introductions help an immigrant species to avoid periods of stressful environments, and increase the genetic diversity in the introduced population as well. For example, common reed (Phragmites australis) was naturalized in North America for a long time before the introduction of a single novel European strain during the early 1800s began its dramatic increase in range and abundance over the last 150 years (Saltonstall 2002). Residence time – how long the species has been introduced – was related to invasion success as well (Scott and Panetta 1993, Rejmánek 2000). Maillet & Lopez-Garcia (2000) found that pre-1900 introductions of weeds from America to France were associated with greater
likelihood of becoming major weeds than more recent introductions. Kolar and Lodge (2001) also concluded that invasion success was greater for longer-established species.

1.2.2 Invasiveness

After Elton (1958), early work on plant invasion suggested that invasive species shared some common genetic, biological, or ecological traits which make them out-perform other competitors (Baker 1974). The term “invasiveness” has been widely used to describe these inherent characters.

A number of putative invasive characteristics have been identified in previous studies, and have been reviewed in many papers (Williamson and Fitter 1996a, Rejmánek 1999, 2000, Kolar and Lodge 2001, Pyšek and Richardson 2007, Theoharides and Dukes 2007, Hayes and Barry 2008). Some of these traits are summarized in Table 1.1 and Table 1.2. I have identified two categories among these traits – simple traits, which are usually single biological characteristics (Table 1.1), and synthetic traits, which are more related to ecology or evolution, and sometimes represent complicated interactions among simple traits (Table 1.2).

Numerous as they are, invasive characteristics, especially simple ones, have varied from study to study (Table 1.1). For example, Rejmánek and Richardson (1996) emphasized the importance of small seed size as a trait common to woody invaders, but Reichard and Hamilton (1997) found seed size to be insignificant. Darwin (1859) suggested that successful invaders usually belong to non-native genera, which was supported by the findings of Mack et al. (1996) and Rejmánek (1996, 1999). Daehler
(2001), however, reached the opposite conclusions, at least for the flora in Hawaii. His results implied that naturalized species tend to belong to native families.

Synthetic traits (Table 1.2), on the other hand, were more consistent among studies. First, invasion history was significantly related to invasiveness in almost all studies (Rejmánek 2000, Kolar and Lodge 2001). As a highly synthetic trait, invasion history best reflected the potential and ability of a species to be introduced, naturalize, become established, and ultimately become invasive. For example, a history of having “invaded elsewhere” was the most important predictor of invasion among woody plants in North America (Reichard and Hamilton 1997). Weed status beyond the original range of a species was also significantly associated with the invasiveness of Australian weeds (Scott and Panetta 1993). Second, the native geographic range of a species was identified as an important factor in many studies, probably because widespread species were more likely to be introduced, and were usually characterized by high dispersal potential and ability to adapt to a wide range of environments (Scott and Panetta 1993, Williamson 1996, Williamson and Fitter 1996b, Goodwin et al. 1999, Maillet and Lopez-Garcia 2000, Prinzing et al. 2002). For example, weed status in Australia was associated with being geographically widespread, and with growing in a wide range of climates in their native habitats (Scott and Panetta 1993). For plants invading New Brunswick, Canada, 70% of the tested species were correctly predicted for their invasiveness using native distribution ranges in Europe (Goodwin et al. 1999).
1.2.3 Invasibility

Since the growth of many invasive plants is actually restricted in their native region (compared with the invaded range), the quality of the invaded environments must be as important as a species’ inherent traits. The potential of a geographic area to be invaded, or invasibility, is affected by both biotic factors, such as community biodiversity (Levine and D'Antonio 1999, Hooper et al. 2005) and abiotic factors, such as climate matching (Hayes and Barry 2008).

Climate matching between native range and invaded range is an important factor (Hayes and Barry 2008), as few tropical species, for example, would be expected to survive in cold zones. Predictions of potential distribution of non-native species has been attempted using climate analyses (Sutherst et al. 1999). Although the match of primary and secondary environments was reasonably close, it was not always perfect (Rejmánek 2000). In North America, for example, latitudinal ranges of naturalized European plant species in the families Gramineae and Compositae were 15-20° narrower than their native ranges in Eurasia and North Africa. The native latitudinal range of an aquatic fern, *Salvinia molesta*, was just 24°S-32°S, while its secondary distribution range was 35°S-30°N (Williamson 1996). This author suggested that climate matching was only a weak predictor because exceptions were widely found. There has been substantial controversy about the role of biodiversity in the stability and productivity of ecosystems (Johnson et al. 1996, Huston 1997, Kaiser 2000), and the importance of biodiversity in the invasibility of a community (Levine and D'Antonio 1999, Hooper et al. 2005). One idea in this argument was based on a “vacant niche” theory, which argued that
communities with fewer native species leave more resource niches available for new, invading, species to exploit; hence, environments with high biodiversity were expected to be more resistant to invasion than those with low biodiversity (Tilman 1997, Knops et al. 1999). Several studies with experimental communities as well as theoretical work supported this view (Rejmánek 1989, Case 1990, Law and Morton 1996, Tilman 1997, Knops et al. 1999).

However, other studies have found the reverse: increasing plant invasions with increasing resident species diversity (Robinson et al. 1995, Palmer and Maurer 1997, Lonsdale 1999). The explanation for these results has been based on the finding that where resources and other factors (climate, disturbance, soil fertility, etc.) favor high resident plant diversity, rates of plant invasion are also favored (McIntyre and Lavorel 1994, Burke and Grime 1996, Levine and D'Antonio 1999, Stohlgren et al. 1999, Naeem et al. 2000).

On the other hand, Davis et al. (2000) proposed that fluctuation in resource availability was a key factor controlling invasibility. They argued that invasibility of a plant community increased when there was an increase of unused resources (supply > uptake). Disturbances, for example, remove the native vegetation and thus reduce the uptake rate of resources, which can lead to susceptibility to invasion. Although the authors did not explain why extra resources can only be used by alien species but not by native species, their hypothesis was supported by theoretical work (Huston 2004), as well as empirical data. For example, Burke and Grime (1996) demonstrated in an experimental study that the magnitude of invasion increased with increasing nutrients and disturbance.
in limestone grassland in UK. Daehler (2003) compared 79 independent native-invasive pairs and concluded that relative performance of native-invasive species often depended on growing conditions. In this study, most (94%) native plants performed equally or superior to invaders at least in conditions of reduced resources (nutrients, light, water) and/or specific disturbance. Global changes, such as increased CO$_2$ level and temperature, were also suspected to have helped plant invasion (Weltzin et al. 2003).

1.2.4 Other factors

Invasive plants are generally thought to experience decreased regulation by herbivores and other natural enemies, which results in their increase in distribution and abundance in their new range (enemy release hypothesis, Keane and Crawley 2002). This intuitive hypothesis, which is the working hypothesis of biological control, lacks supportive evidence. Descriptions and studies of the relationship between natural enemies and invasive plants are often anecdotal or non-quantitative. For those semi-quantitative studies, there is little evidence that alien invasive plant species are less likely to be attacked by herbivores than are native species (Keane and Crawley 2002). Comparisons of plant growth in their native range and new range provide indirect tests of this hypothesis (Thébaud and Simberloff 2001), but there is no obvious trend that invasive plant growth is greater in the new range than in their native range.

Theoretically, invading populations can experience rapid evolution through founder effects, selection pressure, and hybridization with native species (Lambrinos 2004). Blossey and Notzold (1995) proposed that introduced plants that were no longer attacked by specialist enemies should lose costly herbivore defense ability, and re-allocate resources previously spent on defense to traits that enhance competitive ability, such as increased size or fecundity (evolution of increased competitive ability, or EICA). In addition, invasive species have sometimes been capable of out-crossing with native species (Ellstrand and Schierenbeck 2000). The progeny of the hybridization possess extraordinary levels of genotypic and phenotypic diversity, which might potentially increase the invasiveness of the species (Lambrinos 2004). For instance, hybrids between the introduced species *Spartina alterniflora* and the native species *S. foliosa* are far more aggressive than either parent (Daehler and Strong 1997, Ayres et al. 1999).

### 1.3 Prediction

Prediction of biological invasion aims to forecast which species, if introduced to a specific region, will become invasive. Although many factors have been associated with plant invasion, only the invasiveness factor has been widely used for prediction purposes. The reason for this is obvious: we have neither enough historical records of introduction patterns, nor enough knowledge of natural enemies of plants, especially pathogens. Evolutionary processes are hardly predictable. It is difficult to use invasibility in predictions because invasibility can only predict which communities/habitats might be more susceptible to invasion, and the roles of climate match and community biodiversity
are still controversial. That is why only invasiveness – the character of the plant itself – is widely used for prediction purposes, not because it is the most reliable, but because of the limitation of our knowledge and application feasibility.

Are plant traits a good predictor? In another words, can plant species characteristics determine invasive potential, at least in some cases? If the answer is “no” then we would expect that invasive species are randomly selected from the pool of all non-indigenous species. However, it appears that certain species are far more “lucky” in this “lottery draw” than other species – they often, if not always, become invasive in new ranges. These plants, such as *Cyperus rotundus*, *Sorghum halepense* and *Eichhornia crassipes*, are sometimes called the “world’s worst weeds” (Holm et al. 1977). There must be something about these species themselves that make them invasive, and species characteristics can serve as predictors in these cases.

The overall efforts of prediction, however, have been far from successful. Pysek (2001) evaluated one of the earliest attempts (in the early 1970s) to predict potential invaders of arable land in the Czech Republic using recent data on invasion. Only 39.3% of the 28 predicted invasive species could be considered as successful invaders in current time. This is one of the few studies using data from different time periods to evaluate results of predictions made previously. Most other studies have used contemporary data to test their prediction systems. For example, Rejmánek & Richardson (1996) created a discriminant function based on six invasive and six non-invasive *Pinus* species, and applied it to another set of six invasive and six non-invasive species. Goodwin et al. (1999) conducted multiple regression analysis on 110 species pairs (invasive and
non-invasive in New Brunswick, Canada) and tested it on 55 other species pairs. Seventy percent of the tested species were correctly predicted. Prinzing et al. (2002) used 50% of the species to calculate a logistic regression model and correctly predicted 81% of the aliens and 70% of the non-alien species in the remaining species.

Although the prediction results seem to be promising for the above examples, the primary predictors chosen for these studies were very different from each other: Rejmánek & Richardson (1996) used seed mass, juvenile period, and interval between large seed crops; Goodwin et al. (1999) used native range; Prinzing et al. (2002) used frequency and range in native region, preference for warm, dry and nitrogen-rich conditions, and ruderal life strategy. Such inconsistency suggests that prediction based on invasive traits remains contingent on each case.

Invasion history – whether a species has invaded somewhere else – is the most consistent predictor of invasion potential (Maillet and Lopez-Garcia 2000, Rejmánek 2000, Kolar and Lodge 2001). Knowledge of invasion history not only provides information about the impact of invaders on the ecosystem and economy, but also about past management experience. The importance of invasion history has been recognized by the US Department of Agriculture for decades (Reed 1977). However, invasion history is not always a reliable predictor. In New Zealand, Williams et al. (2000) reported that 20% of exotic weedy species collected for the first time in the second half of last century had never been reported as invasive outside New Zealand. Furthermore, many species, especially in less developed countries, have not had abundant opportunities to travel to new ranges (Mack 1996), and thus their invasion potential is unknown.
Some scientists have expressed doubt that invasion can be predicted. Gilpin (1990) wrote in his review that “we are never going to have a scheme to predict the success of invading species.” Williamson (1999) agreed that it is hard to predict invasion, probably due to the difficulties of finding general laws in ecology. Given the variety of pathways by which a species can establish and have an impact, each species can become invasive in its unpredictable and unique way.

1.4 Weeds and invasive plants

Both invasive plants and weeds are noxious plant species or genotypes that cause economic and environmental damage. The definition of invasive plants is “the proliferation and persistence of a species in a new range such that it has detrimental consequences (abiotic or biotic, or both). This persistence is not dependent on deliberate human intervention.” (Mack 1996). The definition of a weed, on the other hand, is a plant that grows “entirely or predominantly in situations markedly disturbed by man (without, of course, being deliberately cultivated)” (Baker 1974).

Weeds are similar to invasive plants in terms of their potential to dominate a community. But they are also different. First, weeds can be native as well as non-native species. Giant ragweed (Ambrosia trifida) is a native plant in Northeastern US, but it has become an important weed in agriculture fields (Regnier et al. 2008). Of 500 weeds common to the northern United States, Muenscher (1955) considered 39.2% to be native species, including Achillia millefolium, Apocynum cannabinum, Asclepias tuberosa, Cerastium arvense, Conyza canadensis, Convolvulus sepium, Oxalis stricta, Panicum
capillare, Phytolaca americana, Polygonum lapathifolium, Polygonum pensylvanicum, Potentilla norvegica, and possibly species of Chenopodium and Amaranthus. Second, only plants that cause economic or environmental harm in “markedly disturbed” areas are called weeds, while invasive plants are not necessarily associated with intensive human activities.

Although invasive plants and weeds can be very different, these two terms are often used in a quite confusing manner and sometimes indiscriminately. Invasive plants are sometimes said to be weedy, while weeds are sometimes called invaders. The term “invasive weeds” is only useful, for example, if there is general agreement that there are also “non-invasive weeds,” although this term is not found in the literature. In addition, there is no general agreement about what constitutes an “intensively disturbed” area, so the borderline between invasive plants and weeds is vague.

On the other hand, weeds and invasive plants do share some common characteristics. Many “invasive traits” such as rapid growth and massive seed production (Goodwin et al. 1999) are very similar to those of the “ideal weed” (Baker 1974, Table 1.3). For this reason, it would be beneficial for invasion biologists to borrow knowledge of weed science when studying invasive plants, especially those growing in frequently disturbed habitats.

1.5 Phenotypic plasticity

Phenotypic plasticity is “the property of a given genotype to produce different physiological or morphological phenotypes in response to different environmental
conditions” (Bradshaw 1965). Although this concept was traditionally studied at molecular, physiological and morphological levels (Trewavas and Jennings 1986, Schlichting and Pigliucci 1993, Via et al. 1995), phenotypic plasticity has recently been connected with ecological phenomena (Dudley 2004, Miner et al. 2005), including weed and biological invasion (Sultan 2001, Griffith and Sultan 2005, Hulme 2008).

Phenotypic plasticity is often described by a reaction norm, which is a graph showing the change of phenotype (trait) values along an environment gradient. Several genotypes are plotted on the same graph to illustrate the genotype by environment interaction (G×E, Figure 1.1). The environmental effect is tested by comparing the mean trait value of all genotypes in different environments. The genotypic effect is tested by comparing the mean trait value in all environments for the different genotypes. Figure 1.1a shows a situation where only the environmental effect (E) is present – there are changes in trait mean value of the three genotypes along an environmental gradient, but the means of each genotype are equal. Figure 1.1b shows the case when only a genotypic effect (G) is present – trait means of each genotype are different; but means within each environment are the same. Figure 1.1c shows that only the genotype by environment effect (G×E) is present – trait means of each genotype and of each environment are unchanged, but each genotype responds to environmental changes differently. Figure 1.1d shows that G, E and G×E effects are all present. In ecological research on weeds and invasive plants, genotypes in reaction norms are usually replaced with species, because ecologists are mostly interested in the different responses at the species level.
A popular hypothesis about phenotypic plasticity of invasive species is that: invasive species are more plastic than native/non-invasive species, which facilitates their adaptation to a wide range of environments. For example, Baker (1974) suggested that an ideal weed “produces some seeds in wide range of environmental conditions; tolerant and plastic” (Table 1.3). Similarly, Grime and Mackey (2002) argued that plants with more phenotypic plasticity are able to optimize resource capture capability in various habitats. The ability to maintain fitness in both stressful and favorable environments is sometimes called a generalist strategy or Jack-of-all-trades (Figure 1.2a), and some invasive species might be successful due to this quality (Richards et al. 2006). On the other hand, Richards et al. (2006) suggested that invasive species can also be Master-of-some (Figure 1.2b), which was also called an opportunist strategy (Sultan 2001). In this case, invasive species exhibit similar fitness as non-invasive species in stressful environments, but achieve a much higher fitness under favorable conditions. This strategy insures survival and spread under stressful conditions, and allows maximum reproductive output when the growing conditions are favorable. Richards et al. (2006) even suggested a third type called Jack-and-master (Figure 1.2c), in which fitness of invasive species is universally high in all environments, but the differences of fitness between invasive and non-invasive species are largest under favorable conditions.

Although the theoretic framework for the role of phenotypic plasticity in biological invasion has been well established, the number of studies to-date is still small and these have revealed mixed results (see citations in Richards et al. 2006). More case studies on a wider range of taxa, geological spans, and ecosystems are needed before general patterns
can emerge and be generalized. In addition, studies on phenotypic plasticity also offer a unique opportunity to investigate biological and ecological traits across different environments, which are largely unknown for many invasive species. This information could be very important because the mechanism behind invasion success might not only lie in the performance in optimum environments, as observed in a greenhouse or in a heavily-invaded field habitat, but also in the responses to stressful conditions.

If phenotypic plasticity could be shown to be consistently associated with invasiveness, this trait could serve as a reliable predictor for invasive potential. Similarly, if a certain response pattern to various environments is shared among invasive species, it can also be used to evaluate the performance of a newly introduced species whose invasiveness is unknown. Such an assessment is very important because non-native crop species continue to be of enormous value to agriculture and other parts of the US economy. It would be unwise and impractical to ban the introduction of all new species, but given the potential environmental and economic harm that might result if the wrong species are introduced, there is a critical need to find a way to evaluate the invasive potential of plants at the border so that only low-risk species are allowed to be imported.

phenotypic plasticity studies, because plants, invasive or non-invasive, will almost always respond to environmental changes (Pigliucci 2001). Some researchers have measured the plastic response of invasive species only (Annapurna and Singh 2003, Herr-Turoff and Zedler 2007), but they have merely documented the ubiquitous phenomena of plasticity and provided little support the hypothesis that the species is invasive due to phenotypic plasticity (Richards et al. 2006). The choice of non-invasive species used for comparison, however, should meet two criteria: First, it should be introduced for a sufficiently long time to avoid the possibility that it is actually invasive, but still in its lag phase of invasion (Sakai et al. 2001). Second, the species should be closely related to its invasive counterpart to avoid confounding differences in phylogeny (Harvey 1996, Hamilton et al. 2005).

This dissertation investigated the role of phenotypic plasticity in the success of plant invasion using three dandelions species (*Taraxacum*, Asteraceae) as a model system, which will be reviewed below.

### 1.6 Review of *Taraxacum* species

*Taraxacum officinale* G.H. Weber ex Wiggers (common dandelion, TOF hereafter) originated in Eurasia and is widely recognized as a major weed in North America. The actual introduction date of TOF into North America is obscure, but the earliest recorded observation was in the New England area in 1672 (Stewart-Wade et al. 2002). TOF usually grows in moderately disturbed habitats such as lawns, roadsides, and no-till agriculture fields. TOF can be found in all Canadian provinces, all US states, and in most
counties in each state (Figure 1.3). Actually, TOF is so widely distributed around the world that it is recognized as one of the world’s worst weeds (Holm et al. 1997). Previous studies have indicated that TOF is adapted to different ecological niches and was considered a generalist species by (Solbrig 1971, Baker 1991), although this characterization was not based on comparative studies with non-invasive species.

*T. laevigatum* Willd. DC. (rock dandelion or red-seeded dandelion, TLA hereafter) is also a non-native species introduced from Eurasia. There is no document indicating when it was introduced into North America, but it was recorded as early as 1913 (Britton and Brown 1913). Where found, it inhabits well drained, sandy soil, and often shaded habitats (Fisher 1988, personal communication with Allison W. Cusick). TLA can be found in most US states and most provinces in Canada, but its distribution is more limited than TOF at the county level (Figure 1.3). For example, TOF is widespread in all 88 counties in Ohio, but TLA has been recorded in only 11 of them, and herbarium OSU records indicate recent observations in only two. Unlike TOF, TLA has never been considered an important weed.

Seeds of *T. kok-saghyz* Rodin (Russian dandelion, TKS hereafter), native to Eurasia as well, were introduced to North America from Russia during World War II in the Emergency Rubber Project effort to develop alternative natural sources of rubber (van Beillen and Poirier 2007). TKS was cultivated in 28 states from 1942 to 1944 to evaluate agronomic characteristics, but the TKS project was terminated when the war ended. Today, TKS is being grown experimentally in three states: Ohio, Oregon, and California for its high rubber content in the fleshy root (Chanon et al. 2008). Considering that the
other two congeneric species are so different in their invasiveness, it is important to
determine whether TKS has the potential to become a weed problem if it becomes widely
cultivated.

All three species of *Taraxacum* are simple perennials growing as rosettes. Flowers of
both TOF and TLA peak in spring and for TOF again in autumn (Fisher 1988). Head
inflorescences are supported by an erect scape, and mature seeds (achenes) are dispersed
by wind with the help of an attached pappus. Although seed production is the major
reproduction and dispersal method for these three species, tap roots are also capable of
producing lateral shoots that can become new individuals.

The reproductive system of TOF has been well documented. Both triploid and
diploid plants are found in the native European habitats, and there are occasional
crossings among them (Tas and Dijk 1999). Triploid individuals, however, only
reproduce apomictically (Richards 1973), and this is the only form found in North America
(Solbrig and Simpson 1974, Lyman and Ellstrand 1984). TLA naturalized in North
America is also triploid and reported as apomictic (Sears 1917). Seeds produced by this
apomictic method have exactly the same genotype as their mother plant.

There has been uncertainty, however, about the reproductive system of TKS.
Warmke (1943) surveyed several TKS samples sent from Russia and found they were all
diploids that reproduced through the normal sexual method. The author further reported
that these plants were highly self-sterile except in late autumn, when seed set was
possible by selfing (Warmke 1944). Unlike many natural polyploids of other species in
the same genus, polyploids (mainly tetraploid and triploid) induced by colchicine were also self-sterile (Warmke 1945).

However, TKS plants used in my study were able to set seeds successfully in the greenhouse without hand pollination during all seasons. The chromosome numbers of these plants were unknown. In an informal test, most inflorescences produced seeds even after I removed stamens and stigmas in un-opened flower buds (the same was true for TOF and TLA, data not shown) Although it is not clear whether sexual or asexual reproduction occurred, seeds collected from one plant will be considered as one “genotype” to be consistent with that of TOF and TLA.

There is a lot of confusion regarding the taxonomy of *Taraxacum*. Scientists from North America generally agree that only two species of Eurasian origin (TOF and TLA) have naturalized in the continent. However, some specialists in Europe argue that those *Taraxacum* species, especially TOF, can be classified into many micro-species (Stewart-Wade et al. 2002). This is understandable considering that North American populations reproduce apomictically and do not cross, thus each genotype line can be regarded as one species. The classification distinction between TOF and TLA is sometimes complicated as well. Hitchcock et al. (1955), as cited in Taylor (1987), listed a series of characteristics, such as leaves, inflorescences, and achenes, to distinguish between TOF and TLA in North America (see Table 1.4). Among these, leaves and achene colors are so far the most frequently used characters. In this study, achene color was used as the only trait to distinguish TOF from TLA – red achenes were produced by TLA and brown achenes were produced by TOF.
There has been no previous work comparing the phenotypic plasticity between TOF and TLA, but there have been some studies comparing TOF to another congener, and among different TOF populations. Brock et al. (2005) compared traits related to seed dispersal ability under conditions of different light quality for TOF and *T. ceratophorum* (a native to USA and with limited distribution). They found that plasticity in scape length at flowering tended to be greater in *T. ceratophorum*, and seed bearing scapes of TOF were taller and more uniform. In another experiment, Brock and Galen (2005) showed that in wet to dry environments, *T. ceratophorum* exhibited higher and more stable water use efficiency than TOF, which had much lower water use efficiency under wet conditions. In a recent study comparing introduced TOF populations in the Andes, Chile, and native populations in the Alps, France, Quiroz et al. (2009) found the Andes populations grown at different soil moisture levels were less plastic in terms of biomass allocation, but were able to maintain more stable survival and reproduction rate than the Alps populations.

1.7 Objectives and hypothesis

The primary objective of this dissertation is to determine whether phenotypic plasticity is associated with the success of TOF compared to TLA. The secondary objective is to determine how the results of the comparison between TOF and TLA can be utilized to predict the potential invasiveness of TKS.

My null hypothesis is that there is no difference in phenotypic plasticity of the invasive TOF and non-invasive TLA. The alternate hypothesis is that compared to TLA,
the response pattern of TOF to various environments follows one of the three scenarios described by Richards et al. (2006): Jack-of-all-trades, Master-of-some, and Jack-and-Master (Figure 1.2).

The second chapter of this dissertation reports on the germination patterns of the three dandelion species in different environments. The objective of this study was to determine how this critical life stage, which marks the beginning of a plant’s life, might contribute to the different success of TOF and TLA. The third chapter describes a greenhouse experiment in which the three species were grown and reproduced in various physical environments, including high and low light, water, and nutrient availability. The objective was to determine whether the plasticity of physiological, morphological, and fitness traits are associated with superior performance of TOF compared to TLA. The fourth chapter, which documents results of a field experiment over three years, aims to determine how the three species respond to different field habitats with or without competitors, and how these responses might facilitate the difference in invasiveness of the three species. The fifth and final chapter gives a summary of this research, and points out what is needed for future study.
<table>
<thead>
<tr>
<th>Biological traits</th>
<th>Relationship</th>
<th>Possible explanation</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Life form</td>
<td>*</td>
<td></td>
<td>(Williamson 1996)</td>
</tr>
<tr>
<td>Relative growth rate</td>
<td>+</td>
<td></td>
<td>(Maillet and Lopez-Garcia 2000)</td>
</tr>
<tr>
<td>Biomass production</td>
<td>+</td>
<td></td>
<td>(Maillet and Lopez-Garcia 2000)</td>
</tr>
<tr>
<td>Height</td>
<td>+/-NS</td>
<td></td>
<td>(Williamson 1996, Rejmánek 2000, Kolar and Lodge 2001)</td>
</tr>
<tr>
<td>Juvenile period</td>
<td>-/NS</td>
<td>early reproduction</td>
<td>(Rejmánek and Richardson 1996, Reichard and Hamilton 1997, Kolar and Lodge 2001)</td>
</tr>
<tr>
<td>Flowering period length</td>
<td>+/-NS</td>
<td></td>
<td>(Goodwin et al. 1999, Kolar and Lodge 2001)</td>
</tr>
<tr>
<td>Number of seeds</td>
<td>+</td>
<td>High reproduction rate</td>
<td>(Kolar and Lodge 2001)</td>
</tr>
<tr>
<td>Seed mass</td>
<td>+/-NS</td>
<td>Easy to disperse, high net reproduction rate</td>
<td>(Rejmánek and Richardson 1996, Kolar and Lodge 2001)</td>
</tr>
<tr>
<td>Dispersal method</td>
<td>*/NS</td>
<td></td>
<td>(Rejmánek 2000, Kolar and Lodge 2001)</td>
</tr>
<tr>
<td>Reproductive systems (perfect flowers or monoecious)</td>
<td>*/NS</td>
<td></td>
<td>(Kolar and Lodge 2001)</td>
</tr>
<tr>
<td>Vegetative reproduction</td>
<td>+</td>
<td>Increase of habitat compatibility</td>
<td>(Rejmánek 2000, Kolar and Lodge 2001)</td>
</tr>
<tr>
<td>Genome size</td>
<td>-</td>
<td>Short generation time</td>
<td>(Rejmánek 1996, Grotkopp et al. 1998)</td>
</tr>
<tr>
<td>Intervals between large seed crops</td>
<td>-</td>
<td>Continuous reproduction</td>
<td>(Rejmánek and Richardson 1996)</td>
</tr>
<tr>
<td>Non-specific mutualisms</td>
<td>+</td>
<td></td>
<td>(Richardson et al. 2000)</td>
</tr>
<tr>
<td>Fire tolerant</td>
<td>+/-NS</td>
<td></td>
<td>(Kolar and Lodge 2001)</td>
</tr>
<tr>
<td>Longevity</td>
<td>NS</td>
<td></td>
<td>(Kolar and Lodge 2001)</td>
</tr>
</tbody>
</table>

Table 1.1 Some of the simple biological and ecological traits related to invasiveness.  
Relationship type between biological traits and invasiveness. (+) positive; (-) negative; (NS) not significant; (*) non-directional significant relationship.
<table>
<thead>
<tr>
<th>Biological traits</th>
<th>Relationship</th>
<th>Possible explanation</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>History of invasion</td>
<td>*</td>
<td>Indication of invasiveness</td>
<td>(Kolar and Lodge 2001)</td>
</tr>
<tr>
<td>Size of primary (native) geographical ranges</td>
<td>+</td>
<td>Fitness homoeostasis and dispersal ability</td>
<td>(Williamson and Fitter 1996a, Goodwin et al. 1999, Rejmánek 2000)</td>
</tr>
<tr>
<td>Belonging to exotic genera</td>
<td>+/-</td>
<td>Possessing traits different from those of native species</td>
<td>(Darwin 1859, Rejmánek 1999, Daehler 2001)</td>
</tr>
<tr>
<td>Origin</td>
<td>*/NS</td>
<td></td>
<td>(Kolar and Lodge 2001)</td>
</tr>
<tr>
<td>Inhabits diverse climates</td>
<td>NS</td>
<td></td>
<td>(Scott and Panetta 1993)</td>
</tr>
</tbody>
</table>

Table 1.2 Selected synthetic biological and ecological traits related to invasiveness.  
Relationship type between biological traits and invasiveness. (+) positive; (-) negative; (NS) not significant; (*) non-directional significant relationship.

1. Germination requirements fulfilled in many environments
2. Discontinuous germination (internally controlled) and great longevity of seed
3. Rapid growth through vegetative phase to flowering
4. Continuous seed production for as long as growing conditions permit
5. Self-compatible but not completely autogamous or apomictic
6. When cross-pollinated, unspecialized visitors or wind utilized
7. Very high seed output in favorable environmental circumstances
8. Produces some seed in wide range of environmental conditions; tolerant and plastic
9. Has adaptations for short- and long-distance dispersal
10. If a perennial, has vigorous vegetative reproduction or regeneration from fragments
11. If a perennial, has brittleness, so not easily drawn from ground
12. Has ability to compete interspecifically by special means (rosette, choking growth, allelochemics)

Table 1.3 Ideal weed characteristics (from Baker 1974)
<table>
<thead>
<tr>
<th>Character</th>
<th>TOF</th>
<th>TLA</th>
</tr>
</thead>
<tbody>
<tr>
<td>Leaves</td>
<td>Oblanceolate, often not deeply cut, lobes broad, the terminal lobe enlarged</td>
<td>More slender, deeply cut their full length, lobes narrow, without an enlarged terminal lobe</td>
</tr>
<tr>
<td>Inflorescence</td>
<td>Relatively large</td>
<td>Relatively small</td>
</tr>
<tr>
<td>Involucre</td>
<td>1.5-2.5 cm high</td>
<td>1-2 cm high</td>
</tr>
<tr>
<td>Inner bracts</td>
<td>13-21, not corniculate</td>
<td>Commonly 13, usually somewhat corniculate</td>
</tr>
<tr>
<td>Outer bracts</td>
<td>Only slightly shorter than inner bracts, relaxed</td>
<td>1/3 to greater than 1/2 as long as inner bracts, appressed to relaxed</td>
</tr>
<tr>
<td>Achenes</td>
<td>Gray-brown to olive-brown, beak usually 2.5-4 times as long as body</td>
<td>Red to reddish-brown or reddish-purple, beak 0.5-3times as long as body</td>
</tr>
</tbody>
</table>

Table 1.4 Characteristics used to distinguish TOF and TLA (Hitchcock et al. 1955)
Figure 1.1 Reaction norms of four types of genotype-environment interaction scenarios: a) environmental effect only, b) genotypic effect only, c) genotype by environment interaction, but no genotypic or environmental effect, and d) environmental, genotypic, and environment by genotype interaction (see text for detail).
Figure 1.2 Three possible fitness plasticity responses of invasive (black line) and non-invasive (gray line) species across an environmental gradient. a) Jack-of-all-trades, b) Master-of-some, and c) Jack-and-Master. Reprint from Richards et al. (2006)
Figure 1.3 Distribution of TOF and TLA in North American, and some of the states in United States. OH: Ohio; MI: Michigan; IN: Indiana; PA: Pennsylvania; KY: Kentucky; WV: West Virginia. Maps came from USDA Plants Database (USDA and NRCS 2008).
CHAPTER 2

GERMINATION PATTERNS IN DIFFERENT ENVIRONMENTS

2.1 Introduction

Germination success in various environments, which acts as a key connection between generations that might be exposed to different habitats, is a characteristic thought to be associated with potential invasiveness. Baker (1974) identified the following two germination traits as ideal weed characteristics: “a) germination requirements fulfilled in many environments, and b) discontinuous germination (internally controlled) and great longevity of seed” (Table 1.3). After analyzing 31 weedy plant species in eastern Germany, Brändle et al. (2003) concluded that the germination niche breadth (the time span within a year during which the species is able to germinate) was correlated to the range size of these species. In a recent review, Pyšek and Richardson (2007) showed ~70% out of 18 studies found alien/invasive species germinate earlier, better, or over a wider range of conditions than their native/non-invasive congeners or related taxa. These studies suggest that species whose seeds are capable of germinating under many conditions are more likely to spread into
and occupy various habitats than species whose seeds have very strict germination requirements.

With its superb dispersal ability, dandelion seeds can spread virtually into any kinds of habitats. Although colonization success is determined by many factors, the first step is to germinate, regardless of whether the site offers an ideal habitat for growth, or a stressful environment with aggressive competitors. Therefore the invasive species *Taraxacum officinale* (TOF) is expected to have fewer restrictions in germination, and to germinate under a wider range of conditions than the non-invasive *T. laevigatum* (TLA). Such plasticity in germination could fall into any of the three categories (Jack-of-all-trades, Master-of-some, and Jack-and-Master, Figure 1.2), as long as TOF germinates better than TLA in most environments.

As a major weed around the world, the germination biology of TOF has been studied frequently (see review in Stewart-Wade et al. 2002). TOF seeds germinate over a wide range of temperatures, from 5°C to 35°C, with less germination at higher temperatures (Mezynski and Cole 1974). Most reports have indicated that TOF seeds germinate better in alternating temperature and light (Stewart-Wade et al. 2002). However, there are few reports on the germination of TLA or *T. kok-saghyz* (TKS), and no comparative studies of the three species.

In this study, I compared the germination behavior of the three dandelion species in various physical environments that differed in temperature, light availability, and water potential. I also tested the germination of seeds that had been exposed to an accelerated aging process. The temperature requirement is important because it determines in which
season (spring or summer) seeds are most likely to germinate. Seeds might be buried in soil and exposed to little light compared to those on the soil surface. So germination tests under different light levels will provide information on how the three species respond to seed burial. Seeds might also land on substrates that vary in water availability, from adequately moist to very dry, which can be characterized by high to low water potential. The ability to germinate successfully in stressful environmental conditions (extreme temperature, buried in soil, very dry substrate) might facilitate the invasiveness of invasive plant species.

Accelerated aging is one of the many methods to test seed vigor, which is defined as “the potential for rapid, uniform emergence, and development of normal seedlings under a wide range of field conditions” (Association of Official Seed Analysts 1983). The principle of this test is to greatly enhance the rate of deterioration of seeds by exposing them to high temperatures (40°C to 50°C) and high relative humidity (>90%) for a short period of time (Association of Official Seed Analysts 1983). This method was initially developed as a test to estimate the longevity of seeds in warehouse storage, but subsequent studies had shown this test was also useful in predicting stand establishment of many crop seeds under field conditions (Baskin 1970, Bishnoi and Delouche 1975, TeKrony and Egli 1977, Anfinrud and Schneiter 1984, Samimy et al. 1987, Egli and Tekrony 1995). The decline in germination after accelerated aging is thought to be proportional to the initial physiological potential of the seeds and their performance in the field under a wide range of environmental conditions (Delouche and Baskin 1973). For example, high vigor seeds show small decreases in germination following accelerated
aging, while low vigor seeds show large decreases. This method was used in this study to show how the three dandelion species respond to different aging periods, which simulated various degrees of deterioration. A successful invader is expected to exhibit low decreases in germination following accelerated aging and therefore a greater ability to persist in the seed bank. Furthermore, more aggressive species are also expected to have better establishment in the field, which is partly associated with germination after aging (Baskin 1970, Samimy et al. 1987, Egli and Tekrony 1995).

The objectives of this study were to: 1) evaluate the germination behavior of three Taraxacum species under a wide range of physical environments that might be associated with invasiveness, and 2) determine whether the germination pattern of TKS under different conditions is similar to that of invasive species.

2.2 Materials and Methods

2.2.1 Study system

A detailed review of the three dandelions species was provided in Section 1.6. In 2005 autumn, seeds of TOF were collected from 9 individuals in different habitats around the Columbus and Wooster campuses of The Ohio State University (Table 2.1). Since the distribution of TLA was very limited in Ohio, only one population (Table 2.1) was located using OSU herbarium records. Nine individuals from this population were dug in fall 2004, and transplanted in the greenhouse. Seeds from each individual were collected. For TKS, seeds were collected from a large population in the Republic of Uzbekistan in 2005. Seedlings from those seeds were grown in a greenhouse, and selections of 9
genotypes representing the range of variation were made from these seedlings by harvesting seed heads. To reduce the possibility of maternal effects on seed germination (Baskin and Baskin 1998), seeds of all three species were germinated and one individual from each of the 27 individuals was grown in the same greenhouse for seed collection. Each original individual and all its progeny will be referred to as one genotype in the following text (9 genotypes for each of the three species).

Collected seeds were stored in a seed storage facility with 5°C constant temperature and 30% RH until use. Such a storage environment is less likely to decrease seed viability compared to storage at room temperature (Letchamo and Gosselin 1996). Since a significant number of seeds were empty (no embryo inside the achene), all seeds were cleaned following the procedure described in APPENDIX A before being used in experiments. A sample of cleaned seeds of each genotype was X-rayed to make sure >95% of the seeds had embryos (Figure 2.1).

2.2.2 Germination temperature experiment

Germination responses to temperature for all genotypes of the three species were studied under three temperature regimes: 5°C/15°C, 15°C/25°C, and 25°C/35°C (night/day) with a 12-h photoperiod. Three replicates with 50 seeds of each genotype were germinated in 9 cm diameter transparent disposable Petri dishes. Seeds were placed on two layers of blotter paper, and 9 ml of distilled water were added per dish. Each Petri dish was sealed in a re-sealable plastic bag to prevent water loss during the experiment. Petri dishes were randomly placed in germination chambers with assigned temperature
settings. Shelves inside the chambers were randomly shifted after one week to compensate for possible environmental variation inside the chambers. For each species, a seed mixture of all 9 genotypes was also prepared using equal weight of each genotype. These seed mixtures were germinated under the three temperature regimes using the same method above (50 seeds/Petri dish). The purpose of testing the germination of seed mixture was to evaluate whether or not the average germination of genotypes can be represented by seed mixture of these genotypes. The experiment had a total of 3 species × (9 genotypes + 1 mix) × 3 temperature × 3 replicates = 270 experimental units. A completely randomized design was used, and the experiment was repeated.

Germinated seeds with visible radicles were counted and removed after 7 and 14 days.

2.2.3 Thermo-gradient table experiment

A thermo-gradient table provides a range of continuous temperature change over a wide range so that temperature effects on germination can be studied at a finer resolution than is possible with germination chambers. The table was set to 10°C at one end and 30°C at the other end, but the actual temperature measured was 12.3 ± 0.6°C to 29.3 ± 0.4°C (mean ± standard deviation). Ten temperature lanes were identified and used along this gradient. Petri dishes with 50 seeds each were prepared the same way as in the germination temperature experiment. Half of the Petri dishes were painted black using spray paint and sealed with black tape along the edges to create a dark germination environment. Only seed mixtures of the 9 genotypes for each species were studied.
because the germination temperature experiment revealed that mixed seeds represented
the average germination behavior of the 9 genotypes (see Results). Germination of mixed
seeds was tested in the ten temperature lanes (constant temperature) and 24 h of light. A
randomized complete block design was used. There were 3 replicates in the first run, and
2 replicates each in the second and third run.

Germinated seeds in the light environment were counted and removed once a week
in a 2-week period. Germination in the dark environment was not counted until the end of
the experiment.

2.2.4 Water potential experiment

To evaluate the variation among species in seed germination along a water potential
gradient, I exposed seeds to different concentrations of PEG-8000 (Polyethylene glycol,
Sigma® Chemical Co. MO 63178) solutions that created a range of water potential.
Solutions were prepared using the equation in Michael et al. (1983) for four levels of
water potential: -0.2 MPa, -0.4 MPa, -0.6 MPa, and -0.8 MPa. This method has been
widely used in germination tests to create different levels of osmotic stress. It has been
reported that filter paper such as blotters would absorb water and exclude larger
molecules of PEG, resulting in a higher PEG concentration in the liquid phase (Hardegree
and Emmerich 1990), so the actual water potentials in these treatments might have been
lower than expected. Distilled water was used in the control treatment of 0 MPa water
potential. Petri dishes with 50 seeds of each species were prepared using the same
method as in the germination temperature experiment, except that 9 ml of assigned PEG
solution or distilled water was used. Seeds were germinated at a constant temperature of 20°C to avoid water potential variation under different temperatures (Michel 1983). A completely randomized design was used. There were six replicates in the first experiment and three replicates in the second experiment.

Germinated seeds were counted and removed after 7 and 14 days.

2.2.5 Accelerated aging experiment

Seeds were scattered in one layer in an aluminum dish, which was placed on top of a fine-mesh metal screen supported by a four-legged frame. The frame was placed in a plastic box with 30 ml of distilled water. The water did not have direct contact with the seeds, but created an environment of almost 100% RH when the box was sealed with a lid (Association of Official Seed Analysts 1983, Zhang and McDonald 1996). The box was wrapped in a re-sealable plastic bag and was kept at 40°C in a dark environment. Five aging periods were tested: 0 h (normal seeds), 24 h, 48 h, 72 h, and 96 h. Some of the seeds, especially those treated with longer aging periods, were infected by fungus, so they were cleaned by rubbing gently between paper towels. Germination of these aged seeds was tested using the same equipment as in the germination temperature experiment, with 15°C/25°C (night/day) and a 12-h photoperiod. Seed mixtures of 9 genotypes for each species were studied. The experimental design was a completely randomized design with three replicates for each treatment, and the experiment was repeated.

Germinated seeds were counted and removed once a week over a 2-week period.
2.2.6 Statistical analysis

Germination rate follows a binomial distribution, so traditional analysis methods assuming normal distribution of the data were not appropriate. In this study, all germination data were analyzed using the generalized linear model or GLZ (Crawley 1993, Littell et al. 2006). The generalized linear model approach has the advantage of handling non-normal distribution data such as binomial and Poisson distributions, and it always gives predictions in the allowable range. The Proc Glimmix procedure in SAS/STAT software (SAS 9.1.3) was used, and a logit link function was applied. Generalized chi-square/df values were all close to 1, so there was no need to adjust for over-dispersion (Littell et al. 2006). When models failed to converge using Proc Glimmix, Proc Mixed was used instead. In these cases, germination percentage data were first arcsine square-root transformed to meet normality assumptions (Zar 1999). Satterthwaite’s method was used to compute the denominator degree of freedom for tests of fixed effects (Littell et al. 2006, pg 114). Least square means, together with their standard errors, were estimated and back transformed data are presented in the final results. If any of the transformed data (including estimate ± standard error) were greater than 1.5708, or smaller than 0 (which corresponds to 100% and zero germination respectively), they were manually changed to 1.5708 or 0. Species and all applied environmental factors (i.e. temperature, light, water potential, and aging period) were treated as fixed effects, and experiment (including its interactions with other fixed effects) was treated as a random effect (Table 2.2).
In the germination temperature experiment, germination of the seed mixture and germination of genotypes were analyzed separately. Two methods were used to analyze the germination data of genotypes. The first method treated genotypes (nested within species), and the interaction between temperature and genotype as random effects. This method allowed testing the species effect as a whole in the background of genotypic effects. The second method analyzed each species separately and treated genotypes as a fixed effect, so that genotypic differences within species could be revealed. Model construction for each analysis is summarized in Table 2.2.

2.3 Results

Germination of the three species was significantly affected by most of the environments tested (Table 2.3). All of the species effects as well as most species-by-environment interactions were significant, except for species × aging period. These results indicated complicated germination responses of the three species exposed to various environmental conditions.

2.3.1 Germination temperature

Genotypes of each species were examined separately in this experiment. There were significant genotype by temperature interactions among the nine genotypes of TLA and TKS (P=0.0346 and P=0.0014), but only the temperature effect was significant in TOF (P=0.0389, Table 2.3). Germination patterns of all 27 genotypes are shown in Figure 2.2a. All species achieved >80% germination in the low (5°C /15°C) and the mid (15°C /25°C)
temperature regimes, but germinated best and more uniformly at 15°C /25°C. Germination was reduced at high (25°C /35°C) temperatures for most genotypes, especially for TOF and TLA. There was no overlap of germination rates among TOF and TLA genotypes, but some overlap among TKS and TOF genotypes at this temperature.

When genotype data were analyzed on a species basis (genotypes as random effects), species, temperature, and their interaction were all significant (Table 2.3), indicating different germination responses to temperature for different species (Figure 2.2b). Significant differences were found between mid and high temperatures in all three species (P=0.0111, P<0.0001, and P=0.0016 for TOF, TLA, and TKS, respectively). Germination of TOF (93.8%) and TLA (93.7%) was lower than TKS (99.2%) at the mid temperature (P=0.0169 and P=0.0165). At high temperatures, TOF had higher germination (71.2%) than TLA (15.7%, P=0.0056), and similar germination to TKS (91.3%, P=0.0732).

The germination of the seed mixture showed a pattern similar to that of the average germination of the genotypes (Figure 2.2b and Figure 2.2c). TKS had the most consistent germination across three temperatures (95.1%, 99.7% and 86.8%, at low, mid, and high temperatures, respectively). TLA germinated best (91.5%) at mid temperatures but only achieved 15.2% germination at high temperatures. Germination of TOF was somewhat between TKS and TLA, with 96.4% at low, 91.5% at mid, and 73.7% at high temperatures.
2.3.2 Thermo-gradient table experiment

Germination was significantly affected by temperature, light, and species, and by all interactions except the temperature by light interaction (Table 2.3). The three-way species×temperature×light effect was also significant (P=0.0037), indicating complicated responses of the three species to light and temperature. Generally, TKS germinated best among the three species in both dark (17.7% to 57.8%) and light (77.6% to 98.4%) conditions across the temperature gradient (Figure 2.3). When seeds were exposed to light, germination of TOF (39.2% to 89.6%) and TLA (28.9% to 91.3%) was similar and declined gradually when temperature increased. Germination of TKS, however, was consistently high (>90%) except at a very high temperature (30°C), when only 77.6% of the seeds germinated. Dark environments reduced germination in all of the three species, but TOF was the most sensitive to darkness (4.2% to 31.1% germination compared to 2.7% to 51.1% of TLA and 17.7% to 57.8% of TKS), especially when temperature was low (Figure 2.3). Germination also decreased with rising temperature in the dark for the three species.

2.3.3 Water potential

Species, water potential, and their interaction all had significant effects on germination (Table 2.3). Germination declined with decreasing water potential, which is analogous to increasing drought (Figure 2.4a). TKS germinated best (7.3% to 99.7%) among the three species, and TOF exhibited the lowest germination rate (0.0% to 90.7%) at all water potential levels. Germination of the three species was most different at -0.2
MPa, -0.4 MPa, and -0.6 MPa, where only 2.6%, 10.6%, and 54.0% of TOF seeds germinated, compared to 14.5%, 33.8%, and 66.3% of TLA, and 36.3%, 66.9%, and 95.3% of TKS (Figure 2.4a). The germination curves of the three species were also different. For TOF, there was a sharp decrease in germination from 0 MPa to -0.4 MPa. In TLA, seed germination decreased at a constant rate from 0 MPa to -0.8 MPa. On the other hand, there was only a small decline in germination for TKS at -0.2 MPa compared to 0 MPa, followed by a constant decrease from -0.2 MPa to -0.8 MPa (Figure 2.4a).

2.3.4 Accelerated aging

Germination was significantly affected by aging period (P=0.0003), and the species effect was marginally significant (P=0.0448). No interaction between species and aging period was found (P=0.3522), which means the three *Taraxacum* species responded to aging period in a similar way. Germination declined in an “S” shape with increasing aging time, from 0 to 96 hours (Figure 2.4b). Again, TKS exhibited the highest germination (7.8% to 99.3%) and TOF the lowest (0.3% to 91.3%) for all aging periods.

2.4 Discussion

Both TOF and TLA achieved similar and relatively high germination rates at low and middle temperatures (Figure 2.2). Alternating temperature and exposure to light promoted germination significantly. These findings were consistent with previous studies of TOF (Stewart-Wade et al. 2002) and no similar studies have been reported for TLA.
Surprisingly, TLA germinated better than TOF in most of the environments tested, and TKS always germinated best among the three.

2.4.1 Genetic variation and taxonomy

It has been widely reported that TOF populations in North America are highly genetically variable for such an introduced species that produces only asexually (Taylor 1987). Lyman and Ellstrand (1984) found 47 discernible clones among 518 individuals using seed color and allozyme morphs. Many of these clones were restricted to a single population and there was one widespread clone found in all but 3 of the 22 populations surveyed. Using rDNA-cDNA combinations, King (1993) identified 145 distinct genotypes in 318 plants. Rogstad et al. (2001) used VNTR (variable number tandem repeat) loci to examine patterns of genetic variation among TOF collected in North America. They found that genetic diversity was moderately high and was maintained at similar levels at different spatial scales. Genetic/morphologic variation within populations was similar, or greater than that among populations (Taylor 1987, Rogstad et al. 2001).

With such high levels of variation, one might expect that germination behavior and other traits would be highly variable as well. It might even be expected that the variation within TOF would exceed the variation among the three species examined in this study. If this was the case, it would be more meaningful to study each genotype of each species rather than to study each species as a whole. Due to the large number of genotypes (27 in total) involved in this study, it was impractical to examine each of them in every
experiment except for the germination temperature test. The results, however, failed to reveal significant differences among the nine TOF genotypes collected (Table 2.3). On the other hand, TLA and TKS seemed to be more variable, with either significant genotype effects or genotype by temperature interactions. The low level of variation among TOF genotypes might be due to the fact that seeds were collected in a relatively limited range (Table 2.1). TLA, on the other hand, exhibited a surprisingly high level of variation considering that seeds were collected from only one population at a cemetery in western Ohio (Table 2.1).

When comparisons were made among species, germination at the low and mid temperatures was very similar for all genotypes and species. But the species did show different response at high temperatures (Figure 2.2a). Furthermore, germination behavior of the seed mixture resembled reasonably well to that of genotypic averages (Figure 2.2b and Figure 2.2c). These results provided support for the method of evaluating the response at the species rather than the genotype level, as well as for the use of the seed mixture to evaluate germination patterns in other experiments.

After an extensive study of Taraxacum populations in northwestern US, Taylor (1987) found that the morphological characteristics listed in Hitchcock et al. (1955) to distinguish between TOF and TLA (Table 1.4) were poorly correlated. The author argued that the morphological variations used for classification were more likely due to phenotypic plasticity rather than inherent genetic differences (a stressed environment tended to produce TLA-type characteristics). This conclusion, however, is not supported by this study. Achenes used in the germination tests were collected from plants grown in
the same greenhouse environments to eliminate maternal environment effects. Plants identified as TOF always produced brown colored achenes and TLA always produced red colored achenes. The leaves of TLA also tended to be more deeply cut than those of TOF, although this characteristic was not as easily recognized as the achene color. This observation suggests that leaf shape and achene color were not controlled by the environment but rather by the genotype. The populations used in this study were classified as TOF or TLA by their achene color, and the clearly separated cluster of genotypes in germination rate under high temperature (Figure 2.2a) supports the separation of these two species using achene color alone. Other characteristics mentioned in Hitchcock et al. (1955) such as bracts and involucres (Table 1.4), however, seemed to be inconsistent within species (data not shown).

2.4.2 Invasiveness and fitness plasticity

Germination patterns in response to alternating temperature appeared to follow the expectation that the invasive TOF germinated better over a wide range of temperatures than did the non-invasive and much less common TLA. The ability of TOF to germinate well even in high alternating temperatures (25°C/35°C) may provide the possibility of continuous germination throughout the growing season (including summer), if sufficient moisture is available. TLA, on the other hand, germinated well only under cool conditions, such as those prevailing during spring and autumn.

This pattern of higher germination of TOF in various environments, however, did not hold in other experiments. At constant temperature (thermo-gradient table experiment),
germination behavior was similar for TOF and TLA when seeds were exposed to light (Figure 2.3). Dark environments inhibited germination for both species, but TLA germinated better than TOF. TOF also had lower germination at water potentials between -0.6MPa and -0.2MPa (Figure 2.4a). The same was true for the accelerated aging experiment in which TOF showed a consistently lower germination rate than TLA when exposed to high temperature and humidity for various times (Figure 2.4b). In short, the non-invasive TLA performed better than the invasive TOF under unfavorable conditions such as dark, drought, and aging.

Although these results disagreed with previous studies in which invasive species generally germinated better, or under a wider range of conditions than non-invasive species (Pyšek and Richardson 2007), TOF might actually benefit from such germination behavior. Depth of seed burial is negatively correlated to establishment success in TOF (Bostock and Benton 1983), thus low germination in the dark could prevent germination of seeds buried too deeply in the soil and thus failure to emerge. If germination is restrained when moisture is inadequate, seedlings may escape the risk of death due to drought. In another words, TOF seeds may germinate best in environments that favor growth, and not risk germination when the conditions could be stressful for new seedlings. There are varying reports on the viability of TOF seeds buried in soil: 1-6% remained viable after 4 years (Chepil 1946, Roberts and Neilson 1981), and some last up to 20-30 years (Stewart-Wade et al. 2002). Therefore ungerminated seeds could remain in the soil for several seasons until favorable condition occur. Furthermore, neither TOF nor TLA seeds would be expected to germinate in dry places during a hot summer. In wet spots at
high temperature, however, TLA seeds would be expected to remain ungerminated. But TOF seeds may germinate and take advantage of the warmth and moisture for growth. This combined adaptation to temperature and soil moisture conditions offers TOF a unique opportunity, or niche, for growth during the summer season.

Compared to TLA, the germination pattern of TOF did not fall into any of the three phenotypic plasticity categories that are expected to explain invasion success (Jack-of-all-trade, Master-of-some, and Jack-and Master, Richards et al. 2006) because TOF exhibited lower germination than TLA in stressful environments. The only exception was germination at alternating temperatures, where TOF appeared to be a Jack-of-all-trades type.

It has been suggested that the magnitude of plasticity alone is not necessarily associated with invasion success (Sultan 2001, Richards et al. 2006). Invasive species might be more plastic in fitness (Master-of-some), or more stable (Jack-of-all-trades) than native/non-invasive species. This study further demonstrated that for a specific fitness component such as germination, neither higher values nor lower values per se were associated with invasion success. TOF had higher, similar, or lower germination than TLA in various stressful environments, but TOF is still a much more successful weed than TLA. This suggests that germination pattern at different conditions contributed to the success of TOF in very complicated way.
2.4.3 Other studies on germination and invasiveness

There have been a few studies using similar methods to compare the germination patterns of closely related invasive and non-invasive species. Forcella et al. (1986) found that rapidity of seed germination and breadth of native distribution contribute to the success of the most invasive species among three non-native *Echium* congeners in Australia. Early germination and frost tolerance were important to determine the invasiveness among three *Impatiens* species in British Isles (Perrins et al. 1993). Lambrinos (2002) found that *Cortaderia selloana*, which was widely spread in California, had consistently higher germination in both lab and field experiments than *C. jubata*, which had a restricted distribution. Mihulka et al. (2003) found that the ability to germinate in light was a significant predictor of invasion success among non-native *Oenothera* congeners in six European countries. After comparing a series of life history traits of invasive *Senecio madagascariensis* and non-invasive *S. lautus*, Radford and Cousens (2000) found that the invasive *Senecio* had higher rates of germination in both light and dark conditions. Van Kleunen and Johnson (2007) compared germination patterns of 30 Iridaceae species that become naturalized outside their home range and 30 congeneric species that have been failed to naturalize. They found that naturalized species emerged faster and more profusely than their non-naturalized congeners.

Most of these studies demonstrated that invasive species germinated faster and more successfully than non-invasive species in at least some environments. In a meta-analysis review, Colautti et al. (2006) concluded that germination success/rate, together with reproductive output and propagule pressure were positively associated with invasiveness.
My results are not in agreement with this conclusion. However, many of these studies also showed that it is not simply the higher germination that makes one species invasive. Instead, germination patterns often worked together with other life history traits and environmental conditions to determine invasiveness (Perrins et al. 1993, Radford and Cousens 2000). This is probably true for the germination pattern of TOF and TLA as the post-germination growth could play an important role. In addition, it is possible that results of studies where invasive species had lower germination (or similar germination between invasive and non-invasive species) were under-reported. There were minimal differences, for example, among three Centaurea congeners with different invasiveness in their seed germination responses (Gerlach and Rice 2003).

Other studies have had more complicated conclusions. In a comparison of four invasive and non-invasive Atriplex species, Mandak (2003) found significant differences in dormancy and germination patterns under various environments in one pair (A. sagittata – A. hortensis group), but no differences were revealed in the other pair (A. tatarica – A. rosea group). The invasive A. sagittata had deeper dormancy (and thus lower germination rate) than the non-invasive A. hortensis, and its success was explained as the ability to time germination and consequently extend the germination period over several years. On the other hand, the success of A. tatarica over A. rosea probably relied on other life history traits such as competitive ability, resource allocation, or resistance to predators. The author concluded that it was impossible to identify general life history traits associated with invasiveness because of the interaction of particular species with particular environments in which they grow. This conclusion might also apply to TOF
and TLA, because their germination patterns seem to interact with environments in a complicated way.

2.4.4 TKS

The germination behavior of TKS was somewhat beyond expectations. It germinated best among the three species under all conditions (Figure 2.2 - Figure 2.4). This might be due to the selection of these populations for high and consistent germination as a potential crop. However, this does not imply that TKS would have a strong potential to become invasive because, as discussed before, high germination was not associated with invasiveness in TOF. On the other hand, the ability to germinate well in all environments offers TKS the advantage to succeed – as a crop or as a weed – if it is able to grow and produce well under such conditions. Further study is needed to demonstrate this before conclusions can be made on whether or not TKS could be potentially invasive.

2.4.5 Further study

TOF had lower germination than TLA and TKS after the accelerated aging process. Although previous studies have showed that accelerated aging results can sometimes represent germination performance in field conditions for some crop species, there have been no previous studies on this aspect for Taraxacum. How these three species germinate in the field is worth investigating. If TOF does not germinate as well as TLA in the field, this could somewhat compensate for its advantage in high temperature environments, and further reduce its advantage in dark and dry conditions.
Germination is only one stage of life history, so it is inappropriate to draw too many conclusions about invasiveness by studying germination only. The results of this study suggest that TOF may have an advantage in warm environments by germinating well in high temperatures. Whether this extends to a fitness advantage depends on how TOF seedlings actually grow in such environments. Similarly, the hypothetical advantage of TOF’s low germination in dark and drought conditions depends on whether or not the ungerminated seeds are able to germinate when favorable conditions arrive. It also depends on the performance of TLA seedlings in dark and dry environments. If TLA seedlings emerge from deep in the soil, or grow well even in dry habitats, then the germination patterns of TLA are more favorable than those of TOF. In this case, there may be other traits that contribute to the invasiveness of TOF. Furthermore, studies of seedling behavior in various environments is also required to determine the invasiveness of TKS.

2.5 Conclusion

The comparison between invasive TOF and non-invasive TLA provided interesting insights into how germination behavior might contribute to invasiveness. The germination of TOF did not strictly fall into the expectation of “germination requirements fulfilled in many environments,” nor did it follow the plasticity hypotheses of Jack or Master. Instead, neither fitness plasticity nor absolute fitness value appear to be good predictors for invasiveness in this case. It is likely that the germination traits, environments, their interactions, and sometimes other related traits (e.g. post-germination
growth) contribute to the greater invasive success of one species relative to another less successful species in a particular habitat. Due to the complicated results, the invasiveness of TKS based on germination behavior remains inconclusive. More studies on growth after germination in various environments are needed to fully understand why TOF and TLA are so different in their invasiveness, and to make reliable prediction about the invasive potential of TKS.
<table>
<thead>
<tr>
<th>Species</th>
<th>Genotype</th>
<th>Collected Date</th>
<th>Location</th>
<th>Habitat</th>
<th>Longitude/latitude</th>
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<td>TOF</td>
<td>1</td>
<td>Oct. 11, 2005</td>
<td>OSU Columbus campus</td>
<td>Lawn in front of H&amp;CS department</td>
<td>40°0'N, 83°2'W</td>
</tr>
<tr>
<td>TOF</td>
<td>2</td>
<td>Sep. 28, 2005</td>
<td>OSU Columbus campus</td>
<td>Weedy patch in Waterman Farm</td>
<td>40°1'N, 83°3'W</td>
</tr>
<tr>
<td>TOF</td>
<td>3</td>
<td>Sep. 27, 2005</td>
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<td>Weedy patch between Parks Hall and Aronoff Laboratory</td>
<td>40°0'N, 83°1'W</td>
</tr>
<tr>
<td>TOF</td>
<td>4</td>
<td>Sep. 28, 2005</td>
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<td>Weedy patch in Waterman Farm</td>
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<td>TOF</td>
<td>5</td>
<td>Sep. 27, 2005</td>
<td>OSU Columbus campus</td>
<td>Mirror Lake north bank, among ground cover of English ivy</td>
<td>40°0'N, 83°1'W</td>
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<td>TOF</td>
<td>6</td>
<td>Oct. 4, 2005</td>
<td>OSU Columbus campus</td>
<td>Lawn of west campus parking lots</td>
<td>40°0'N, 83°2'W</td>
</tr>
<tr>
<td>TOF</td>
<td>7</td>
<td>Sep. 16, 2005</td>
<td>OSU Wooster campus</td>
<td>Lawn under crab apple (Malus) trees</td>
<td>40°47'N, 81°55'W</td>
</tr>
<tr>
<td>TOF</td>
<td>8</td>
<td>Sep. 16, 2005</td>
<td>OSU Wooster campus</td>
<td>Lawn along roadside</td>
<td>40°47'N, 81°55'W</td>
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<td>TOF</td>
<td>9</td>
<td>Sep. 16, 2005</td>
<td>OSU Wooster campus</td>
<td>Lawn in front of a rose garden</td>
<td>40°47'N, 81°55'W</td>
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<tr>
<td>TLA</td>
<td>1-9</td>
<td>Oct. 28, 2004</td>
<td>Freedom Township, Wood County, Ohio</td>
<td>Sandy soil in Fish Cemetery, W. of Zepernick Rd., S. of Housekeeper Rd.</td>
<td>41°22'N, 83°30'W</td>
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<td>TKS</td>
<td>1-9</td>
<td>2005</td>
<td>population in the Republic of Uzbekistan</td>
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Table 2.1 Description of sample collection
<table>
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<th>Models for</th>
<th>Fixed effect</th>
<th>Random effect</th>
<th>Model</th>
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<tr>
<td>Germination temperature: each species was analyzed separately</td>
<td>Gen</td>
<td>Temp</td>
<td>Exp×Gen</td>
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<tr>
<td>Germination temperature: all genotypes, genotype as random effect</td>
<td>Spp</td>
<td>Temp</td>
<td>Gen(Spp) Gen(Spp)×Temp</td>
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<tr>
<td>Germination temperature: Mixed seed</td>
<td>Spp</td>
<td>Temp</td>
<td>Exp Exp×Spp</td>
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<td>Thermo-gradient table</td>
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<td>Temp</td>
<td>Light</td>
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<td>Spp</td>
<td>Water_potential</td>
<td>Exp Exp×Spp</td>
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<td>Accelerated aging</td>
<td>Spp</td>
<td>Aging_period</td>
<td>Exp Exp×Spp</td>
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Table 2.2 Description of models used in the analysis. Gen – genotype; Temp – temperature; Spp – species; GLZ – generalized linear model; Mixed – Mixed model; “ | ” means all simple effects and interactions of the terms. For example, Spp | Temp means Spp, Temp and Spp×Temp effects.
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<tr>
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<th>F-value</th>
<th>P b</th>
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<td>Species×Aging period</td>
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</table>

Table 2.3 ANOVA tables for all germination experiments

\( a \): See Statistic Analysis for details

\( b \): Bold number indicates significant effect at 0.05 level

\( † \): Data analyzed using generalized linear model (Proc Glimmix)

\( ‡ \): Data analyzed using mixed model (Proc Mixed) because generalized linear model was unable to converge
Figure 2.1 X-ray image of seeds after cleaning. Most seeds were filled with embryos. Picture shown is TOF seeds.
Figure 2.2 Germination percentage (least square mean ± SE) in alternating Low (5°C/15°C), Mid (15°C/25°C), and High (25°C/35°C) temperature regimes. (a) All 27 genotypes of the three species (each species was analyzed separately). (b) Average across nine genotypes for each species (genotype as random effect). (c) Seed mixture of nine genotypes for each species. TOF: solid line; TLA: dotted line; TKS: dashed line.
Figure 2.3 Germination percentage (least square mean ± SE) of the three species in various constant temperatures and light or dark conditions.

Figure 2.4 Germination percentage (least square mean ± SE) of the three species in: (a) various water potentials, and (b), various accelerating aging period. TOF (solid line and filled circle), TLA (dotted line and open triangle), and TKS (dashed line and filled square)
CHAPTER 3

GROWTH AND REPRODUCTION IN DIFFERENT GREENHOUSE ENVIRONMENTS

3.1 Introduction

Phenotypic plasticity is thought to play an important role in the success of invasive species (Sultan 2001, Griffith and Sultan 2005, Hulme 2008). A popular hypothesis is that invasive species have greater phenotypic plasticity than native or non-invasive species, which facilitates their adaptation to a wider range of environments (Richards et al. 2006). Although not always expressed explicitly, “plasticity” mentioned in the above hypothesis usually refers to morphological or physiological features (such as leaf shape or metabolic pathway) that provide the possibility of growth flexibility in different environmental conditions. On the other hand, fitness, which is a measure of reproductive success (Dejong 1994), is also considered to be a component of phenotypic plasticity in some studies (Sultan 2001, Richards et al. 2006). Thus a logical prediction of the above hypothesis would be that fitness traits are more stable, rather than more plastic, for invasive species across environments. Confusion can arise if these two components are
not clearly identified and distinguished for their different responses across various environments.

For this reason, I propose to restate the above hypothesis as follows: invasive species are generalists that are capable of maintaining fitness stability across a wide range of growth conditions, by means of plastic responses in morphology or physiology to environmental changes (Figure 3.1). For example, when growing in a low-light condition, invasive species might exhibit larger changes in height than non-invasive species, a shade-avoidance mechanism to access more light resources (Smith 1982, Smith and Whitelam 1997), which would result in less fitness reduction compared to the level of fitness without shade. Similarly, an invasive species might increase its investment in root tissue when facing drought or a nutrient deficit in soil, which would allow it to explore water and mineral elements more effectively, and thereby maintain higher fitness than a less responsive non-invasive species.

I propose that if phenotypic plasticity is a trait that allows certain species to be more successful invaders than other species, there are two aspects of phenotypic plasticity that must be examined with respect to fitness: 1) Invasive species maintain a more stable fitness across an environmental gradient than non-invasive species (Figure 3.1a); and 2) The stable fitness of an invasive species is achieved by more plastic responses of morphological and physiological traits (Figure 3.1b). The concept that plasticity in one trait can lead to stability in another trait is not a new one. Trewavas, and Jennings (1986) suggested that stability in higher level traits, such as morphology, resulted from a great deal of plasticity at lower levels of organization (e.g. molecular, cellular, and histological
structure). So it is reasonable to suggest that the stability of fitness, a high-level trait, can be achieved by large plasticity of low-level traits of morphology and physiology.

This study uses a model system of three closely related species in the genus of *Taraxacum* (Asteraceae) to evaluate the above hypotheses. One of the species (*T. officinale*, or TOF) is known as a notorious non-native weed throughout North America. Another species, *T. laevigatum* (TLA), is a closely related but relatively rare non-invasive alien. The third species, *T. kok-saghyz* (TKS), has been introduced to North America as a latex producing species, and its invasive status is unknown (van Beillen and Poirier 2007). Therefore, a secondary rationale for this study was to evaluate the invasive potential of *T. kok-saghyz*, by comparing its phenotypic plasticity with that of the closely related invasive and non-invasive species.

These three species were studied at the individual plant level through a greenhouse experiment in which they were grown under a range of light, water availability, and fertility conditions. Combinations of these environmental factors represent the characteristics of the habitats where dandelion species (especially TOF) were found, from grass lawns (moist, high fertility with low or high competition for light) to roadsides (dry, moderate to low fertility, and various levels of light competition). Previous studies comparing wide-spread species with those of limited distribution have shown different responses to light (Brock et al. 2005, Griffith and Sultan 2005), water availability (Brock and Galen 2005), and fertility (Milberg et al. 1999, Burns 2004). The specific objective of this study was to determine the relationship between plasticity of physiological,
morphological, and fitness traits (growth and reproduction) of the three *Taraxacum* species.

### 3.2 Materials and Methods

#### 3.2.1 Study system

A detailed review of the three dandelions species was provided in Section 1.6. The collection of each species was described in Section 2.2. Eight genotypes of each species were randomly selected from the nine genotypes for this study. Seeds used in this experiment were from either the original plants or their progeny grown in the greenhouse.

#### 3.2.2 Experimental design

Individuals of each species were grown in a factorial combination of eight treatments (two light conditions × two fertility levels × two water availability) in a split plot design with eight replications. Light treatment was the main plot effect. To insure that phenotypic plasticity was properly measured rather than being confounded with the genotype effect, I designed the experiment in a way that each block contained individuals from the same genotype of each species (Sultan 2001). Thus, eight genotypes of each species were assigned to 8 blocks. There were 3 species × 8 treatments × 8 replicates = 192 individuals in total.

On February 21, 2006, I sowed seeds in flats with 9×18 cells (2.7×2.7×4.5 cm) filled with a commercial growing medium (Sureclone 360, Michigan Grower Products, Inc. Galesburg, MI, USA). Seeds were lightly pressed into the media and flats were placed on
greenhouse benches where water misted the pots every 10 minutes. Germination occurred in one week. I provided fertilizer solution (20-10-20, 50 ppm) to emerged seedlings once per week. On March 10 2006, when the seedlings had 2-3 fully expanded true leaves, they were transplanted into standard plastic pots (15 cm in height and ~2L in volume) filled with the same growing medium and assigned amount of fertilizer (see below). Seedlings were allowed to adapt to the pots for 3 weeks before light and water treatments were applied. Pots were placed on two greenhouse benches, with 30 cm spacing between pots. There was 60 cm distance between two blocks so that the green-shade treatment (see below) had minimum effect on plants in adjacent blocks.

**Light condition**

I grew each individual either in full light (F) or green shade (G). Green shade, rather than neutral shade (which absorbs light of all wavelengths equally), was selected for this experiment in an effort to better mimic the effect of vegetation shading. Due to their low height, dandelions are frequently found in habitats where vegetation shading from turf grasses or crops is common. Compared to natural solar radiance, sun light penetrating green vegetation is characterized by a much higher red : far-red (R:FR) ratio, which has numerous effects on plant growth, such as resource allocation pattern, time to reproduction, and leaf size (Smith 1982, Smith and Whitelam 1997, Brock et al. 2005). Therefore dandelions would be expected to respond differently to green shade than to neutral shade, and green shade should provide more realistic information about the species’ performance in field conditions.
I created green shade using a single layer of green film filter (Roscolux #4430, Rosco Laboratories Inc., Stamford, CT, USA). The light absorption curve of this material is shown in Figure 3.2, measured using an LI-1800 portable spectroradiometer (LI-COR, Inc, Lincoln, NE, USA). The R:FR ratio (655-665/725-735 nm, Smith 1994) is 0.556 ± 0.006 under green shade compared to 1.170 ± 0.002 under full daylight in the greenhouse (four measurements in a clear August midday). The green filter created a light environment similar to a grass-ward habitat (R:FR ratio = 0.61 - 0.92) as described in Morgan and Smith (1981).

The experiment was set up as split-plot design and the light effect was the main plot treatment. I suspended the green filter 50 cm above the 12 pots (3 species × 4 treatments) in each block. Four pieces of side “drapes” (30 cm in height) were also attached to surround the plants. From July 6 to August 17, light intensity was measured using an LI-1776 Solar Monitor (LI-COR, Inc, Lincoln, NE, USA) during seven sunny mid-days under full light and green shade treatments, right above the highest leaves. Photosynthetic photo flux density (PPFD, 400-700 nm) was 880.8 ± 106.3 µmolm⁻²s⁻¹ (means ± 1 SD) in full light, compared to 414.3 ± 68.9 µmolm⁻²s⁻¹ in green shade. The green filter was wiped from time to time during the experiment to avoid dust accumulation.

**Fertility**

Two levels of soil fertility were applied, and are referred to as high fertility (H) and low fertility (L). Into the growing medium, I mixed 13 g (H) or 4 g (L) of slow release fertilizer (Scotts® Osmocote® Classic 14-14-14, The Scotts Company, Marysville, OH,
USA) at the time of seedling transplanting. These dosages were recommended for high and low fertility as described on the product label. On July 11, when the plants had been transplanted for 4 months – which was the recommended time for the fertilizer to be effective – the assigned amount of fertilizer was re-applied by spreading the granules over the growing medium.

Soil moisture

Two levels of soil moisture, wet (W) and dry (D), were applied. To each pot, I connected a pressure-compensated dripper which adjusted for water flow rate. High flow-rate drippers (2L/h) were used for wet (W) treatment plants, and low flow-rate drippers (1L/h) for dry (D) treatment plants. The drippers for pots containing full-light/wet (FW), green-light/wet (GW), full-light/dry (FD), and green-light/dry (GD) treatment plants were controlled by four independent programs so that they could be easily turned on and off, and adjusted for different irrigation time and frequencies. This allowed maximum flexibility to provide the amount of water needed for each plant.

The W-treatment plants received 2 minutes of irrigation twice a day at the beginning of the experiment. I increased the irrigation time and frequency gradually as the plants grew bigger, and as the weather became warmer with higher light intensity. At the final stage before harvest, the irrigation was on for 10 minutes (FW) and 5 minutes (GW), 3 times a day. Since plants in different treatments (soil fertility and light condition) grew at different rates, the programmed irrigation scheme did not necessarily meet the water requirements for all plants each day. Therefore, I checked the weight of each pot daily to
determine whether or not sufficient water was supplied. Additional water was manually applied as needed.

Programmed automatic irrigation did not work well for dry (D) treatments because some plants received too much water while others too little. Therefore, plants were manually watered under the criterion that if the plants showed signs of wilting, 100-200 ml of water (depending on the weather condition) was supplied once a day. If a daily check was impossible, the irrigation was turned on for that day, with irrigation time and frequency adjusted for the forecasted weather on that day. This precaution was necessary because plants under the D-treatment were very close to wilting, and a day without water (especially for a hot day) would surely have killed them.

I measured the soil moisture of each pot every two weeks (four blocks on alternate weeks) using a time-domain reflectometer (TDR, Trase System I, 6050X1, Soilmoisture Equipment Corp., Santa Barbara, CA, USA), which measured volumetric water content (waveguide rod length = 12.5 cm). Moisture level for wet pots was 29.84 ± 6.84% (means ± 1 SD), and 2.49 ± 2.15% for dry pots.

The relationship between the absolute amount of water and the TDR measurement is shown in Figure 3.3a. This was done by first drying a pot containing the same growing medium in a drying oven (55 °C) for 3 days, then gradually adding water, mixing well, and taking a measurement using TDR. The relationship between water potential and TDR measurement was also quantified (Figure 3.3b). Sixteen pots with the growing medium were prepared ranging from very dry to near field capacity. The water content was first measured using TDR. Then a sample of the growth medium was taken from the pot
Immediately, and water potential was measured using WP4-T Psychrometer (Decagon Devices, Pullman, WA, USA).

Since the plants were frequently infested by aphids, thrips, and powdery mildew, granular insecticide (Marathon® 1% G, OHP Inc., Mainland, PA, USA) and liquid fungicide (Heritage®, Syngenta Crop Protection, Inc., Greensboro, NC, USA) were applied as needed during the experiment. Daily maximum temperature was 26.8 ± 2.1°C, and minimum temperature was 21.0 ± 1.5°C.

3.2.3 Measurements and calculations

Reproduction

The reproductive behavior of each individual was monitored on a near daily basis. I recorded the number of ripe capitula with matured seeds and collected them for each individual. These data were aggregated weekly to show the pattern of reproduction. Scapes (the supporting structure for one capitulum) were collected frequently during the experiment, and stored in paper bags at room temperature.

Biomass and leaf area

The experiment was stopped on August 29, and the green shade was removed. I measured the height (from soil level to the highest leaf) and diameter of each plant. From August 30 to September 6, leaves of each plant were cut (block by block) and roots were washed. All plant parts, including scapes, leaves, and roots were put into paper bags and dried at 55°C for 7 days before weighing. Total biomass was the sum of these three parts.
plus seed biomass after cleaning. I computed the reproductive biomass as the sum of scape and seed biomass. Investment in each part (leaf, root, reproduction, and seed) was calculated by dividing the biomass of that part by the total biomass. The shoot:root ratio (SRR) was the biomass ratio of leaves and root.

Leaf morphology

On August 6, one typical leaf of each plant was collected, carefully pressed, and scanned (together with a ruler for later calibration) into digital images. I then processed the images using ImageJ software (Rasband 1997-2008) to obtain leaf area. The length and width of each leaf was also measured (see Appendix B for detail procedures and notes). Leaf shape index was computed as the leaf area/bounding rectangle area ratio to describe the indentation degree of the leaves. A leaf is more indented if the value is lower, and vice versa.

Seeds

Collected seeds were stored in a seed storage facility with 5°C constant temperature and 30% RH. From October 5, seeds were cleaned following the procedure described in Appendix A. After cleaning, I measured the weight of 100 seeds and repeated the process for three times for each individual. For those producing less than 300 seeds, seed number was counted and all seeds were weighed together. Then the weight of 100 seeds was calculated. If the seeds exceeded 300, the weight of all seeds was measured, and then the total number of seeds was calculated using the 100-seed weight.
I grouped these measured and calculated variables into four categories (morphology, allocation, reproduction, and biomass) for ease of presentation and interpretation. The morphology category includes size characteristics (i.e. height and diameter), and leaf shape index. Investment in leaf, root, reproduction, and SRR make up the allocation category. These two categories belong to physiological and morphological traits. The reproduction category includes investment in seeds, total seed number, seed biomass, and seed weight. Finally, the biomass category consists of total biomass, leaf, root, and reproduction biomass. These two categories belong to fitness traits. Although seed production and characteristics might be the best measurement of fitness, biomass also contributes to perennial species success, so it was included in the fitness component.

3.2.4 Second run

The second run of the experiment was conducted from January to June, 2008. Since the data of the first run indicated that there were no differences in responses to light condition among the three species, this treatment was eliminated from the second run. A randomized complete block design was used with 8 replicates. Each block consisted of 12 treatments (3 species × 2 water availability × 2 fertility levels). I used the same set of 8 genotypes of each species, but their placement in each block was re-assigned randomly. Procedures and methods (such as potting mix, fertilizer, chemical uses) were the same as the first run.

I started seedlings on January 18, 2008, and transplanted them into pots on February 11 with the assigned amount of fertilizer. The dry treatment began three weeks later
(irrigation withheld). Because natural light intensity was not as high as in the first run, supplemental light was provided, which was programmed to turn on if environmental light intensity was below 200Wm$^{-2}$ between 8:00 and 16:00. Matured seed heads were counted and collected twice a week, and seeds were stored for later cleaning and counting. Plants were measured and harvested between June 2 and June 5. Biomass of all parts (scape, leaf, and root) was weighed on June 11. I did not measure leaf morphology in this run.

Room temperature during the experiment was 27.4 ± 3.0°C (daily maximum, mean ± SD) and 15.5 ± 1.3°C (daily minimum). Daily maximum PPFD was 1106.7 ± 443.9 µmolm$^{-2}$s$^{-1}$. Soil moisture was 38.10 ± 9.19% for the wet treatment, and 3.18 ± 2.87% for the dry treatment.

3.2.5 Statistical Analysis

ANOVA and least-square mean

For the first run, all variables were analyzed using the following linear model:

\[
\text{Variable} = \text{Light}\mid\text{Water}\mid\text{Fertility}\mid\text{Species} + \text{Block(Species)} + \text{Light}\times\text{Block(Species)}
\]

Italicized terms are random effects. The term “Light\mid Water\mid Fertility\mid Species” denotes all simple effects and the interactions (including two-, three-, and four-way interactions) among the terms, and they were considered as fixed effects. Block(Species) specifies the block effect nested in species. Light\times Block(Species) was also included because a split
plot designed was used. These two terms were considered as random effects. Blocks are nested in species because each physical block consisted of individuals of one single genotype of each of the three species. As a result, the “block effect,” which is actually a combination of block effect and genotypic effect, is different for each species. The Block(species) effect assigned separate block effects to each species, and was more appropriate. Models using “Block(species)” usually had smaller residual errors than models using “Block”, and thus resulted in more significant test results for some effects. However, the species effect was usually less significant using “Block(species)” due to the fact that the denominator degree of freedom (which was estimated using Satterthwaite’s method (Littell et al. 2006, pg 114)) for the species effect was much smaller than in models using “Block”.

The light treatment was excluded in the second run, so the following linear model was used:

\[
\text{Variable} = \text{Water}|\text{Fertility}|\text{Species} + \text{Block(}\text{Species}\text{)}. 
\]

Since the invasive status of TOF and TLA is known and that of TKS is unclear, it is more meaningful to identify the differences between TOF and TLA, rather than examining the differences among all three species. The initial analysis showed that many TKS characters were very different from TOF and TLA, so a significant effect in a three-species analysis could be caused by TKS alone, and did not necessarily indicate a difference between TOF and TLA. Therefore, it was more meaningful to conduct two sets of analysis, one excluding TKS, and another including all three species. The first analysis aims to compare invasive TOF with non-invasive TLA. The second one was
conducted to generate least square means for each effect (ANOVA table was also included).

The normality of the residuals was first checked. Data were log- or square-root-transformed if normality assumptions were not met. Proc Mixed in SAS/STAT software (SAS 9.1.3) was used for analysis, and two sets of ANOVA tables were created for the two and three species comparisons. The significance level use in the ANOVA table was 0.05. This level was not adjusted for multiple comparisons for the reasons discussed in (Moran 2003). Furthermore, there was a clear pattern that species, water×species, and water×fertility×species effects were more likely to be found significant (especially in the first run, Table 3.1), so it was unlikely they were significant due to chance only.

Back-transformed estimates from the three-species analysis are presented. Statistical comparisons between estimates were performed on the 3-species analysis results. It was not necessary to present all estimates due to the large number of treatment combinations involved. Plots of means are presented for significant effects that involved species effects (e.g. water×species, or fertility×species), because such effects implied different species responses to the environmental conditions. In addition, estimates of all treatment combinations (four-way interactions) are presented for all variables. Standard errors are not shown in plots for clarity.

The results were somewhat different in the two runs of the experiment. In order to compare their results more closely, mean plots of the experiments were drawn, side by side, to show species responses to the four environments (DL, DH, WL, and WH). For the plots of the first run, only the results from the full light treatment are presented.
because the second run did not include the light treatment. Plots were adjusted to the same scale range to make comparisons easier.

Assessment of phenotypic plasticity

The phenotypic plasticity of each species was quantified by calculating the coefficient of variance (CV), which is the ratio of the standard deviation of a trait’s value across environments divided by the overall mean in those environments. The CV has been used in several studies to assess trait plasticity when there were more than two growing conditions (Schlichting and Levin 1984, 1986, Sultan 2001). However, the CV usually has been calculated on mean values across replicates so that there was only one CV value for each species, which eliminated the possibility of statistical comparisons among species. In this study, the CV was first calculated for each replicate across the eight multi-factor environments for each species. This value was treated as one replicate. As a result, there were eight CV replications for each species in total. These data were then analyzed to test species effects (fixed effect). The model was first tested for heterogeneity of variance among species because for some of the traits, the variances were very different among species. If no heterogeneity was found (the null model likelihood ratio test had $P>0.05$), then variances were pooled. Otherwise, the CV was analyzed using a heterogeneity variance model in which each species was assigned a different variance. Least square means and standard errors were estimated, and the mean differences among species were tested using Tukey’s HSD.
3.3 Results

3.3.1 Overview

Since the main purpose was to evaluate the differences between TOF and TLA, the following statements concerning significant effects refer to the test results of the 2-species ANOVA table (Table 3.1 for the first run, and Table 3.3 for the second run).

Overall, water, fertility, and their interactions explained most of the variance in both runs, as indicated by large F values (Table 3.1 and Table 3.3). In the first run, many variables were significantly affected by the water×species or water×fertility×species interactions, but only a few was affected by light×species or higher interactions. The results of the second run were slightly different. The two-species ANOVA (Table 3.3) showed no significant water×fertility×species effect for any of the traits examined, but the water×species effects were still significant for many variables.

3.3.2 Morphology

Plant morphology (height, diameter, and leaf shape) was significantly affected by environments and species in both runs (Table 3.1 and Table 3.3). In the first run, plants grew higher and with wider diameters under high fertility and wet conditions. Green shade further enhanced this trend (Figure 3.4d and Figure 3.4e). TOF grew 2.3% – 36.2% higher and 0% – 21.0% larger in diameter than TLA across environments (Figure 3.4d and Figure 3.4e), but no species related interaction was found to be significant (Table 3.1). The leaf shape index was higher for TOF (0.21 – 0.26) than TLA (0.21 – 0.24) in most environments (Figure 3.4f), which suggested that TOF leaves were less indented.
than those of TLA. Exposure to full light tended to make the leaves more indented but this pattern was not observed for TLA under wet conditions (Figure 3.4f).

Similar patterns were observed for height and diameter in the second run, with TOF growing 14.2% – 43.7% higher and 16.3 – 27.0% wider than TLA in all environments (Figure 3.8c and Figure 3.8d). No species×environment interactions were found to be significant (Table 3.3). However, plants grew smaller than in the first run, especially under wet conditions (Figure 3.8a and Figure 3.8b vs. Figure 3.8c and Figure 3.8d). For example, TOF and TLA reached 25.3 cm and 24.3 cm in height during the first run in wet/high-fertility (WH) environment, but they only grew to 15.8 cm and 11.0 cm in the same condition during the second run.

Compared to TOF, TKS did not grow as tall (79.9% – 91.7%) or as wide (78.4% – 94.0%), and was more similar in stature to TLA (Figure 3.4d, Figure 3.4e, Figure 3.8c, Figure 3.8d). The size of TKS responded to environmental changes following the same pattern as the other two species.

No differences in CV were statistically significant for morphological traits in either run, except that TLA had a larger CV for height (0.485 ± 0.03) than TKS (0.387 ± 0.03) in the first run (Figure 3.4a – Figure 3.4c, Figure 3.8e, Figure 3.8f).

3.3.3 Allocation

Overall, all three species responded to green shade by increasing investment in leaf and decreasing allocation to roots, which resulted in larger SRR (Figure 3.5e – Figure 3.5g). High fertility caused greater biomass allocation to leaf tissue and less to roots.
Exposure to drought enhanced the investment in roots, and reduced the investment to reproduction (Figure 3.5e – Figure 3.5g, Figure 3.9e – Figure 3.9h).

In the first run, allocation to leaf, root, and reproduction was significantly affected by water×species, suggesting different allocation patterns for TOF and TLA under different water availability (Table 3.1). Allocation to leaf, root, and hence SRR was very similar for TOF and TLA when water supply was sufficient (Figure 3.5i – Figure 3.5k), with 33.0% and 30.6% of biomass to leaf (P = 0.253), 40.4% and 39.3% to root (P = 0.757), and SRR of 0.82 and 0.78 for TOF and TLA (P = 0.634), respectively. But the allocation pattern diverged in the dry environments: TLA had almost no change in leaf investment compared to wet condition (29.8%, P = 0.609), but a much higher allocation to roots (54.0%, P<0.001). TOF, on the other hand, exhibited a significantly higher investment in both leaf (42.9%, P<0.001) and root (47.7%, P<0.001, Figure 3.5i, Figure 3.5j). As a result, SRR for TOF in dry conditions (0.90) was not significantly changed compared to wet condition (P = 0.196), but SRR of TLA (0.54) was significantly decreased (P<0.001, Figure 3.5k). Increased allocation to leaf and root tissue under dry condition was compensated by decreased allocation to reproduction (scape and seed). In wet environments, 26.6% and 30.2% of total biomass went to reproductive structures for TOF and TLA, but in dry environments only 9.4% and 16.2% went to reproduction (both P<0.001 compared to wet).

Allocations to roots and reproduction were significantly affected by water×fertility×species interactions (P = 0.022 and P = 0.003, Table 3.1). TLA invested more in roots (56.5% in DL and 51.4% in DH) and reproduction (16.9% in DL and
15.5% in DH) than did TOF (allocation to roots: 52.0% in DL and 43.4% in DH; allocation to reproduction: 7.8% in DL and 11.1% in DH, Figure 3.5m, Figure 3.5l). Allocation to these parts was similar for the two species in WL, but TLA allocated more to reproduction than TOF (31.8% vs. 25.5%), and less to roots (32.3% vs. 36.5%) under WH conditions (Figure 3.5m, Figure 3.5l).

In the second run, however, water×species interactions were not significant for investment in leaf and SRR (P = 0.638 and P = 0.185), but were significant for investment in root and reproduction (P = 0.037 and P = 0.045, Table 3.3). Different patterns of leaf investment and SRR between TOF and TLA were not detected in the second run (Figure 3.9e, Figure 3.9g). Rather, these two traits were quite similar for the two species (Figure 3.9f, Figure 3.9g). In the first run, TLA had 8.7% – 18.5% higher allocation to roots than TOF in dry conditions (Figure 3.9b), but investment in roots was 7.3% – 11.0% lower in the second run under the same condition (Figure 3.9b vs. Figure 3.9f).

Allocation patterns of TKS were quite different from those of TOF and TLA in that for both first and second run, TKS exhibited the highest investment in root (43.2% – 74.1% in the first run, and 54.2% – 72.0% in the second run, Figure 3.5f, Figure 3.9f) and the lowest investment in reproductive structures (1.9% – 12.5% in the first run, and 13.3% – 25.8% in the second run) among the three species (Figure 3.5h, Figure 3.9h). Investment in leaf and SRR were lower than the other two species during the second run (Figure 3.9e, Figure 3.9g).
There were no significant differences for CVs except for investment in reproduction in the first run (Figure 3.5d). TOF was more plastic than TLA (0.66 vs. 0.38), which was largely due to its smaller value in dry conditions (Figure 3.5h).

3.3.4 Reproduction

In the first run, TLA produced 66.1% to 4.8 times more seeds than TOF across environments (Figure 3.6f). The same was true for investment in seeds and seed biomass (Figure 3.6e, Figure 3.6g). Plants produced most seeds in the WHF environment, where TLA set 6980 seeds and weighed 2.86g in total. TOF set 3050 seeds weighing 1.51g in the same environment. The seeds of TLA, however, were 0.5% – 17.2% lighter than those of TOF across environments (Figure 3.6h). Seeds tended to be heavier when resources were more available. The 100-seed weight of TOF was between 33 mg and 50 mg, which was within the reported range from 0.33 mg and 0.68 mg (Collins 2000). Most reproduction variables were significantly affected by water×fertility×species interactions (P= 0.040 – 0.045) except seed weight, which was significantly influenced by fertility×species (P = 0.012, Table 3.1). TLA had higher seed biomass than TOF in DL, DH, and WL (0.374 g – 0.945 g vs. 0.092 g – 0.541g), but the difference was largest in WH (2.12 g vs. 1.08 g, Figure 3.6k). The same pattern was observed in total seed (Figure 3.6j). Seed weight was not significantly different in low fertility environments for TOF and TLA (P=0.1786), but the difference was significant under high fertility (P=0.0009).

There were no significant differences between CVs for seed biomass and seed number of TOF and TLA, but TOF exhibited significantly larger CVs for investment in
seed (0.723 ± 0.08 vs. 0.386 ± 0.02) and seed weight (0.173 ± 0.01 vs. 0.110 ± 0.01) than did TLA (Figure 3.6a –Figure 3.6d). Larger CV for seed weight was a result of a wider seed weight range of TOF (0.33 mg – 0.50 mg) than TLA (0.33 mg – 0.42 mg, Figure 3.6h). The range of values for investment in seeds, however, was similar for the two species (TOF: 0.004 – 0.029, TLA: 0.028 – 0.056), and the larger CV for TOF was mainly due to its smaller mean (Figure 3.6e).

Similar to the first run, TLA exhibited 7.6% – 75.7% higher investment in seed and TOF produced 1.5% – 18.1% heavier seeds across environments in the second run (Table 3.3, Figure 3.10e, Figure 3.10h). However, no significant differences were found in total seed and seed biomass for any effects (Table 3.3), which suggests that TOF and TLA produced similar amount of seeds (TOF: 1890 – 5560, TLA: 2210 – 5300) and seed biomass (TOF: 0.79 g – 3.04 g, TLA: 0.87 g – 2.44 g) across environments (Figure 3.10f, Figure 3.10g). This result disagreed with that of the first run, in which TLF produced significantly more seeds and had higher seed biomass than TOF especially in high resource environments. A possible explanation is that the peak of TLA reproduction was not reached when the experiment was terminated earlier during the second run. The seed head count for the first run indicates that during the first two months of experiment, reproduction was similar for both species (Figure 3.12a). When the reproduction peak began in mid-June, however, TLA produced many more seed heads than TOF. During the second run, seed heads matured about the same time (mid-April, Figure 3.12b) even though plants were started a month earlier. The experiment was stopped in early June,
just before the reproduction peak began (Figure 3.12b). This probably explains why the reproduction advantage of TLA was not detected during the second run.

TKS had relatively low seed production except in WHG (1990 per plant) and WHF (3910 per plant) in the first run (Figure 3.6f), and except in WH (4910 per plant) during the second run (Figure 3.10f). In WHG and WHF during the first run, TKS investment in seed, total seed, and seed biomass, were similar to those of TOF, but were 35.9% – 46.6% lower than TLA (Figure 3.6e – Figure 3.6g). TKS, however, produced much fewer scapes with many more seeds on each scape than did the other species (data not shown), which resulted in less scape biomass allocation, and thus a low investment in reproductive structures in WH. The 100-seed weight of TKS (36 mg – 47 mg) was similar to TOF (33 mg – 50 mg), and larger than TLA (33 mg – 42 mg), expect for WLF (33 mg) and WHG (39 mg) in first run (Figure 3.6h), during which very light seeds were produced. No reasonable explanation was found for this result. In the second run, TKS seed weight (44 mg – 54 mg) was similar and sometimes larger than TOF (40 mg – 55 mg, Figure 3.10h).

### 3.3.5 Biomass

TOF accumulated more biomass (total, leaf, and root) across all treatments than did TLA in both runs (Figure 3.7e –Figure 3.7g, Figure 3.11e –Figure 3.11g). In the first run, maximum total biomass was achieved in the WHF environment for TOF (72.0 g), but in the WHG environment for TLA (52.6 g). Maximum leaf biomass was achieved in the
WHG environment (Figure 3.7f) for both species (26.4 g and 20.6 g) due to high allocation to leaf when shaded.

There were significant differences between TOF and TLA for biomass accumulation under different growing conditions. Total and leaf biomass were significantly affected by the fertility×species interaction (P<0.001 and P = 0.005), and root biomass was affected by the water×species interaction (P = 0.01, Table 3.1). The water×fertility×species effect was only marginally significant (P=0.0495). For total biomass, there was no significant difference between TOF and TLA under low fertility conditions (P=0.067), but total biomass of TOF was 25.4% higher than TLA in high fertility (45.6 g vs. 35.4 g, P<0.001, Figure 3.7i). TOF accumulated 48.8% and 49.5% more leaf biomass in low and high fertility conditions (P=0.0037, and P<0.001, respectively) than did TLA, and the difference was larger in the high fertility treatment (15.4 g vs. 10.3 g, Figure 3.7j). For root biomass, there was no significant difference between TOF and TLA under DL, DH, and WL conditions (P=0.589, 0.939, and 0.289), but TOF produced 39.5% heavier root than TLA in WH conditions (P=0.0002, Figure 3.7k). Accumulation of biomass in reproduction structures (including scapes and seeds) reached maximum in WHF for TOF (18.7 g) and TLA (17.8 g), and their overall trends in all environments were similar (Figure 3.7h). Reproduction biomass was significantly affected by the water×species effect (P = 0.004, Table 3.1). TLA accumulated slightly more reproduction biomass (1.9 g) in dry environments than TOF (1.2 g) and slightly less in wet environments (10.8 g vs. 11.4 g, Figure 3.7l), but both differences were insignificant (P=0.1632 and P=0.6786 respectively).
In the second run, no significant environment×species interactions were found for the four biomass components (total, leaf, root, and reproduction, Table 3.3), but the species effect was significant, except for the reproduction biomass (P = 0.079). Although they can not be analyzed statistically, comparison with the first run revealed that biomass accumulations (total, leaf, and root) were similar in the two runs for plants in dry conditions, but plants growth was much smaller under wet conditions in the second run (Figure 3.11a – Figure 3.11d vs. Figure 3.11e – Figure 3.11h). For example, total biomass in WHF in the first run was 72.0 g, 50.9 g, and 65.2 g for TOF, TLA, and TKS, respectively, but was only 38.5 g, 28.5 g, and 41.0 g in WH during the second run. This is mainly because the duration of second run was 3 months rather than 5 months for the first run. Plants in the second run simply did not have time to accumulate equivalent amounts of biomass. The comparison also revealed that biomass differences between TOF and TLA were much larger in the second run, especially for the root biomass in dry conditions (Figure 3.11g). For example, roots in the first run weighed 7.5 g for TOF and 6.6 g for TLA (DLF), and weighed 9.5 g for TOF and 5.4 g for TLA in the same condition (DL) in the second run. This result suggests that the initial root growth of TLA was slower than that of TOF. No significant differences were found among CVs across environments.

Total biomass accumulation of TKS was similar to that of TOF in both runs (Figure 3.7e, Figure 3.11e), but TKS was distinguished from TOF by 7.0% – 53.1% larger root biomass and 14.2% – 90.5% smaller reproduction biomass, especially in favorable environments (Figure 3.7g, Figure 3.7h, Figure 3.11g, and Figure 3.11h).
3.4 Discussion

Since the normal seasonal growing duration in field was better represented by the first run (March ~ September) of the greenhouse experiment, discussion will be mainly focused on the results from the first run, without ignoring the inconsistencies between the results of the first and second run of the experiment. Possible explanations will be provided for the discrepancy between the two runs when possible,

3.4.1 Allocation in different water availability

It is a common response for plants to allocate more resources to root tissue and less to above ground parts when facing drought (Lambers et al. 1998), as a result of reduced leaf growth and an effort to explore more available water under such a stressful condition. This response was usually reflected by a decreased shoot:root ratio. TLA seemed to follow this general rule but TOF did not. This difference in allocation pattern between the two species was unexpected. It is possible that the root system of TOF is more efficient in water acquisition, especially during drought. Thus even though less biomass was allocated to root, TOF plants were still able to support growth. However, total biomass in dry condition was not significantly different between TOF and TLA (Figure 3.7e), which suggested that TOF gained little benefit from a different allocation pattern under dry conditions. On the contrary, less investment in root for perennials like dandelions could be risky because the root system serves as the storage organ during winter.
The discrepancy in allocation pattern between the two runs might suggest that growth was different for TOF and TLA in early life stages, especially under dry conditions. In the second run when plants grew for a shorter time, TOF invested more in root than TLA in dry treatments, but the relationship was reversed in the first run (Figure 3.9b vs. Figure 3.9f), which lasted for a longer time. This might indicate that when facing drought, TOF allocates more resources in root growth during early life stages, which is presumably a better strategy because a larger root system can improve survivorship when water supply is insufficient. Later, when establishment was successful, more energy was allocated to photosynthetic tissue above ground.

3.4.2 Fitness: biomass and reproduction

Two hypotheses were proposed regarding the successful invasion of TOF over TLA: 1) TOF is able to maintain higher, stable fitness than TLA in both stressful and favorable conditions, and 2) such a stable fitness is achieved by more plastic morphology and allocation under stressful conditions. Results of this experiment suggest that TOF grows bigger (taller, wider in diameter) and accumulates more biomass than TLA in most environments, but the difference is largest under good rather than poor growing conditions. The pattern of biomass accumulation failed to support the first hypothesis. The second hypothesis, which was based on the validation of the first one, was not valid by default. Furthermore, differences in biomass accumulation under favorable conditions were not achieved by greater plasticity in morphology or allocation. Morphological (height, diameter, and leaf shape) responses to environmental changes were quite similar.
between the two species. Patterns of allocation to leaf and root tissues were different between TOF and TLA, but mainly under low resource (dry) conditions.

On the other hand, TLA produced more seeds and therefore accumulated greater total seed biomass than TOF in most environments. This result was unexpected because prolific seed production has often been cited as a trait that contributes to the success of a weed (Baker 1974, Francis and Warwick 2007). The results of this study suggest that not only did the successful weed, TOF, produce fewer seeds than TLA, the difference was also largest under high resource growing conditions.

Richards et al. (2006) suggested that other than the generalist strategy (“Jack-of-all-trades,” Figure 1.2a), invasive species can also be “master-of-some” (Figure 1.2b), which was also called an opportunist strategy (Sultan 2001). In this case, an invasive species exhibits similar fitness to a non-invasive species in stressful environments, but achieves a much higher fitness under favorable conditions. There is also a third strategy, designated “Jack-and-master” (Figure 1.2c), in which fitness of an invasive species is universally high in all environments, but the differences are largest under favorable conditions. Biomass production of TOF clearly falls into the Master-of-some or Jack-and-Master category, but seed production failed to fit any proposed pattern.

The reversed relationship of TOF and TLA in biomass and reproduction, two typical fitness measurements, raises the question of a possible mechanism behind the overwhelming success of TOF over TLA in nature. Vavrek et al. (1997) demonstrated that for TOF grown in the field, survival and second-season fertility were positively
correlated with individual plant size. This implies that biomass accumulation is probably more important than seed production for perennial species like dandelions. In addition, life history traits at other life stages, such as seed dispersal and seedling establishment, could also play important roles. Individual seed weights of TOF are heavier than those of TLA in all environments, and the differences were highest under favorable conditions. Higher nutrient storage in each individual seed might promote greater establishment success of TOF offspring, which could compensate, or even override, the factor of less seed production. For example, in a study of *Cytisus scoparius*, an invasive species whose population grew more rapidly in prairie than in urban settings, Parker (2000) demonstrated that seedling establishment made the largest contribution to the difference in growth rate between the two habitats. If this holds true in *Taraxacum*, it suggests that TOF and TLA rely on different life history strategies for population growth, and TOF’s strategy is better adapted to high resource habitats.

Many plants can be characterized as one of the two life history strategies. The first is characterized by a short life span (annual or biennial), small size, rapid growth, massive seed production with small seeds, and good dispersal ability. These species are sometimes referred as r-selected species (Pianka 1970) that occur during early succession and are well-adapted to high-disturbance habitats. They take advantage of temporarily available resources, complete their life cycle in a short time, and produce abundant seeds to seek new, suitable habitats. Another type of species is characterized by higher competitive ability, long life expectancy, large body size, and fewer but larger offspring.
Sometimes called K-selected species, they often become dominant in later succession and are adapted to more stable environments (Pianka 1970).

TOF has generally been considered an r-strategist (Gadgil and Solbrig 1972), based on its colonizing ability and massive seed production. However, the comparison with TLA suggests that TOF is closer to a K-selected species whereas TLA is closer to r-selected species. TOF is typically found in lawns and reduced-tillage crop fields where soil disturbance is relatively infrequent. As a perennial species growing in such habitats, the “K” strategy is probably more successful than the “r” strategy. In addition, Grime et al (1986) suggested that perennials of relatively stable habitats often respond to stress by deferring reproduction, a mechanism to protect the parent plant, whereas ephemeral plants of temporary habitats tend to sustain reproduction when facing stress. Both TOF and TLA decreased their investment in reproduction in stressful environments (Figure 3.5h), but the decrease was less for TLA than for TOF. This suggests that TOF is more conservative in reproduction, so that adult survivor rate can be maintained. In other words, the TOF strategy of high competitive ability, and high adult and offspring survivor rate, is more adapted to these relatively stable habitats than is the TLA strategy.

TOF accumulated more biomass but produced fewer seeds than TLA in high-resource environments, which make it difficult to determine whether or not TOF exhibits higher overall fitness than TLA in such conditions. Although previous studies on phenotypic plasticity and biological invasion have focused on fitness components such as fecundity, seed characteristics, dispersal ability, and germination (Sultan 2001, Brock et al. 2005, Mihulka et al. 2006), population growth rate, which reflects the ability of a
species to survive, persist, reproduce, and recruit, might be a better measurement (Parker 2000). Therefore, future research should focus on population level studies, and measurements on population growth rate.

3.4.3 Invasiveness traits of TKS

One objective of this study was to evaluate the potential invasiveness of TKS, a potential crop for latex production in US (van Beillen and Poirier 2007, Chanon et al. 2008). The results showed that TKS accumulated similar levels of biomass as TOF, and seed production was also similar under optimum conditions. In another words, fitness responses of TKS resemble those of the weedy TOF more than the non-weedy congener TLA. One distinguishing characteristic of TKS, however, was its high investment in roots and large root biomass in all environments. This feature is why this species was been studied as crop from which latex in root tissue is obtained (van Beillen and Poirier 2007). For perennial species, the root system is especially important as it serves as an energy storage organ during winter. Roots also play a major role for dandelions in the re-growth of above-ground tissues when they die back or have been removed. The superior ability to regenerate from roots is a major reason that TOF is so difficult to eliminate (Mann and Cavers 1979, Stewart-Wade et al. 2002). It is likely that TKS, with an even larger root system, might be equally, if not more, difficult to remove completely if it escapes from cultivation. Based on these results, I expect that the overall performance of TKS will be similar to that of TOF, and it has the potential to become invasive if widely cultivated.
3.4.4 Plasticity and plasticity index

In this study, phenotypic plasticity alone was inadequate to explain, let alone predict, the invasiveness of a certain species. The results did not indicate whether a high or low degree of plasticity is associated with invasiveness. High levels of plasticity could be the result of an opportunist strategy (Master-of-some, or Jack-and-Master), and low plasticity could indicate a generalist strategy (Jack-of-all-trades), both of which might favor invasion success. Sultan (2001) also found that neither plasticity nor constancy per se were necessarily associated with ecological breadth. A detailed analysis of species traits in each environment can often provide more information.

This study also suggests that the CV is not a useful index to evaluate plasticity, mostly because the differences in plasticity among these species were not large enough to be statistically significant, even though significant differences were detected in species-by-environment interactions. For example, total biomass was significantly affected by the fertility×species interaction (Table 3.1) and TOF appeared to be more plastic than TLA (Figure 3.7i). The CV value of TOF was slightly higher than that of TLA but the difference was not significant. The same was true for seed number and seed biomass where TLA was more plastic but the CV failed to capture this trend Figure 3.6b, Figure 3.6c, Figure 3.6j, and Figure 3.6k). Although it is possible to find a more effective index to assess plasticity, it is probably not necessary to do so because the magnitude of plasticity alone is not a good indicator of invasiveness. It is unlikely that a single index can be used to describe the complex responses of a species under various environments,
and one will certainly lose much valuable information by reporting an index that is
difficult to relate directly to invasiveness.

3.4.5 Suggestions for future study

The results of this study suggested that TOF might rely on higher survival and
seedling establishment rates to be successful, and its advantage should become more
evident over longer time periods. Future studies should be focused on the demographic
aspect of these two species in multi-year experiments in field, and population growth rate
should be used as a fitness measurement. No evidence was found that different responses
of TOF and TLA in biomass and seed production were caused by the morphological or
physiological traits examined. Other characteristics, such as water use efficiency and
relative growth rate might contribute to these differences and can be examined in future
studies.

This study also demonstrated the importance of comparative experiments of closely
related species under a range of environments. It is difficult to identify traits that
contribute to invasiveness without a comparison of invasive and non-invasive species.
Similarly, without comparison in multiple environments, variation of the traits can not be
fully revealed. But it is probably not wise to focus only on phenotypic plasticity in the
future. There have been arguments against the use of phenotypic plasticity to evaluate
plant invasion (Hulme 2008). A detailed analysis of species responses along
environmental gradients would likely be more valuable.
3.5 Conclusion

This study showed that the invasive TOF accumulated more biomass, but produced fewer seeds than its non-invasive congener in both stressful and favorable conditions. The greatest responses occurred under favorable (i.e. high resource) environments. Plasticity in these two fitness components cannot be explained by plasticity of the morphological and physiological traits examined. Based on these results, I am unable to determine whether TOF is more of a generalist or opportunist than is the non-weedy TLA. Further studies at population level are needed to answer this question. The possible future agronomic crop species TKS was more similar to TOF than to TLA in fitness responses across environments, and will probably benefit from its unique, huge root system. In this respect, this species appears to have potential to become a weed if it is widely grown and escapes from cultivation.
Table 3.1 ANOVA of 2-species (TOF and TLA) analysis for the first run. Bold *P* values are significant at 0.05 level.
Table 3.1 continued

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<td>14.33 &lt;0.001</td>
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<td>542.08 &lt;0.001</td>
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Reproduction Biomass

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<th>Seed weight</th>
<th>Total biomass</th>
<th>Leaf biomass</th>
<th>Root biomass</th>
<th>Reproduction biomass</th>
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<td>P</td>
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Table 3.2 ANOVA of 3-species (TOF, TLA, and TKS) analysis for the first run. Bold $P$ values are significant at 0.05 level.
Table 3.2 continued

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<th>Effect</th>
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<th>Investment in seed</th>
<th>Reproduction</th>
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<th>Reproduction biomass</th>
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<td>Height</td>
<td>Diameter</td>
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<td>Investment in root</td>
<td>Shoot:root ratio (SRR)</td>
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Table 3.3 ANOVA of 2-species (TOF and TLA) analysis for the second run. Bold P values are significant at 0.05 level.
### Table 3.3 continued

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<th>Seed weight</th>
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<td>P</td>
<td>F</td>
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<td>11.33</td>
<td><strong>0.001</strong></td>
<td>19.33</td>
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<td>0.16</td>
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<td></td>
<td>26.48</td>
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<td></td>
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<td></td>
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<td>77.39</td>
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<tr>
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<td>8.40</td>
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<td>0.93</td>
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<tr>
<td>Fert*Sp</td>
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<td>0.34</td>
<td>0.714</td>
<td>2.54</td>
<td>0.087</td>
<td>0.56</td>
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<td>6.64</td>
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<td>0.628</td>
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Table 3.4 ANOVA of 3-species (TOF, TLA, and TKS) analysis for the second run. Bold $P$ values are significant at 0.05 level.
<table>
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<th>Effect</th>
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<th>Biomass</th>
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<td>Seed biomass</td>
<td>Seed weight</td>
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<td>F</td>
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<tr>
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<td>0.16</td>
<td>0.848</td>
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</tbody>
</table>
Figure 3.1 Hypothetical phenotypic responses of an invasive species (solid line) and a non-invasive (dashed line) species in a) fitness component, and b) morphological or physiological component. A successful invasive species would be expected to maintain higher and more stable fitness over stressful to favorable environments, and this would likely be achieved by more plastic morphological or physiological changes.
Figure 3.2 Photon spectral irradiance in full light (solid line) and green shade (dashed line). R:FR ratio (655-665/725-735nm) is 1.170 in full light and 0.556 in green shade.

Figure 3.3 Relationship between: a) measurement of TDR (%) and absolute amount of water (ml) added in a standard pot filled with completely dry grow mix, and b) water potential (MPa) and TDR measurement. See text for details.
Figure 3.4 Coefficient of variation (CV) and least square mean of morphological traits of the three species in the first run. TOF: *Taraxacum officinale*; TLA: *T. laevigatum*; TKS: *T. kok-saghyz*. a – c: CV for height, diameter, and leaf shape index. Error bar shows 1 standard error. Different letters on the bars indicates means are different at 0.05 significant level as indicated by Tuckey’s HSD test. No letters were added if no significant differences were found among the three species. d – f: Means across all treatment combinations (dry (D) vs. wet (W) soil, low (L) vs. high (H) fertility, and green shade (G) vs. full light (F)) for height, diameter, and leaf shape index for TOF (solid line and filled circle), TLA (dotted line and open triangle), and TKS (dashed line and filled square).
Figure 3.5 Coefficient of variation (CV) and least square mean of allocation traits of the three species in the first run. TOF: *Taraxacum officinale*; TLA: *T. laevigatum*; TKS: *T. kok-saghyz*. a – d: CV for investment in leaf, investment in root, shoot : root ratio (SRR), and investment in reproduction. Error bar shows 1 standard error. Different letters on the bars indicates means are different at 0.05 significant level as indicated by Tuckey’s HSD test. No letters were added if no significant differences were found among the three species. e – h: means across all treatment combinations (dry (D) vs. wet (W) soil, low (L) vs. high (H) fertility, and green shade (G) vs. full light (F)) for investment in leaf, investment in root, SRR, and investment in reproduction for TOF (solid line and filled circle), TLA (dotted line and open triangle), and TKS (dashed line and filled square). i – k: species means in dry and wet soil for investment in leaf, investment in root, and SRR. l, m: species means in DL, DH, WL, and WH for investment in reproduction and investment in root.
Figure 3.5
Figure 3.6 Coefficient of variation (CV) and least square mean of reproduction traits of the three species in the first run. TOF: *Taraxacum officinale*; TLA: *T. laevigatum*; TKS: *T. kok-saghyz*. a – d: CV for investment in seed, total seed, seed biomass, and seed weight. Error bar shows 1 standard error. Different letters on the bars indicates means are different at 0.05 significant level as indicated by Tuckey’s HSD test. No letters were added if no significant differences were found among the three species. e – h: means across all treatment combinations (dry (D) vs. wet (W) soil, low (L) vs. high (H) fertility, and green shade (G) vs. full light (F)) for investment in seed, total seed, seed biomass, and seed weight for TOF (solid line and filled circle), TLA (dotted line and open triangle), and TKS (dashed line and filled square). i – k: species means in DL, DH, WL, and WH investment in seed, total seed, and seed biomass. l: species means in low and high fertility for seed weight. m: species mean in LG, LF, HG, and HF for investment in seed.
Figure 3.6
Figure 3.7 Coefficient of variation (CV) and least square mean of biomass of the three species in the first run. TOF: *Taraxacum officinale*; TLA: *T. laevigatum*; TKS: *T. kok-saghyz*. a – d: CV for investment in total biomass, leaf biomass, root biomass, and reproduction biomass. Error bar shows 1 standard error. Different letters on the bars indicates means are different at 0.05 significant level as indicated by Tuckey’s HSD method. No letters were added if no significant differences were found among the three species. e – h: means across all treatment combinations (dry (D) vs. wet (W) soil, low (L) vs. high (H) fertility, and green shade (G) vs. full light (F)) for total biomass, leaf biomass, root biomass, and reproduction biomass for TOF (solid line and filled circle), TLA (dotted line and open triangle), and TKS (dashed line and filled square). i, j: species means in low and high fertility for total biomass and leaf biomass. k, l: species mean in dry and wet soil for root biomass and reproduction biomass. n: species mean in DL, DH, WL, and WH for root biomass.
Figure 3.7
Figure 3.8 Least square means and coefficient of variation (CV) of morphology traits of the three species in first run (a, b), and second run (c – f). TOF: *Taraxacum officinale* (solid line and filled circle); TLA: *T. laevigatum* (dotted line and open triangle); TKS: *T. kok-saghyz* (dashed line and filled square). Environment: dry (D) vs. wet (W) soil, low (L) vs. high (H) fertility. a, b: species means of first run (full light only) in DL, DH, WL, and WH for height and diameter. c, d: species means of second run in DL, DH, WL, and WH for height and diameter. e, f: CV of second run for height and diameter. Error bar shows 1 standard error. No significant differences were found among the three species.
Figure 3.9 Least square means and coefficient of variation (CV) of allocation traits of the three species in first run (a – d), and second run (e – n). TOF: *Taraxacum officinale* (solid line and filled circle); TLA: *T. laevigatum* (dotted line and open triangle); TKS: *T. kok-saghyz* (dashed line and filled square). Environment: dry (D) vs. wet (W) soil, low (L) vs. high (H) fertility. a – d: species means of first run (full light only) in DL, DH, WL, and WH for investment in leaf, investment in root, SRR, and investment in reproduction. e – h: species means of second run in DL, DH, WL, and WH for investment in leaf, investment in root, SRR, and investment in reproduction. i – l: CV of second run for investment in leaf, investment in root, SRR, and investment in reproduction. Error bar shows 1 standard error. No significant differences were found among the three species. m, n: species means of second run for investment in root and investment in reproduction in dry and wet soil environments.
Figure 3.9
Figure 3.10 Least square means and coefficient of variation (CV) of reproduction traits of the three species in first run (a – d), and second run (e – p). TOF: *Taraxacum officinale* (solid line and filled circle); TLA: *T. laevigatum* (dotted line and open triangle); TKS: *T. kok-saghyz* (dashed line and filled square). Environment: dry (D) vs. wet (W) soil, low (L) vs. high (H) fertility. a – d: species means of first run (full light only) in DL, DH, WL, and WH for investment in seed, total seed, seed biomass, and seed weight. e – h: species means of second run in DL, DH, WL, and WH for investment in seed, total seed, seed biomass, and seed weight. i – l: CV of second run for investment in seed, total seed, seed biomass, and seed weight. Error bar shows 1 standard error. No significant differences were found among the three species. m: species means of second run for investment in seed in low and high fertility environments. p, n, o: species means of second run for investment in seed, seed biomass, and seed weight in dry and wet soil environments.
Figure 3.10
Figure 3.11 Least square means and coefficient of variation (CV) of biomass traits of the three species in first run (a – d), and second run (e – l). TOF: *Taraxacum officinale* (solid line and filled circle); TLA: *T. laevigatum* (dotted line and open triangle); TKS: *T. kok-saghyz* (dashed line and filled square). Environment: dry (D) vs. wet (W) soil, low (L) vs. high (H) fertility. a – d: species means of first run (full light only) in DL, DH, WL, and WH for total biomass, leaf biomass, root biomass, and reproduction biomass. e – h: species means of second run in DL, DH, WL, and WH for total biomass, leaf biomass, root biomass, and reproduction biomass. i – l: CV of second run for total biomass, leaf biomass, root biomass, and reproduction biomass. Error bar shows 1 standard error. No significant differences were found among the three species.
Figure 3.12 Matured seed head count of the three dandelion species in the first run (a), and second run. TOF: *Taraxacum officinale* (solid line and filled circle); TLA: *T. laevigatum* (dotted line and open triangle); TKS: *T. kok-saghyz* (dashed line and filled square). Data were summed for each week and averaged across all treatments from the first collection date. Error bars represent 1 standard error.
4.1 Introduction

Phenotypic plasticity is thought to facilitate invasiveness, either by maintaining fitness over a wide breadth of environmental conditions or by achieving very high fitness in highly favorable environments (Baker and G.L. Stebbins 1965, Richards et al. 2006). Most previous work has focused on species responses to various abiotic environments (such as water, nutrients, and light) in greenhouse or well-controlled field settings (Sultan 2001, Gonzalez and Gianoli 2004, Brock et al. 2005, Leishman and Thomson 2005, Muth and Pigliucci 2007). Few studies, however, have explicitly investigated the role of phenotypic plasticity on invasiveness across different field habitats (but see Thébaud et al. 1996, Lambrinos 2002, Gerlach and Rice 2003, Leger et al. 2007, Leicht-Young et al. 2007). Field habitats are characterized not only by different abiotic conditions, but also by other organisms that are constantly interacting with the invasive species. These co-occurring species include, but not limited to, soil microbes, mycorrhiza, pollinators, competitors, and herbivores. Some of these interacting organisms have effects on invasion processes (Callaway and Aschehoug 2000, Lambrinos 2002, Callaway et al.)
2004). Although one can argue that biotic factors ultimately influence the performance of a plant through abiotic means (for example, competition from a neighbor depletes light, water, or nutrient supply to the target plants; soil microbe suppress plant growth through certain chemicals), it is very difficult, if not impossible, to simulate these effects by environmental manipulations.

Among these biotic factors, competition with other plant species is of special interest. Invasive plants rarely grow alone without surrounding vegetation. Even for those aggressive species that form monocultures, there is a phase when they compete with other species before replacing them. Furthermore, competition with neighbors can interact with abiotic factors, and determine the distribution of an invading species. A plant species might end up growing in a sub-optimal abiotic environment because competition in more favorable sites is too intensive.

The ability to maintain fitness in both stressful and favorable environments is a generalist or Jack-of-all-trades strategy (Richards et al. 2006). Alternatively, a species can exhibit unremarkable growth in stressful environments but achieve especially high fitness under favorable conditions, which has been called a Master-of-some (Richards et al. 2006) or opportunist strategy (Sultan 2001). This strategy insures survival and spread under stressful conditions, and allows maximum reproductive output when growing conditions are favorable. Richards et al. (2006) proposed a third strategy, called Jack-and-master, in which fitness is universally high in all environments, but the differences are largest under favorable conditions.
I propose that phenotypic plasticity is not only displayed as a set of responses to different abiotic environmental factors, but also as a set of responses to a range of field habitats, which involve different biotic as well as abiotic components. The ecological significance of phenotypic plasticity in biological invasion lies in the argument that invasive species exhibit wider ecological niche breadth due to their plasticity (Sultan 2001, Hulme 2008). In another words, this plasticity allows them to grow in a wide range of environments (or thrive in optimum ones) and thereby establish, survive, and spread in habitats in which they did not evolve. Here I report on an effort to test this hypothesis in field situations.

This study uses a model system of three closely related species in the genus of *Taraxacum* (Asteraceae). One of the species (*T. officinale*, or TOF) is known as a notorious non-native weed throughout North America. Another species, *T. laevigatum* (TLA), is a closely related but relatively rare non-invasive alien. The third species, *T. kok-saghyz* (TKS), has been introduced to North America as a latex producing species, and its invasive status is unknown (van Beillen and Poirier 2007). Therefore, a secondary rationale for this study was to evaluate the invasive potential of *T. kok-saghyz*, by comparing its phenotypic plasticity with that of the closely related invasive and non-invasive species.

I grew the three dandelion species in a factorial set of field environments and documented their performance. Specifically, these habitats were a frequently mowed lawn, un-mowed grass, and bare ground (no grass), in a factorial combination with high and low fertility levels. Lawn is a typical place where TOF is found. Bare ground with no
other vegetation is unusual, but this one served as a no-competition control and was expected to be the optimum habitat. None of the species are commonly found among dense and tall vegetation, so it was expected to be a stressful environment. The fertility factor was included to determine if there were interactions between abiotic and biotic factors. The experiment was designed to follow the performance of these species over more than one growing season in order to provide information on plastic responses over a relatively long time.

The specific objectives of this study were 1) to determine if the invasive TOF, and non-invasive TLA maintain fitness over a range of environments (Jack-of-all-trades), or thrive only in optimum environments (Master-of-some); and 2) to evaluate the invasive potential of TKS based on its comparative performance with TOF and TLA in these environments.

4.2 Materials and methods

4.2.1 Study system

A detailed review of the three dandelions species was provided in Section 1.6. The collection of each species was described in Section 2.2. This study included 12 replicates. Each replicate was assigned with one genotype of each species. Since there were only 9 genotypes for each species, 3 randomly selected genotypes were repeated twice.
4.2.2 Experimental design

The experiment was conducted at the OSU Turfgrass Research Center (40°1'N, 83°3'W). The study area was dominated by tall fescue (*Festuca arundinacea*), and was previously maintained by frequent mowing during the growing season. Plots were moderately infested with *Taraxacum officinale*, *Plantago major*, *Trifolium repens*, *Digitaria sanguinalis*, and *Cyperus esculentus*. Before the experiment began in mid April of 2006, I treated the field with a single application of Trimec® 992 (PBI/Gordon Corporation, Kansas City, MO, USA) to control broadleaf weeds.

There were 18 treatments in this study: 3 *Taraxacum* species × 2 fertility levels × 3 grass conditions. I used a split-plot design with six environmental factors as main plots, and individuals of the three species grown in these plots as sub-plot factors (Figure 4.1). The study was designed to continue for three years. At the end of each year, I planned to harvest and measure the growth of a third of the plants so that their long term performance could be studied. For this reason, each plot accommodated 3 individuals of each species (i.e. 9 plants) for three harvest seasons (Figure 4.1). Main plots were squares measuring 1.5 m wide. The 9 plants were planted in three rows spacing 0.5 m between individuals. The distance between two plots was 1 m, as was the distance between blocks (Figure 4.1). A total of 648 plants were transplanted and monitored in this study (9 plants × 6 plots × 12 replicates).

On March 22, 2006, seeds were sown in 9×18-cell flats filled with a commercial growing mix (Sureclone 360, Michigan Grower Products, Inc. Galesburg, MI, USA). Seedlings were maintained in the greenhouse, and supplied with fertilizer solution...
(20-10-20, 50 ppm) once a week. Two weeks before transplanting, flats were moved outdoors to a sheltered site for acclimation. In order to improve transplanting survival, I spot-sprayed glyphosate on May 13th in field plots where seedlings were to be transplanted. On May 22, dandelion seedlings with soil plugs were transplanted in the assigned locations. Each seedling received ~350 ml of water immediately after transplanting.

Grass

Three grass treatments were applied: no grass, grass, and tall grass. For the no grass treatment, the assigned plots were sprayed with glyphosate on April 28, 2006. All vegetation died within two weeks, which created a bare ground habitat after the residual shoots decomposed. After dandelion seedlings were transplanted, the plots were maintained with a combination of hand weeding and spot-applications of glyphosate (with dandelion plants covered). Short grass plots were maintained by mowing with a rotary mower at 10 cm every two weeks during the growing season (April – November). The tall grass plots were mowed in the same manner during 2006 to allow the dandelion plants to become established. Beginning in 2007, grasses in the tall grass plots were allowed to grow freely during the growing season and reached about 1 m in height during the summer.
Fertility

Two fertility levels were applied, and are designated high and low. Low fertility plots were not fertilized. The high fertility plots were sprayed four times a year (in April, May, June, and September) with granular fertilizer designed for turf grass (Lesco® Professional Turf Fertilizer, 21-4-11, Lesco Inc, Cleveland, OH, USA) at the rate of 1 lb nitrogen/1000ft². This application schedule was similar to that used by the Turfgrass Research Center maintenance group. No fertilizer was applied in any plot during 2006, and high fertility treatment did not begin until 2007.

4.2.3 Maintenance and measurement

A high percentage of seedlings (especially TLA) died soon after being transplanted in 2006, even with diligent efforts to provide irrigation. I censused the dead seedlings and replaced them with new ones in June, August, and October, which was the last replacement. The main focus was to get seedlings established that year, and this is why tall grass and high fertility treatments were not imposed. In the following two years, dead plants were counted, but not replaced. No measurements were taken in 2006 except for the mortality data.

In 2007 May, I counted surviving plants and measured their diameters. Matured seed heads were counted and removed as needed, at least once a week, and sometimes three times a week during peak blooming. In October, surviving plants were counted and their diameters were measured again. Selected individuals, which were the largest plant (according to the diameter measurement in October) of the species in each treatment plot,
were harvested by digging them up from the field. I harvested the largest plants rather than random ones because there were large variations in size among the plants in the same treatment plot. Therefore, the selection of “best performers” was more reasonable. Roots and leaves of harvested plants were separated, dried in a 55°C oven for at least 7 days, and then weighed. After harvesting, only a small number of TLA remained in the field (Table 4.1). These individuals were not monitored in 2008. The same was true for TOF and TKS in the tall grass treatment.

I applied the same maintenance and measurement in 2008, except that diameter was not measured. In 2008 November, all plants were harvested; their root and leaf biomass measured as described above.

4.2.4 Data Analysis

A large number of individuals died unexpectedly during the experiment, leaving many missing values. This made the final data set unbalanced. For this reason, data were not analyzed using ANOVA; instead, only means and standard errors were calculated and reported.

Survival rate

The experiment was not designed as a population level study. However, since a large number of individuals were involved (648 in total) and mortality rate varied from treatment to treatment, it was logical to summarize and present the survival rate for each treatment. In 2006 when seedlings were transplanted and dead ones were replaced, an
individual was considered dead if it was replaced at least once from June to October.

Plant counts for those that were not replaced were pooled across all 12 replicates.

Fertility and tall grass treatments were not applied until 2007, so the data were pooled into two environmental treatments (short grass and no-grass) for each species. Survival rate was calculated as the number of survived plants in each treatment divided by 144 (short grass) or 72 (no grass), which is the total number of seedlings transplanted. Dead plants were all replaced in 2006 October and censused in May 2007. An over-winter survival rate (2006 - 2007) was calculated using the same method.

When plants were censused again in November 2007, the survival rate during 2007 was calculated as the number of live plants in November divided by the number of live plants in May. This time, fertility and grass treatments were imposed, so survival data for all 18 treatments were calculated. About half of the plants were dug and harvested in November 2007. The remaining plants were used to calculate over-winter survival of 2007 using census data in April 2008. The same method was used to compute survival for 2008 using the final census data taken in November 2008.

Only nine TLA plants in all treatments remained in the field after harvesting in November 2007 (Table 4.1). This sample size was too small to calculate meaningful survival rates, so TLA was excluded from the data analysis of 2008.

*Reproduction*

Reproduction data were collected as number of seed heads produced during 2007 and 2008. Only individuals that were recorded alive in the end-of-season census were
included in the analysis. Some plants that died before the census still produced a significant number of seed heads, but these data were excluded because the objective was to capture reproduction dynamics in different seasons (e.g. spring vs. autumn). Seed head counts were summed over the growing season, as well as aggregated every two weeks for each year. Means and standard errors are reported.

_Diameter and Biomass_

Diameter data (2007 May and 2007 October) and biomass data (2007 and 2008 harvest) were averaged for each treatment. Standard errors were calculated and reported.

### 4.3 Results

#### 4.3.1 Survival

The number of surviving plants after each census (or harvest) is summarized in Table 4.1. Among the total of 648 plants, 429 survived to the end of 2006. After dead plants were all replaced in October 2006, 535 plants remained after winter, and 308 survived to November 2007. A total of 147 plants were harvested in 2007, which left 161 in the field. Those plants declined to 111 at the end of November 2008. TLA had the highest mortality in all environments. Only 69 out of 216 individuals were alive in fall of 2006 and 32 in fall of 2007.

The survival rates of TOF were consistently over 0.8 in all seasons and environments except for in the tall grass treatments (Figure 4.2 and Figure 4.3). The same was true for
TKS, whose survival rate was over 0.6, except in tall grass. The TLA survival rates, however, were under 0.5 in all environments during the 2007 growing season.

Plants grown in the tall grass treatments experienced the highest mortality in 2007 (average survival = 0.27 vs. 0.79 in short grass and 0.68 in no grass, Figure 4.3b). Survival in short grass and no grass was the same for TOF in the 2007 growing season (0.99). For TLA and TKS, survival was a little higher in short grass (0.25 and 0.78) than in no grass (0.17 and 0.44, Figure 4.3b). Survival rates in tall grass-low fertility plots were higher than in tall grass-high fertility plots for all three species (0.55 vs. 0.26, 0.08 vs. 0.00, and 0.48 vs. 0.13 for TOF, TLA, and TKS, respectively, Figure 4.3b). Other than that, there were no observed differences in survival for plants growing at different fertility levels.

4.3.2 Reproduction

The seed head count was highest in the no grass environment for all three species. TOF in 2007, for example, reached 172.0 ± 11.5 heads per plant compared to 9.3 ± 2.4 in tall grass and 5.8 ± 0.8 in short grass (Figure 4.4). Although plants in tall grass environments appeared to produce more seed heads than those in short grass, the production mostly occurred in May 2007 (Figure 4.5). During that time, grasses were not fully grown and were still very short. Reproduction was almost zero in these plots in the following month.

TOF exhibited the highest reproduction of all three species in all environments. A more detailed analysis revealed that TOF experienced two reproduction peaks, one in
spring and one in autumn (Figure 4.5 and Figure 4.6), while the other two species only set seeds in spring. Soil fertility had little effect on reproduction, except that TLA produced more seeds (109.6 ± 10.9 seed heads/plant) in no grass-high fertility environments than in no grass-low fertility (35.0 ± 12.1 seed heads/plant) plots in 2007 (Figure 4.4a). Another exception was in 2008, when TOF and TKS in short grass-low fertility plots produced more seed heads (8.3 ± 1.1 and 7.2 ± 1.4 heads/plant) than those in short grass-high fertility environment (2.3 ± 0.5 and 1.7 ± 0.5 heads/plant).

4.3.3 Size and biomass

General speaking, TOF was largest in size and TLA the smallest as measured by diameter and biomass in almost all environments (Figure 4.7 – Figure 4.9). During the 2007 growing season, the diameter of TLA in no-grass plots declined significantly (from 33.5 ± 1.1 cm in May to 10.7 ± 2.3 cm in low fertility, and to 14.4 ± 2.6 cm in high fertility in October), but TOF and TKS was not affected (Figure 4.7). The biomass of TLA was very low compared to that of TOF and TKS in all treatments (Figure 4.8). In 2007, for example, total biomass in no-grass/high-fertility plots was 74.5 ± 17.7 g, 4.1 ± 1.1 g, and 48.0 ± 12.0 g for TOF, TLA, and TKS, respectively. Biomass accumulation was similar between TOF and TKS in 2007 (Figure 4.8), but TKS grew smaller than TOF in 2008 (25.9 ± 4.2 g vs. 40.9 ± 4.2 g in no grass plot, and 1.0 ± 0.2 g vs. 2.0 ± 0.2 g in short grass plot).
4.4 Discussion

4.4.1 Environmental effects

The status of surrounding vegetation had large effects on the growth of the three dandelion species, which exhibited significant decreases in performance in tall-grass environments as indicated by higher mortality, much lower reproduction, and smaller plant sizes after this treatment was applied during 2007. This result is consistent with previous findings that TOF density decreased with increasing grass height (Molgaard 1977), at least partly due to shading. Survival in short grass plots was dramatically improved, accompanied with increased reproduction, and plant diameter, but with little increase in biomass. TOF is frequently found in lawns, so its persistence in short grass environments was expected. Growth of TOF and TKS plants in no-grass treatments was extremely good; plants were very large, robust, and produced many flowers in spring and autumn (TOF) each year. This demonstrated the growth potential of these two species in optimum field conditions without competitors.

Fertility level, on the other hand, had little effect on the growth of the three species, especially in no-grass plots. In short and tall grass habitats, however, dandelions in low fertility soil seemed to grow better than in high fertility conditions (Figure 4.3b, Figure 4.4b, Figure 4.9). This was probably because high nutrient availability promoted vigorous growth of grass and made it more competitive toward dandelions. Grass in high fertility plots appeared to be thicker and greener (personal observation). Previous studies also suggested that TOF growth could be suppressed in well fertilized turfgrass swards (Johnson and Bowyer 1982, Hall et al. 1992).
4.4.2 Mechanism behind the different success of TOF and TLA

This field experiment provides evidence that TOF is more successful than TLA due to a higher survival rate, more prolific seed production in spring and autumn, and massive biomass accumulation. Previous studies have found that invasive species achieved higher fitness than the non-invasive (or native) species in certain environments, but had similar performance in at least some habitats (Lambrinos 2002, Gerlach and Rice 2003). In this study, however, TOF had overwhelming advantages over TLA across all habitats in all three years. TOF clearly exhibited a Jack-and-master type strategy (Richards et al. 2006) compared to TLA.

TOF had a very high (>80% over all, and near 100% in some plots) survival rate in all conditions except in tall grass where average survival was 40%. Survival in tall grass and low fertility conditions was 55%, while almost all TLA were dead in this environment (Figure 4.3b). The ability to survive among tall vegetation could play a very important role in the success of TOF. In some weedy spots (roadsides, crop field edges) that only get mowed once or twice a year, vegetation can grow very high, shading plants with rosette growth habits. Low-growing species that cannot tolerate this short-term shading might be unable to survive. TOF, however, seems to be able to survive in such conditions. As long as it is still alive, TOF could take advantage an opening in the canopy after mowing to accumulate biomass and produce seeds. It is this ability to perform consistently well under a breadth of conditions that makes TOF a successful weed.
It is not clear, however, what caused the high mortality in TLA. Many plants died in the establishment stage, which is the period after transplanting. However, many seedlings established successfully and apparently healthy also died suddenly without any symptoms. This finding was especially surprising because only 1 out of 64 TLA plants died in the greenhouse experiment, which involved a range of conditions from very stressful (dry, low light, low fertility) to very favorable environments (moist, high light, and high fertility). Several explanations were sought. Since TLA is often found in well-drained habitats (Fisher 1988), I considered that the field soil was not suitable for it. To test this possibility, I conducted a study in which 50 TOF and TLA seeds were germinated and grown in each of the 6” pots filled with field soil for 5 months in a growth chamber. Pots were treated with either persistent standing water, well watered and drained, or very dry soil. TOF had slightly higher survival (58 %) than TLA (42%) in flooded pots, a little lower survival (21% vs. 34%) in dry pots, and similar survival (46% vs. 41%) in well drained soil, but the differences were not as dramatic as in the field. I also suspected that soil pathogens might be involved in the death of TLA. But in another informal study, no significant difference in performance was found between TOF and TLA grown in sterilized field soil and non-sterilized soil.

Considering that TLA is still a widely distributed species with a handful of populations in most US states, it poses an interesting question regarding how this species maintains its population. In this study, TLA was not able to sustain itself for more than two growing seasons. It is possible that the most suitable growing conditions (niche) for TLA were not included in this study. TLA might prefer a sandy substrate and lightly...
shaded conditions, although the plants from which the experimental material was derived were growing in full sun. A second possibility is that TLA relies more on seed production than on the persistence of adult plants to maintain populations. Before many individuals died in summer of 2007, a significant number of seeds (55.7 ± 5.7 heads/plant in no-grass plots) were produced by these plants. Populations could be maintained if these seeds germinate successfully, and at least some reach the reproduction stage. Although this kind of life history is more frequently found in annual species, an exotic perennial like TLA, which cannot survive for more than one year, might be forced to follow this route.

4.4.3 Invasive potential of TKS

The overall performance of TKS in field was not as good as that of TOF, but it was much better than TLA in terms of survival, reproduction, and biomass. Survival rate of TKS was smaller than TOF in tall grass environments, but much higher than TLA (survival in tall grass plots in 2007 was 0.40, 0.04, and 0.30 for TOF, TLA, and TKS, respectively, Figure 4.3b). TKS produced much fewer seed heads (65.9 ± 9.9 heads/plant in 2007) than TOF (172.0 ± 8.1 heads/plant) in no grass habitats (Figure 4.4) even though the size of TKS individuals was only slightly smaller than TOF (73.1 ± 10.1 g vs. 53.9 ± 8.7 g for TOF and TKS, Figure 4.8). TKS accumulated less root biomass than TOF in both 2007 and 2008 (Figure 4.7 and Figure 4.8). This was different from the results of greenhouse experiments in which TKS had a larger root system then TOF. In the field, however, TKS tended to develop more adventitious shoots from the roots than TOF did, which may suggest better regeneration ability. These results suggest that TKS is not
superb in terms of reproduction ability by seed, but it can be robust and thrive under favorable condition, and persist in stressful habitats. These qualities, which resemble a Jack-of-all-trades strategy, make this species a perfect candidate as a potentially aggressive weed should it escape from cultivation, which is very likely for a wind-dispersed plant.

4.5 Conclusion

This study demonstrated that TOF exhibited much higher fitness than TLA over a range of field environments, which suggests that it is a Jack-and-Master type in terms of phenotypic plasticity patterns. TLA had high mortality in the field but the cause is unknown. The performance of TKS indicates that it has potential to behave as a successful weed if it escapes from cultivation.
<table>
<thead>
<tr>
<th>Treatment</th>
<th>TOF</th>
<th>TLA</th>
<th>TKS</th>
<th>Sum</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>2006 October</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Short grass</td>
<td>123</td>
<td>45</td>
<td>110</td>
<td>278</td>
</tr>
<tr>
<td>No grass</td>
<td>70</td>
<td>24</td>
<td>57</td>
<td>151</td>
</tr>
<tr>
<td>Sum</td>
<td>193</td>
<td>69</td>
<td>167</td>
<td>429</td>
</tr>
<tr>
<td><strong>2007 May</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Short grass</td>
<td>139</td>
<td>100</td>
<td>126</td>
<td>365</td>
</tr>
<tr>
<td>No grass</td>
<td>71</td>
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<td>46</td>
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<tr>
<td>Sum</td>
<td>210</td>
<td>153</td>
<td>172</td>
<td>535</td>
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<tr>
<td><em>(Seedlings were all replaced in 2006 October)</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Tall-Low</td>
<td>18</td>
<td>2</td>
<td>15</td>
<td>35</td>
</tr>
<tr>
<td>Tall-High</td>
<td>9</td>
<td>0</td>
<td>4</td>
<td>13</td>
</tr>
<tr>
<td>Short-Low</td>
<td>35</td>
<td>9</td>
<td>26</td>
<td>70</td>
</tr>
<tr>
<td>Short-High</td>
<td>36</td>
<td>9</td>
<td>30</td>
<td>75</td>
</tr>
<tr>
<td>No-Low</td>
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<td>3</td>
<td>17</td>
<td>56</td>
</tr>
<tr>
<td>No-High</td>
<td>35</td>
<td>9</td>
<td>15</td>
<td>59</td>
</tr>
<tr>
<td>Sum</td>
<td>169</td>
<td>32</td>
<td>107</td>
<td>308</td>
</tr>
<tr>
<td><strong>2007 November after harvest</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Tall-Low</td>
<td>8</td>
<td>0</td>
<td>6</td>
<td>14</td>
</tr>
<tr>
<td>Tall-High</td>
<td>3</td>
<td>0</td>
<td>1</td>
<td>4</td>
</tr>
<tr>
<td>Short-Low</td>
<td>23</td>
<td>3</td>
<td>14</td>
<td>40</td>
</tr>
<tr>
<td>Short-High</td>
<td>20</td>
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<td>17</td>
<td>39</td>
</tr>
<tr>
<td>No-Low</td>
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<td>1</td>
<td>9</td>
<td>33</td>
</tr>
<tr>
<td>No-High</td>
<td>22</td>
<td>3</td>
<td>6</td>
<td>31</td>
</tr>
<tr>
<td>Sum</td>
<td>99</td>
<td>9</td>
<td>53</td>
<td>161</td>
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<tr>
<td><strong>2008 April</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Short-Low</td>
<td>23</td>
<td>1</td>
<td>14</td>
<td>38</td>
</tr>
<tr>
<td>Short-High</td>
<td>17</td>
<td>1</td>
<td>16</td>
<td>34</td>
</tr>
<tr>
<td>No-Low</td>
<td>22</td>
<td>1</td>
<td>9</td>
<td>32</td>
</tr>
<tr>
<td>No-High</td>
<td>22</td>
<td>2</td>
<td>5</td>
<td>29</td>
</tr>
<tr>
<td>Sum</td>
<td>84</td>
<td>5</td>
<td>44</td>
<td>133</td>
</tr>
<tr>
<td><strong>2008 November</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Short-Low</td>
<td>22</td>
<td>1</td>
<td>9</td>
<td>32</td>
</tr>
<tr>
<td>Short-High</td>
<td>15</td>
<td>1</td>
<td>11</td>
<td>27</td>
</tr>
<tr>
<td>No-Low</td>
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<td>7</td>
<td>28</td>
</tr>
<tr>
<td>No-High</td>
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<td>0</td>
<td>3</td>
<td>24</td>
</tr>
<tr>
<td>Sum</td>
<td>79</td>
<td>2</td>
<td>30</td>
<td>111</td>
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</tbody>
</table>

Table 4.1 Survival count in each census. Data of 2006 October and 2007 May was aggregated into only two groups (short grass and no grass) because fertility and tall grass treatments were not applied before these two censuses. Individuals in tall grass treatment were not censused after 2008 April because sample size was too small.
Figure 4.1 Experiment design and layout. Each 1.5 m × 1.5 m plot received one of the 6 environmental treatments and contained 9 plants, 3 from each species (as indicated by different symbols). On replicate (block) measured 7.5 m × 5.0 m, and included 6 small plots as described above. The entire experiment had 12 replicates with 3 × 4 layouts in field.
Figure 4.1

One plot:
3 plants * 3 species = 9 plants

One replicates:
9 plants * 2 fertility * 3 grass = 54 plants

Whole experiment:
with 12 replicates:
54 * 12 = 648 plants

Figure 4.1
Figure 4.2 Over winter survival rate of a) 2006-2007 and b) 2007-2008: TOF (grey), TLA (white), and TKS (hatched). Short/No refers the status of surrounding vegetation. High/Low refers the fertility level. 2006-2007 data was aggregated into only two groups (short grass and no grass) because fertility and tall grass treatments were not applied until 2007 spring. TLA and individuals in tall grass treatment were not censused in 2007 - 2008 because sample size was too small.
Figure 4.3 Seasonal survival of year a) 2006, b) 2007, and c) 2008: TOF (grey), TLA (white), and TKS (hatched). Tall/Short/No refers the status of surrounding vegetation. High/Low refers the fertility level. 2006 data was aggregated into only two groups (short grass and no grass) because fertility and tall grass treatments were not applied until 2007 spring. TLA and individuals in tall grass treatment were not censused in 2008 because sample size was too small.
Figure 4.4 Total seed head count (mean ± 1 standard error) of three dandelion species in different habitats in a) 2007 and b) 2008: TOF (grey), TLA (white), and TKS (hatched). Tall/Short/No refers the status of surrounding vegetation. High/Low refers the fertility level. Data of tall grass habitat and TLA in 2008 was not measured. Insert shows seed head counts of tall grass and short grass in a different scale.
Figure 4.5 2007 seasonal seed head count (mean + 1 standard error) of three dandelion species in different habitats: TOF (solid line and filled circle), TLA (dotted line and open triangle), and TKS (dashed line and filled square). Tall/Short/No refers the status of surrounding vegetation. High/Low refers the fertility level.
Figure 4.6 2008 seasonal seed head count (mean + 1 standard error) of two dandelion species in different habitats: TOF (solid line and filled circle) and TKS (dashed line and filled square). Short/No refers the status of surrounding vegetation. High/Low refers the fertility level.
Figure 4.7 Diameter (mean ± 1 standard error) of three dandelion species in different habitats measured in a) 2007 May, and b) 2007 October: TOF (grey), TLA (white), and TKS (hatched). Tall/Short/No refers the status of surrounding vegetation. High/Low refers the fertility level.
Figure 4.8 Biomass (mean ± 1 standard error) of three dandelion species in different habitats during 2007 growing season: TOF (grey), TLA (white), and TKS (hatched). Tall/Short/No refers the status of surrounding vegetation. High/Low refers the fertility level. Insert shows biomass of tall grass and short grass in a different scale.
Figure 4.9 Biomass (mean + 1 standard error) of two dandelions species in different habitats during 2008 growing season: TOF (grey), TKS (hatched). Short/No refers the status of surrounding vegetation. High/Low refers the fertility level. Insert shows biomass of short grass in a different scale.
CHAPTER 5

SUMMARY AND FUTURE DIRECTIONS

5.1 Research summary and general conclusions

This dissertation revealed that the germination, growth, and reproduction of the three dandelion species responded to various environments in complex manner. Seeds of the invasive TOF germinated better than those of the non-invasive TLA under different regimes of alternating temperatures, but exhibited less germination in other stressful environments (dark, low water potential, and after accelerated aging, Chapter 2). In the greenhouse with different combinations of abiotic factors, TOF grew bigger than TLA in favorable conditions. TLA, however, exhibited higher reproduction than TOF in high resource environments (Chapter 3). The superior invasive quality of TOF was revealed in the field experiment. TLA experienced very high mortality in all treatment combinations of competitors and soil fertility, and the causes of mortality were unknown. On the other hand, TOF thrived in favorable habitats, and persisted in stressful ones (Chapter 4).

These results support the hypothesis that there are differences in the phenotypic plasticity of TOF and TLA at various life stages. However, these responses did not consistently fall into one of the three scenarios proposed by Richards et al (2006, Figure
1.2). Compared to TLA, TOF appeared to be a Jack-of-all-trades in terms of germination in alternating temperatures, and a Master-of-some for biomass accumulation in the greenhouse experiment. But field growth and reproduction patterns suggested that TOF was a Jack-and-Master type. In contrast, TLA exhibited higher fitness than TOF in other stressful germination environments, and also in reproduction under high resource greenhouse conditions. These findings suggested that phenotypic plasticity alone is not a reliable indicator of invasive potential for TOF and TLA. Response patterns are complicated and depend largely on which environments, life stages, and fitness traits are studied.

Although phenotypic plasticity was not clearly associated with the invasiveness of TOF, these comparative studies between TOF and TLA over a wide range of environments provided information that might reveal the mechanisms behind TOF’s success, and allow us to evaluate the invasive potential of TKS. TOF seeds only germinated over a narrow environmental range, possibly linked to ideal conditions for seedling growth. Seeds dispersed into stressful habitats may remain in the soil ungerminated until suitable germination conditions occur (Chapter 2). TOF allocated more energy to vegetative growth than to reproduction, probably enhancing its ability to establishment and survival, which resembles a K-strategist (Chapter 3 and 4). On the other hand, TLA did not survive well in the field, so it may rely on higher rates of reproduction to sustain its small populations. TKS germinated best among the three species in all environments (Chapter 2). Other than this, TKS species behaved more like TOF than TLA in the greenhouse and field (Chapter 3 and 4), which suggests it has the
potential to behave as a weed, just like other crops such as canola (*Brassica napus*), hairy vetch (*Vicia villosa*), and buckwheat (*Fagopyrum esculentum*).

### 5.2 Terminology concerns

The term “phenotypic plasticity” is sometimes misleading in studies of biological invasion. Most studies on phenotypic plasticity focus on the developmental, morphological, and physiological aspects of organisms (Trewavas and Jennings 1986, Dewitt and Scheiner 2004, Hulme 2008). Fitness related traits, which are frequently used in biological invasion studies, are rarely considered “phenotypic” responses. If a plant changes its leaf shape in different environments, then it can be comfortably called a “phenotypic plasticity” response. However, when a plant grows bigger and sets more seeds in favorable growing conditions but is stunted in stressful conditions, “phenotypic plasticity” seems to be an awkward term to use. Traits like these, which are sometimes called “labile attributes” (Hulme 2008), are not readily accepted as true phenotypes by some scientists (Hulme 2008). For these reasons, I suggest that for future studies, we should omit “phenotypic” and replace “plasticity” with “elasticity”. For example, the difference in biomass accumulation along an environmental gradient can be referred to as “growth elasticity” and those of seed output as “reproduction elasticity”. This new terminology is easier to understand for those who never heard of “phenotypic plasticity”, and is more appropriate for these traits. For morphological and physiological traits such as leaf shape and biomass allocation, however, the term “phenotypic plasticity” is still recommended.
5.3 Future directions

This dissertation demonstrated that comparative studies of invasive and non-invasive species across different environments can yield fruitful results. More studies like this on other species and in other ecosystems are needed. However, it is probably not necessary to focus on phenotypic plasticity alone. Detailed analysis in each environment would be more useful. This dissertation also suggested that neither germination, biomass, nor reproduction were the best measurements of fitness to evaluate phenotypic plasticity and its link to biological invasion.

Future work should focus on the population level and make measurements on population growth rate. Demographic data on all life stages (germination rate, seedling establishment rate, adult survival rate, seed reproduction, dispersal, and seed decay and predation rate) can be collected in all kinds of environments for each species. A demographic model such as a matrix model (Caswell 2000) can be built using these data and projections of population growth can be made. One can also compare these models among species and environments to determine the most critical life stage(s) that make one species different from another under certain conditions using a life table response experiment, or LTRE (Caswell 2000, Parker 2000, Caswell et al. 2003). This method not only offers invaluable information on invasive processes at the population level, but also on which life stage(s) is/are most vulnerable for the species. More efficient management methods can thus be developed for controlling invasion using this knowledge.
The experiment materials used in this dissertation were obtained in limited geological locations, especially for TLA. Collections over a wider range might reveal different response patterns to environment variation. Finally, additional research is needed to reveal the causes of TLA mortality in field.
APPENDIX A

SEED CLEANING PROCEDURES FOR *TARAXACUM* SPECIES

1. Pappus was first separated from seeds by gently rubbing between two rubber blocks.

2. Mixture of pappus and seeds went through a #40 sieve to remove small debris.

3. The mixture was blown in a vertical air column. The speed inside the air column was
adjusted so that the light-weighted pappus and empty seeds were able to be separated
from the heavy filled seeds.
APPENDIX B

LEAF MORPHOLOGY MEASUREMENT PROCEDURE

One typical leaf from each plant was collected and scanned. The image was processed using ImageJ® software to obtain leaf area and perimeter. The length and width of each leaf was also measured by drawing a bounding rectangle.

Process procedure:

1. Erase color check card, scale and other background
2. Convert to 8 bit format
3. Convert to binary format using automatic threshold
4. Set scale: 792 pix/20cm
5. particle analysis, minimum area 2cm²
6. Measure area, perimeter, Feret’s diameter, and bounding rectangle

The bounding rectangle is always drawn in x and y axis direction rather than the area’s major axis. Thus for a leaf placed with an angle when scanned, the bounding rectangle failed to reflect the leaf’s width and length. Feret’s diameter is used instead for
leaf length. The angle of leaf is measured using arcos (bounding rectangle length/Feret’s
diameter). If the angle is more than 15 degrees, the width is re-measured manually.
Otherwise, the width of bounding rectangle is regarded as the leaf width.
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