THE FATE OF CHINESE UNDERSTORY SPECIES IN CONIFEROUS FORESTS OF THE PACIFIC NORTHWEST: THE ROLE OF LIGHT

By

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To the Faculty of Washington State University:

The members of the Committee appointed to examine the thesis of MOLLY MUIR BROOKE find it satisfactory and recommend that it be accepted.

Chair

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Abstract

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An effective method to predict invasive plant species could prevent annually billions of dollars of environmental damage in the U.S. In this study, I propose such a method based on the identification of likely sources of future invaders and factors that could determine the fate of these introductions. Many ornamental species from temperate China may hold a risk of invasion for the Pacific Northwest because of the climatic similarities between temperate coniferous forest regions of China and the Pacific Northwest. Further, these two regions are floristically related and contain many congeneric species that occupy similar ecological niches. Such similarly adapted species could potentially displace their congeners in the introduced range. However, if the non-native species cannot tolerate the shade levels in these forests, they pose no risk of invasion. I experimentally subjected four Chinese understory species, three native congeners for comparison and one bamboo species to two shade levels commonly found in Pacific Northwest forests and monitored their growth rates, leaf morphologies and chlorophyll contents. The Chinese *Allium tuberosum* demonstrated greater leaf morphology plasticity and relative growth rates than the native *A. cernuum* but little difference in chlorophyll acclimation. The Chinese *Philadelphus kansuensis* displayed greater leaf morphology plasticity and more rapid branch elongation than the native *P. lewisii* but little difference in chlorophyll acclimation. The native *Spiraea douglasii* appeared light-limited in both shade treatments and the non-native *S. japonica* and *S. wilsonii* exhibited no greater abilities to acclimate to shade than the native. The Chinese *Fargesia rufa* survived and grew in both shade treatments, but the lack of a native bamboo prohibits further comparisons. I predict that *A. tuberosum* and *P. kansuensis* are more likely to be able to naturalize in these shade regimes in the Pacific Northwest than are *S. japonica* or *S. wilsonii*. The fate of *F. rufa* in these shade conditions cannot be predicted without further trials. This study illustrates one step in a practical, field-based protocol for evaluating potential plant invaders into intact forest ecosystems where shade may limit invasion success. Horticultural introductions, particularly those from temperate China, may well contribute future plant invaders to the Pacific Northwest.

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INTRODUCTION

1. Invasive species

One of the most challenging environmental problems today is the eradication and control of invasive species. Although a single definition of an "invasive species" is not universally accepted, an organism is generally termed "invasive" if it proliferates outside of its native range and has a negative impact on its new environment (see discussion in Davis and Thompson 2000, Mack *et al.* 2000). Among the approximately 50,000 known non-native species in the U.S., only a few thousand have become invasive. Nevertheless these invaders collectively cause about $120 billion in economic losses annually, nearly $35 billion of which is caused by invasive plants alone (Pimentel *et al.* 2005). The primary economic costs of invasive plants include increases in the frequency and intensity of wildfires, reduction in the quality of livestock rangelands, direct competition with crops, hindrances to navigation and threats to human health (Mooney 2005).

The environmental damage caused by invasive species will likely have more profound impacts on biodiversity than the costs to any nation's economy. Invasive plant species can alter fire and nutrient cycling regimes, attack native species as parasites or competitors, deplete water supplies, change the course of evolution and cause the extinction of native species (Mooney 2005). Biological invasions reputedly rank second only to habitat destruction as threats to biodiversity (Wilcove *et al.* 1998). Approximately 50% of the species currently listed as threatened or endangered by the Endangered Species Act have invasive species as a primary driver of their status (Wilcove *et al.* 1998). For example, three endemic Hawaiian shrubs, *Kokia drynarioides, Caesalpinia kavaiensis* and *Colubrina oppositifolia,* are endangered due to the extreme fire hazard created by *Pennisetum setaceum*, an invasive perennial grass, around their few native locations (pers. comm. Curt Daehler). Clearly such serious economic and environmental threats cannot be overlooked. The safest way to avoid such negative consequences would be to prevent all future plant introductions, but this solution is infeasible for both practical and political reasons (Ruesink *et al.* 1995). We must instead develop an accurate way to predict likely invaders and focus our energy on prohibiting these high-risk species from entering the U.S. (National Research Council 2002).

2. Prediction

Predicting, and subsequently preventing, the entry of potential invasive species is important because prevention of invasive species preempts the environmental and economic costs associated with the eradication of these species (National Research Council 2002). Until now, much of the research on invasive plant species has focused on creating prediction tools built upon species' ability to invade elsewhere, biological traits (e.g. mode of reproduction, seed dispersal ability, fruit type, frost tolerance etc.), a similar climate between the native and potential introduced range, or some combination of these approaches (National Research Council 2002). One intuitive model employs a 14-step decision tree with woody plant traits that assign to one of three categories: reject entry, defer entry pending further analysis/monitoring, or accept entry (Reichard and Hamilton 1997). With the later addition of 10 steps to the model, Widrelechner *et al.* (2004) claim the predictive power of the decision tree increases from 65% to 90%. However, even with a 90% classification rate, the model results in a 3.3% false negative error rate, allowing invaders to be introduced, as well as a 13.3% false positive error rate, limiting the introduction of potentially beneficial horticultural or agricultural non-native species

(Widrlechner *et al.* 2004). For example, the Asian *Berberis thunbergii*, an invasive species in the Midwestern U.S. was accepted by this model (Widrlechner *et al.* 2004).

Similar results were obtained through tests of the 49-question Australian Weed Risk Assessment model (WRA) (Pheloung *et al.* 1999). Modified versions of the WRA were applied to New Zealand (Pheloung *et al.* 1999) and Hawaii (Daehler *et al.* 2004) and both correctly identified the majority of high risk and low risk invaders. However, the weakness in all these models appears when determining the fate of the species that are not clearly high or low risk species. This ambiguity in the "moderate risk" category can lead to the harmful introduction of species or needless exclusion of beneficial species. Furthermore, species are currently evaluated retrospectively by testing known invasive and non-invasive non-native species and these estimates are likely to be overly optimistic (Lonsdale and Smith 2001).

The ecology of an invasive species is likely more complicated than can be accurately predicted by a model constructed from the correlative tools provided by a species' past history, its traits, or the similarity of its native and introduced range climates. Indeed the only fail-safe prediction method is to evaluate the species' performance in the habitat in question. A similar, but more practical, alternative is to experimentally subject the non-native species to the environmental conditions of the potential new habitat. If the species can survive, grow and reproduce under these environmental conditions, the species could likely become naturalized or invasive if introduced into this new habitat. This approach has been used repeatedly through evaluations in growth chambers. By subjecting the species to varying photoperiods and temperature levels in a controlled environment, such studies predicted the potential range expansion of these invasive species, which led to management recommendations (Patterson *et al.* 1990, Hall and Patterson 1992, Patterson 1994, Patterson 1997 and others). A more accurate method would be to subject the species to the complete spectrum of conditions in the habitat in question through a controlled field study. Although the need for such a practical, field-based method has long been recognized, no such method has yet been developed (National Research Council 2002, Mack 2005).

3. The Role of Light in Species' Distribution

A non-native species must tolerate all of the aspects of its new environment to persist. If a species is introduced as a seed, it must be able to meet its germination requirements, tolerate seed predation and fungal attack before the seedling stage (Harper 1977, Baskin and Baskin 2001, Howe and Brown 2001, Schafer and Kotanen 2003, Garcia and Houle 2005). At the seedling stage, the species must again tolerate predation, light and moisture regime of the habitat, and meet its energy demands with the available light (Harper 1977, George and Bazzaz 1999, Messaoud and Houle 2006). If the species cannot harvest enough light to balance its energy budget it will not reproduce or even persist in the vegetative state (Smith and Smith 2006). The vast majority of introduced species are thwarted by at least one environmental constraint of the introduced habitat and do not persist or proliferate to cause harm to the new environment. However, those species that are introduced into a habitat similar to their native habitat may be "pre-adapted" for the conditions of the new habitat and therefore stand a greater chance of becoming naturalized (Richardson and Pysek 2006).

One important environmental factor in determining plant species' distribution is the amount of light in its habitat (Grime and Jarvis 1975, Koike 2001, Begon *et al.* 2006). In habitats where light is a limiting factor, such as the understory in a tropical forest, the effects of light limitation can be striking. For instance, Davies *et al.* (1998) demonstrated strict niche partitioning among 11 tree species in the genus *Macaranga* based on the shade tolerance of each species. Shade-tolerant species were found strictly in the understory and the others existed along a continuous gradient of decreasing shade tolerance up to the largest canopy trees (Davies *et al.* 1998). Similarly, understory species in forests of the Pacific Northwest must tolerate shade. Native species are adapted to tolerate these conditions and any naturalized species must either be pre-adapted or be able to acclimate to the shade regime in these forests. Observing the ability of a non-native species to acclimate to light conditions in the potential introduced range could help predict the fate of the species if it were introduced.

Plants frequently exhibit shifts in carbon allocation when acclimating to a light-limited environment. In general, shade-acclimated plants exhibit lower rates of photosynthesis and respiration and lower light compensation points such that less light is required to balance the carbon budget (Chapin 1991, Larcher 1995, Smith and Smith 2006). Shade acclimated plants also display higher specific leaf area (Grime 2001). The resulting thinner and broader leaves give the plant more photosynthetic surface area to maximize the limiting resource (Grime 2001). The overall reduction in photosynthate production leads to decreased production of dry matter and, therefore, slower growth rates (Grime 2001). Shade-acclimated leaves also often exhibit lower chlorophyll *a* to *b* ratios than sun-acclimated leaves (Larcher 1995). Therefore, species with higher specific leaf area and lower chlorophyll *a* to *b* ratios (or with plasticity in these traits), but no reduction in growth rate when exposed to the shade levels of the potential introduced range are likely to be able to acclimate to the shade conditions of the new habitat.

4. Selecting a Pool of Potential Invaders

a. Congeners

Ecologists have long sought to predict invasions before they occur (Richardson and Pysek 2006 and references therein). Because it would be impractical to evaluate the invasion potential of every species, ecologists first narrow the field by identifying a pool of likely invaders (Mack 1996). The approaches for creating this pool of potential invaders are varied but can form two general categories: species traits and environmental characteristics (Mack 1996, Richardson and Pysek 2006 and references therein). Many attempt to predict future invasive species by characterizing the traits of current invaders and by examining the history of invasion of each species in other regions (Mack 1996, Goodwin *et al*. 1999, Sharma *et al*. 2005). Others look at environmental traits of invasible habitats by comparing the current native and naturalized ranges of a species and extending the potential range to include other similar climates (Mack 1996, Widrlechner 2001, Sharma *et al*. 2005). Although each predictive method has met with some success, none has yet been demonstrated superior to the others (Mack 1996).

The opportunity for another predictive tool arises when a native congeneric species occurs in the potential new range for a species introduction (Mack 1996). Congeners are species of the same genus and, especially when they are closely-related, are often adapted for similar habitat types (Mack 1996). Where possible, the presence of a congener in the native habitat allows for direct experimentation and comparison between the species to assess similarities and differences that may confer advantages to the non-native species (Mack 1996). As early as 1859, Charles Darwin proposed that intense competition between closely-related congeners could result in fewer congeneric recruits to a habitat than recruits from less-related taxa (Darwin 1859). Darwin's naturalization hypothesis (DNH) has been tested repeatedly and the overwhelming majority of the evidence does not support it (Richardson and Pysek 2006 and references therein). For instance, in a simple statistical analysis of invaders in New Zealand, Duncan and Williams (2002) found that genera with at least one native species were significantly more likely to become naturalized than those without congeners in the region. It appears that in many cases the benefits of being pre-adapted, even at the genus level, for a new habitat outweigh the costs of competition with a closely-related species (Richardson and Pysek 2006).

Although the DNH hypothesis can be evaluated in a correlative manner, few studies have studied the traits of native and non-native congeners in the field (but see Caldwell *et al.* 1981, 1983; Nowak *et al.* 1986). In addition, I am unaware of any studies that investigate the traits of congeners before widespread naturalization of the non-native species has occurred. In this study, I compare native and non-native congeners before the non-native species has been widely introduced. If the non-native species are pre-adapted for the habitat, they could perform similarly to the native species in field trials. Moreover, if the non-native species possess traits that allow them to acclimate to the habitat more readily than the native species, they should exhibit more aggressive characteristics than the native species, such as faster growth. Species exhibiting characteristics that convey competitive advantages could potentially become invaders in these habitats.

b. Horticultural Introductions

Identifying probable modes of introduction is another way to eliminate some species from the pool of likely future invaders (Mack 2005). Although many microbes, invertebrates and some crop weeds were accidentally introduced, the vast majority of plant introductions have been intentional (National Research Council 2002, Pimentel *et al.* 2005). The majority of these plant introductions are deemed beneficial (Mack 2005), however, most of our current invasive plant species were also intentionally introduced for agricultural or horticultural purposes (Mack and Erneberg 2002, Mooney 2005, Pimentel *et al*. 2005). To date, there are several thousand naturalized plant species in the U.S.; these species may comprise as much as 25% of the U.S. flora (Pimentel *et al*. 2005 and references therein). However, because the majority of invasive plant species are intentionally introduced, the potential for prediction and prevention of future invasive plant species is high compared to insects and other accidentally introduced alien species. Ecologists can conduct rigorous studies of invasion risks for each species before it is introduced and decide whether introduction should be authorized.

Historically, plants were introduced for practical purposes such as food, medicine, or erosion control but also solely for ornamental value (National Research Council 2002, Mack 2005 and references therein). Today the number of plant species in the latter category is steadily increasing (Reichard and White 2001, Mack 2005). The search for ornamentals that are easily cultivated and produce showy flowers or fruits often results in artificial selection of ornamentals with traits that may increase the risk for invasion (Mack 2005). In contrast to the strict regulation of non-native species in New Zealand and Australia, in the U.S. there are few restrictions on plant introductions and no plant screening methods (Mack 2004). As a result, many species have escaped cultivation and become naturalized or invasive in the surrounding habitats (Reichard and White 2001, Mack 2005 and references therein). Woody species present a particularly high risk: approximately 85% of the current invasive woody species were introduced as ornamentals or for erosion control (Reichard and Hamilton 1997). Thus, plant nurseries serve as a significant point of dissemination for potential invasive species.

Currently, the horticultural industry generates over $13 billion a year and ranks second only to the production of corn and soybeans in importance to the U.S. agricultural economy

(Regelbrugge 2003). With ever-increasing public interest in new plant horticultural introductions, international traffic in plants will likely continue to increase, bringing new economic and environmental threats (Perrings *et al.* 2005). Fortunately, awareness of the damage caused by invasive species is increasing within the horticultural industry (Baskin 2002, Mack 2005). Plant nurseries are ideal locations to implement proper screening methods for future introductions because they have space to test the non-native species in the local climate (Mack 2005). Moreover, the incentive to distribute only species with a low risk of environmental damage is intrinsic to any responsible business (Reichard and White 2001) and the horticultural industry has already begun to make voluntary steps in this direction (Baskin 2002).

5. China – a future source of horticultural species

a. Ecological similarities between U.S. and China

Identifying likely native or donor areas for new horticultural selection for the U.S. is a powerful tool in narrowing the search for potential invaders (National Research Council 2002). Some countries may be at an elevated risk of supplying the U.S. with invasive species due to characteristics of its climate, flora or history.

Climatic matching between the native and potential donor ranges has proven useful in these investigations (Mack 1996, National Research Council 2002). In this respect, China stands out as a strong candidate for new invasive species in the U.S. because the two regions share many physical characteristics (Mack 1996, Qian and Ricklefs 1999). Both countries are located within approximately the same latitudes (Qian and Ricklefs 1999). Each country contains regions from tropical to boreal, elevations from sea level to 6,000 m and moisture gradients from more moist coastal areas to xeric interior areas (Qian and Ricklefs 1999). In particular, the U.S. Pacific Northwest and temperate portions of Yunnan Province in China share many similar macroclimates (Domrös and Gongbing 1988, Schneider 1996). No other large area shares as many physical similarities with the U.S., and it is therefore likely that no other flora is as similarly adapted to the climate in the U.S. (National Research Council 2002).

b. Floristic similarities between U.S. and China

The similarities between the floras of China and the U.S. are striking and have long attracted the attention of biologists (Gray 1840, 1846, 1878; Li 1952, Fryxell 1967, Graham 1972, Boufford and Spongberg 1983, Ying 1983, Tiffney 1985, Ricklefs and Lathan 1992 and others). Jonas P. Halenius, a student of Linnaeus, first recognized the similarities between these disjunct floras in 1750 (Boufford and Spongberg 1983). However, Asa Gray is credited with the seminal work on this topic (Boufford and Spongberg 1983). Prior to the publication of Darwin's *On the Origin of Species*, Gray hypothesized that the similarities between the floras of China and the U.S. must be a result of "a peculiar intermingling of the Eastern American and Eastern Asian floras" and that the differences in the modern flora result from change over time after the two continents separated (Gray 1859, Boufford and Spongberg 1983). These ideas, revolutionary in Gray's era, are upheld today in the light of more evolutionary and geologic study (Wolfe 1978, Boufford and Spongberg 1983).

Today we know that North America and Asia were intermittently connected by land bridges throughout the Tertiary (Tiffney 1985, Qian and Ricklefs 1999). These connections created what was effectively one large northern temperate flora (Tiffney 1985, Qian and Ricklefs 2004). Even after direct movement of species across land bridges was no longer possible, the continuing climatic similarities of the two regions resulted in the evolution of several closely-related taxa through parallel evolution from common ancestors (Tiffney 1985). Remnants of this united northern temperate flora are seen in the similarities between the modern temperate floras of the U.S. and China (Li 1952, Fryxell 1967, Graham 1972, Boufford and Spongberg 1983, Tiffney 1985, Qian and Ricklefs 1999 and others).

The relationship between the modern floras of the eastern U.S. and China has been extensively studied and the two regions are now known to possess approximately the same taxonomic diversity at the levels of orders and families (Qian and Ricklefs 1999). However, China, with nearly twice as many species in its flora, has much more species richness than the U.S. at the genus and species levels (Qian and Ricklefs 1999). More importantly, the two floras contain many species that appear to occupy similar ecological niches in their respective native habitats (National Research Council 2002). This similarity between the eastern U.S. and China, not only in floristics, but also in the ecological requirements/tolerances of these species has attracted the attention of ecologists investigating invasive species.

Unfortunately, ecologists have largely overlooked one important part of Gray's work on the floras of China and North America. Gray found the greatest degree of similarity between Asia and the eastern U.S., but also noted considerable similarities between Asia and the western U.S. (Boufford and Spongberg 1983, Gray 1859). To my knowledge, no one has yet conducted studies like those of Qian and Ricklefs (1999) with the flora of the western U.S. Such studies are warranted because of Gray's findings of floristic similarities between these two regions. The similarity between the physical environments and flora of the U.S. and China is an indication, however provisional, that species introduced from temperate China in general and specifically Yunnan pose risk for invasion into ecosystems in the Pacific Northwest and elsewhere.

c. Risks heightened by historical circumstances

The threat of new invasive species originating in temperate China is heightened by historical circumstances. Although temperate Yunnan was a site of intense plant collection by western biologists and horticulturists throughout the 19th and early 20th centuries (Mack 2001), political upheavals suspended all such collecting and even plant importation from China for almost 60 years (Spongberg 1993). Before this embargo, plant collectors had introduced many new species into the U.S. (Spongberg 1993) and some of these have become some of the most aggressive plant invaders in the U.S. (National Research Council 2002 and references therein). This group includes *Rosa multiflora, Lythrum salicornia, Buddlelia davidii*, *Hedychium coronarium* and *Mimosa pudica* (Randall & Marinelli 1996, Wu 1999). Nevertheless, the introduction of such attractive species sparked interest in importing ornamentals from China (Spongberg 1993). When these trade restrictions were totally reversed in 1980, approximately 60 years of constrained enthusiasm was released and the volume of trading and travel between the two regions has subsequently exploded (National Research Council 2002, Mack 2001, Spongberg 1993). Other than aesthetic value and hardiness in the introduced habitat, nothing is more valuable to a plant collector than novelty (Mack 2001). Thus, in the past 25 years, many new Chinese species have been introduced into the U.S. (Spongberg 1993), with little regard for threats they might pose as potential invaders (Mack 2001).

d. Pool of potential invaders from China

Today, temperate China and specifically the species rich flora of Yunnan represent the largest single region from which new plant introductions are arriving into North America (see Zhang *et al.* 1998). Horticulturalists invest considerable time and expense in travel to remote regions of China to ‘discover’ new ornamental species for U.S. commercial trade (Zhang and

Dirr 2004). For example, Zhang and Dirr (2004) recommend 20 woody species for use as ornamentals in the U.S. and conclude by saying, "(n)ew ornamental plants from China are far more than we mentioned above. How to further explore the potential ornamental plants, how to bring these plants back to U.S., and how to collectively market these plants should be addressed." Some plant nurseries are fulfilling this mandate through private collecting trips to China. In the Pacific Northwest, Heronswood Nursery (Kingston, WA) was a pioneer in introducing many species specially selected to flourish in this region (Heronswood Nursery 2005).

In his review of horticultural introductions into the U.S. from eastern Asia, Spongberg states: " Previously little-known plants and totally new ones as well are destined to enter the horticultural marketplace as the twenty-first century approaches" (Spongberg 1993). This trend is worrying because the importation of species from temperate China before their embargo in the 1920s has already yielded several plant invaders (Randall and Marinelli 1996, Wu 1999*)*. It is likely then that some fraction of new introductions contain species with similar invasive ability. The U.S. would do well to identify them and prohibit their entry.

6. Design of Current Study

The development of a rapid, field-based prediction method that maximizes economic benefits while minimizing risk of invasion is long overdue (National Research Council 2002, Mack 2005). This method needs to accurately identify benign species for importation that will benefit the horticultural industry while excluding the species that will ultimately cause the U.S. significant economic and ecological losses. Ecologists can narrow the field of probable future invaders by identifying likely sources and modes of introduction. Europe and North America have been extensively explored for potential ornamental species, consequently it is unlikely that many new invaders will come from these regions (National Research Council 2002). Likewise, South America and Australia have been well-collected for horticultural species and may not provide many new invaders, although some horrific invaders have come from both continents (e.g. *Eichhornia crassipes* and *Melaleuca quinquenervia*) (National Research Council 2002). China, however, is a much more likely source because so many more opportunities occur there as its flora has not been thoroughly exploited as a source of ornamental species (National Research Council 2002). Because many of these species have overlapping ecological amplitudes with species in the U.S., it is possible that some of these new introductions will pose threats to our native plant communities (National Research Council 2002). More specifically, we can identify the Pacific Northwest as a potential recipient of invasive species from the Yunnan Province of China because of the striking similarities in the climates and general floristic composition of these two regions (National Research Council 2002).

I selected a group of Chinese understory species that are currently marketed as ornamental species in the Pacific Northwest. Each species is native to regions of China that are climatically and floristically similar to coniferous forests of the Pacific Northwest. Additionally, each species (with the exception of the bamboos) has a native congener in the Pacific Northwest (see “Study Species” in this manuscript). The presence of a congener in a similar ecological role suggests that the non-native species may behave similarly to its native counterpart if introduced to the same habitat (National Research Council 2002). Consequently, each of these species is a potential species of concern as an invader in the Pacific Northwest.

A non-native species must overcome a series of biotic and abiotic barriers if it is to grow, naturalize or become invasive. This study is designed to measure the effects of light limitation on the non-native species. Sufficient light availability is crucial to the growth and survival of a plant and the effects of light limitation are rapidly visible (Smith and Smith 2006). The ability to recognize the effects of light limitation is potentially a useful tool to distinguish benign species from potential invasive species. Light is also an important limiting factor in the dense coniferous forests of the Pacific Northwest and no species could become established in these forests if they cannot tolerate the shade regime of these forests (e.g. Caplan and Yeakley 2006). I subjected native and non-native congeners to shade treatments approximating the shade levels commonly found in an array of coniferous forests of the Pacific Northwest. I then compared the performance of these congeners and looked for evidence that the non-native species could acclimate at least as well as their native counterparts to the native shade regime. Non-native species that demonstrate the ability to acclimate, survive, grow and reproduce at least as well as their native counterparts in these light conditions have the potential (subject to their performance under other environmental conditions) to become naturalized, or even invasive, in these forests.

My research is driven by a stark observation - the consequences of an invasive understory species in the coniferous forests of the Pacific Northwest would be devastating to the native plant communities. The Pacific Northwest, in particular the wilderness areas, currently has fewer invasive plant species than any other region in the U.S. (Parks *et al*. 2005). These vast public lands in the Pacific Northwest are a national treasure but may ironically represent a potential threat to native plant communities. On one hand, the large areas of relatively undisturbed land are havens for natural plant communities into which few non-native species have been introduced (Parks *et al*. 2005). However, as human activities encroach upon these wilderness areas, the opportunities for non-native plant introduction increase accordingly (Parks *et al*. 2005). Consequently, these vast public lands potentially pose a problem in that a non-native species might spread for years without detection (Mack *et al*. 2000). Invasive understory species would be particularly difficult to detect because it is unlikely they would be seen aerially and would, therefore, have to be detected through ground surveys. By the time the invasion was discovered, it would likely be too late to eradicate and very costly to control (Simberloff 1997). Predicting which species could become invasive before they are introduced is a much better solution.

Several objectives for this study emerge from the issues raised above. The overall objective was to develop a field-based tool to identify potential invaders among horticultural plants introduced into the Pacific Northwest. First, I evaluated the utility of shade tolerance as a mechanism of understory species exclusion in the Pacific Northwest forests. Additionally, I evaluated the utility of congeneric species as a basis for comparison to predict the likelihood of invasion. Finally, I evaluated the likelihood that China will be a donor of new potentially invasive species to the Pacific Northwest. Specifically:

1. To what extent does light availability in a new range influence (thwart or facilitate) the establishment of these non-native species?
    a. How does shade affect plant growth and survival?
    b. To what extent can these non-native species acclimate to the shade conditions of native forests (leaf morphology , chlorophyll content and photosynthetic characteristics)?
2. Can the presence of a native congener be used to predict the likelihood of invasion by a non-native species? Do congeneric species respond similarly to one another in native conditions?

3. Are Chinese understory species likely to be pre-adapted to the conditions of the forests of the Pacific Northwest? Is there cause for concern about plant introductions from China?
4. Can field experimentation predict the fate (i.e., naturalized, extirpated) of Chinese understory species in the northern Rocky Mountain coniferous forests? Can field trials in these forests provide insight on an experimental protocol that could be widely implemented in the U.S.?

MATERIALS AND METHODS

1. Study Species

I chose four Chinese understory species based on their commercial availability in the U.S. and the occurrence of a native congener in the Pacific Northwest: *Allium tuberosum* Rottler ex Sprengel, *Philadelphus kansuensis* (Rehder) S. Y. Hu, *Spiraea japonica* L. f., and *Spiraea wilsonii* Duthie. Additionally, I chose a bamboo, *Fargesia rufa* Yi (OHRN), due to its commercial availability in the U.S. and the potential risk for bamboo invasion in the U.S. (Mack 2003). Finally I chose three native congeners of the four Chinese species as a basis for comparison of their similarities to the Chinese species: *Allium cernuum* Roth, *Philadelphus lewisii* Pursh, and *Spiraea douglasii* Hook. These native species are all members of coniferous forest communities in the northern Rockies.

Allium cernuum (Liliaceae) is found throughout much of the U. S. (USDA 2003). It is most prevalent in prairies, forests and montane areas on well-drained soils (Seymour 1990, Brenzel 2001). This clump-forming species grows vigorously, producing basal leaves and scapes up to 60 cm tall (Seymour 1990, Brickell and Zuk 1997). As the common name "nodding onion" suggests, this species produces a nodding cluster of pale pink flowers and generally blooms July through October (Seymour 1990, Flora of North America 1993). *Allium cernuum* is deemed a good landscape plant because it is easily cultivated, will spread through both self seeding and from bulb offsets, requires little maintenance and is resistant to parasites and other pests (Missouri Botanical Garden 2006). It tolerates light conditions from full sun to partial shade and requires little moisture (Missouri Botanical Garden 2006). Horticulturalists recommend this species for planting in zones 4-10 (Brickell and Zuk 1997). In the Pacific Northwest *A. cernuum* is common in moist areas (Hitchcock and Cronquist 1973).

Allium tuberosum is native to southwestern Shanxi in China and is now naturalized in southern China (Wu *et al.* 1994). This species is most commonly found under shrubs at 1000-1100 m elevation or under cultivation, where it is called "Chinese chives" (Wu *et al.* 1994). *Allium tuberosum* has been introduced into the United States as a culinary species; it has escaped and can be found along roadsides and other disturbed sites (Flora of North America 1993). It is currently established in Iowa, Nebraska and Wisconsin (USDA 2003). Similar to *A. cernuum*, *A. tuberosum* is a clump former. It produces many gray-green basal leaves and taller flower-bearing scapes up to 46 cm tall (Brenzel 2001). It produces tiny, star-shaped, white flowers that usually appear in loose clusters August through September; *A. tuberosum* is sometimes planted as an ornamental species (Proctor 1997). Horticulturalists recommend planting this species in approximately the same range as *A. cernuum* (zones 4-8); these sources also report the tendency of this species to spread if not carefully controlled (Brickell and Zuk 1997, Missouri Botanical Garden 2006). This species also tolerates full sun to partial shade, requires little moisture and is resistant to parasites and other pests (Missouri Botanical Garden 2006). The similar ecological requirements and tolerances of this species and the native *Allium* as well as its escape risk, make *A. tuberosum* a species of concern for the Pacific Northwest.

Philadelphus lewisii (Hydrangeaceae) is a deciduous shrub with arching branches. Adult plants can be 3 m tall and at least as wide (Brickell and Zuk 1997, Brenzel 2001). This species is native to California, Idaho, Montana, Oregon and Washington (Brenzel 2001, USDA Plants Database 2003). The shrub's racemes of fragrant, broad, white flowers are conspicuous in the early to midsummer (Brickell and Zuk 1997). This shrub is a prized ornamental because it grows vigorously, is hardy in zones 5-8 and is somewhat drought tolerant (Brickell and Zuk 1997). *Philadelphus lewisii* also tolerates shade better than most other flowering shrubs found in the Pacific Northwest (Seymour 1990). In the Pacific Northwest *P. lewisii* occurs from arid steppe to forests dominated by *Pinus ponderosa* or *Pseudotsuga menziesii* (Hitchcock and Cronquist 1973). This species can tolerate diverse habitat conditions such as riparian areas and rocky hillsides and occurs to 2100 m elevation in the Cascade Mountains (Hitchcock and Cronquist 1973).

Philadelphus kansuensis (synonym: *P. pekinensis* Ruprecht var. kansuensis Rehder) is native to the Gansu, Qinghai and Shaanxi Provinces in China (Wu *et al.* 1994). This shrub may be 7 m tall and is found in thickets at 2400 to 3500 m in elevation (Walters *et al.* 1984, Huxley1992, Wu *et al.* 1994). *Philadelphus kansuensis* has large, ovate-lanceolate, dentate leaves that are coarsely haired above (Walters *et al.* 1984, Huxley1992, Wu *et al.* 1994). Racemes of white flowers are produced on bristly flower stalks in midsummer (Walters *et al.* 1984, Wu *et al.* 1994). The flowers are approximately 2.5 cm across each and occur in clusters of five to seven (Walters *et al.* 1984, Huxley1992). *Philadelphus kansuensis* appears to be approximately as hardy as its Pacific Northwest congener, withstanding temperatures to zone 7 (Huxley 1992) or even zone 9 (Walters *et al.* 1984). However, no specific information on the shrub's light or moisture requirements is available. *Philadelphus kansuensis* is not yet widely used as an ornamental species. The ecological similarities between this species and the native *P. lewisii* make it a potential candidate for naturalization in the Pacific Northwest.

Spiraea douglasii (Rosaceae) is an erect shrub that spreads through suckering. It has oblong leaves that are downy above and white beneath (Webster 1897, Brickell and Zuk 1997, Brenzel 2001). It produces purplish pink flowers in dense clusters on terminal panicles to 20 cm long (Brickell and Zuk 1997, Brenzel 2001). *Spiraea douglasii* occurs in coastal ranges from Northern California north to British Columbia and east to the Rocky Mountains (Brickell and Zuk 1997, Brenzel 2001). This species is reported to "sucker freely and can be invasive" (Brenzel 2001). *Spiraea douglasii* shrubs can be up to 2.5 m tall and can form a dense thicket (Webster 1897, Brickell and Zuk 1997, Brenzel 2001). *Spiraea douglasii* prefers acidic soils and abundant moisture (Brenzel 2001). The species is hardy in zones 5-8 and tolerates full to partial sunlight (Brickell and Zuk 1997, Brenzel 2001). In the Pacific Northwest *S. douglasii* occurs from sea level to subalpine habitats and is usually found in swamps, "damp meadows" or riparian sites (Hitchcock and Cronquist 1973).

Spiraea japonica is native to central and southeastern China as well as in Korea and Japan (Wu *et al*. 1994). *Spiraea japonica* is widespread in its native range; it inhabits forested slopes, riverbanks and alpine steppes (Wu *et al*. 1994). It occurs from 700 to 4000 m elevation and is also widely cultivated in China (Wu *et al*. 1994). This is a clump-forming, deciduous shrub (Brickell and Zuk 1997). Adult shrubs are 2 m tall and1.5 m wide (Brickell and Zuk 1997). Variable pink flowers are borne in terminal corymbs up to 20 cm across in mid to late summer (Brickell and Zuk 1997). This species was introduced into the U.S. before1859, and was apparently popular soon after because at least five cultivars were reported by 1897 (Webster 1897). Today this species is described as an "ideal low maintenance tree" because of its rapid growth, small adult height and resistance to pests (Amato 1998). More than 14 cultivars are now recognized (Brenzel 2001). *Spiraea japonica* tolerates a wide range of soil types, tolerates drought and full sun to partial shade; it is hardy in zones 4-9 (Amato 1998, Brickell and Zuk 1997). *Spiraea japonica* is currently found in much of the U.S. (USDA 2003). This species is recognized as invasive by the Southeast Exotic Pest Plant Council and is given the highest ranking of “severe threat” (Southeast Exotic Pest Plant Council1996). USDA plant hardiness zones throughout much of the naturalized range of *S. japonica* are identical to the zones in the Pacific Northwest, suggesting that this species could also become naturalized in this region. The apparent risk of invasion and pre-adaptation for conditions in the Pacific Northwest make it a species of concern for this region.

Spiraea wilsonii is the third *Spiraea* I investigated; it is native to Gansu, Guizhou, Henan, Hubei, Shaanxi, Sichuan and Yunnan Provinces of China (Wu *et al.* 1994). This species occurs in forests, on rocky slopes and along roadsides at elevations of 1000 to 3200 m (Wu *et al.* 1994). This spreading shrub produces many arching branchlets and typically stands 1.5 to 2.5 m tall (Walters *et al.* 1984, Huxley1992, Wu *et al.* 1994). The shrub has small, obovate leaves with a few teeth at the leaf’s distal end (Walters *et al.* 1984, Huxley1992, Wu *et al.* 1994). The white flowers (6 mm diameter) bloom in mid summer on short side shoots with terminal corymbs (4.5 cm diameter) (Walters *et al.* 1984, Wu *et al.* 1994). No information is available on this species’ light or moisture requirements, but the varied native habitat suggests that it can withstand conditions from full to partial sun and may be drought tolerant. The first record of introduction of this species into the U.S. was made in 1900 (Rehder 1949); I am unaware of any reports of this species escaping cultivation (USDA 2003). Only one mention of *S. wilsonii* is found in the traditional horticultural references suggesting that it has not yet been widely introduced. Its ecological similarity to native *Spiraea* warrants its evaluation in this study.

Fargesia rufa (Poaceae) is a temperate bamboo that is native to forests in the Gansu and Sichuan Provinces in China at 1,000-2,500 m elevation (Whittaker 2005). Unlike tropical bamboos, this species tolerates high-altitude winters and is hardy to -20^0C (zone 6) (Whittaker 2005). Consequently, *F. rufa* may be ideal for gardens in the Pacific Northwest and propagation of this species has been rapid since its introduction in the U.S. in 1995 (Whittaker 2005). The flora of the Pacific Northwest includes no bamboos, so no congener was included in this study. *Fargesia rufa* may grow up to 3.5 m tall but it is usually recommended for shorter hedges due to its low growth habit (Whittaker 2005). The culms are rarely greater than 1 cm in diameter (Whittaker 2005). *Fargesia rufa* reportedly tolerates full sun to partial shade and produces many new culms annually; the number of culms can increase ten-fold in three years (Whittaker 2005). This astounding growth rate and ability to tolerate temperate climates makes *F. rufa* a potential candidate to become invasive in the Pacific Northwest.

2. Plant Material

Native *Allium cernuum*, *Philadelphus lewisii*, and *Spiraea douglasii* seedlings were purchased from Plants of the Wild Nursery (Tekoa, WA) on 4 March 2006. Each seedling was immediately transplanted to a one-gallon pot and was grown in a greenhouse at Washington State University. Plants of all three species were kept dormant at 5 ^{0}C night and 15 ^{0}C day temperatures until 25 February 2006, when the average greenhouse temperatures were gradually increased from 5 ^{0}C night and 15 ^{0}C day temperatures to 15 ^{0}C night and 20 ^{0}C day temperatures in three, 5 ^{0}C incremental steps of approximately one month each through 18 May 2006.

Four pots of *Fargesia rufa* were obtained from Heronswood Nursery (Kingston, WA) in late November, 2005. *Fargesia rufa* culms were kept dormant in 5 ^{0}C night and 15 ^{0}C day temperatures until 25 February 2006, when the average greenhouse temperatures were gradually increased in the same procedure as described above. On 25 February 2006, the culms were divided into 36 plants of approximately equal size, and each was transplanted into a one-gallon pot.

The other non-native species were obtained as seeds from several arboreta (see below). All seedlings were grown in a greenhouse at Washington State University in a mixture of 50% Sunshine LC-1 potting soil and 50% sand.

Seeds of *Philadelphus kansuensis* and *Spiraea japonica* were collected at the Morris Arboretum (Philadelphia, PA) in fall, 2005. *Philadelphus kansuensis* seeds were sown directly into flats of moist soil in December, 2005 and grown under approximately 15 ^{0}C night and 20 ^{0}C day temperatures. On 4 March 2006, seedlings were transplanted into one-gallon pots. *Spiraea japonica* seeds were scattered on flats of moist soil in early December, 2005 and were then stratified in the greenhouse at 5 ^{0}C for six weeks (December 2005 and January 2006). On 27 January 2006, the flats were transferred to a greenhouse bay with approximate 15 ^{0}C night and 20 ^{0}C day temperatures. On 4 March 2006, seedlings were transplanted to one-gallon pots.

Seeds of *Allium tuberosum* were collected at the National Arboretum (Washington, D.C.) in fall, 2005. *Allium tuberosum* seeds were sown directly into flats of moist soil in March 2006 and grown in approximately 15 ^{0}C night and 20 ^{0}C day temperatures. On 30 March 2006 seedlings were transplanted to one-gallon pots.

Seeds of *Spiraea wilsonii* were collected at the Arnold Arboretum (Boston, MA) in fall, 2005. *Spiraea wilsonii* seeds were scattered on moist soil and stratified in the greenhouse at approximately 5 ^{0}C for six weeks in December 2005 and January 2006. On 27 January 2006, the flats were transferred to a room with approximate 15 ^{0}C night and 20 ^{0}C day temperatures. On 4 March 2006, seedlings were transplanted to one-gallon pots.

All species were watered as needed and fertilized approximately every two weeks between 25 Feb and 18 May 2006 with Peter's fertilizer (20-20-20 percent composition, NPK) at

500ppm. On 18 May 2006, the plants were removed from the greenhouse and placed in a lathe house for two weeks to acclimate to ambient conditions.

3. Field Sites

In spring 2005, I established ten plots in which to characterize the light regime found in Pacific Northwest coniferous forests. The study sites included the Washington State University Hudson Biological Reserve and Lyle Grove Reserve (Whitman Co., WA, USA), the University of Idaho Experimental Forest (Latah Co., ID, USA) and the Priest River Experimental Forest (table 1). These sites collectively contain an array of forest habitat types (h.t.) (*sensu* Daubenmire and Daubenmire 1968) and late seral/mature stands. The ten stands, two in each of five habitat types, were chosen to evaluate variation in light reaching the understory across an environmentally broad array of coniferous forests in the Pacific Northwest: *Pinus ponderosa*/*Symphoricarpos albus* h.t. (Hudson Biological Reserve and Lyle Grove Reserve), *Pseudotsuga menziesii*/*Physocarpus malvaceus* h.t. and *Abies grandis*/*Pachistima myrsinites* h.t. (University of Idaho Experimental Forest),and *Tsuga heterophylla*/*Pachistima myrsinites* h.t. and *Abies lasiocarpa*/*Pachistima myrsinites* h.t. (Priest River Experimental Forest). Each stand is approximately 0.5 ha and is surrounded by a 45-m buffer of the same habitat type. Slope was measured using an Abney level and aspect was measured using a compass for each of the ten stands (table 1).

4. Light Measurements

In each stand, I delineated two parallel 50-m transects approximately 25-m apart along the contour and marked them with flagging. The light regime was characterized in each stand during the peak growing seasons with an AccuPAR Linear Par Ceptometer (Decagon Devices, Pullman, WA). The peak growing seasons were defined as April-October in *Pinus ponderosa/Symphoricarpos albus* h.t., *Pseudotsuga menziesii/Physocarpus malvaceus* h.t. and *Abies grandis/Pachistima myrsinites* h.t. stands and June-September in *Tsuga heterophylla/Pachistima myrsinites* h.t. and *Abies lasiocarpa/Pachistima myrsinites* h.t. stands. I visited each site monthly on clear days between 1000 and 1400 hrs PST and recorded light levels at ten locations along a transect outside of the canopy to measure full sunlight. Data from each location is an average of 10 readings over 5 seconds averaged over 8 photodiodes along the 80-cm long ceptometer. After measuring the points outside the canopy, I measured100 points at one-meter intervals along the two, 50-m transects within the stands and then repeated the ten full-sunlight measurements outside the canopy. Finally, I averaged the full sunlight measurements and compared those data to the measurements under the canopy to calculate percent transmittance of light to the understory (percent transmittance = understory PAR/average overstory PAR). Percent shade was then calculated as the percent of light not transmitted to the understory (percent shade = 1 – percent transmittance). The five-number summary, mean and standard deviation were calculated for the percent shade of each habitat type and all habitat types were compared in an ANOVA followed by Tukey's Pairwise Means Comparison Test ($p < 0.05$). using JMP statistical software (SAS Institute 2004).

5. Shade Treatments

Shade experiments were conducted on the Washington State University campus from 30 May-15 August 2006. Two shade treatments were chosen based on preliminary percent shade data collected in 2005 during the growing season to approximate the light levels found in the five representative forest understories. Shade structures (2.4 m x 2.4 m x 1.2 m high) were constructed in May 2006 with ‘70%’ and ‘90%’ black knitted shade cloth (Gothic Arch Greenhouses, Mobile, AL), over PVC supports and fence post anchors. Each shade structure was left uncovered by shade cloth from 0-60 cm above the ground to allow air circulation. This gap was enclosed with hardware cloth as a rodent barrier. The experiment consisted of six replicate shade structures for each of the two light treatments for a total of 12 shade structures. The 12 shade structures were placed randomly in a 30 m x 30 m area such that the structures did not shade each other (fig. 1).

Actual shade values were recorded on four clear days throughout the experiment with an AccuPAR Linear Par Ceptometer (Decagon Devices, Pullman, WA) to ensure that the shade values were consistent throughout the experiment. Measurements were made hourly between 0900 and 1400 PST, both inside and outside each structure on each of the four days. Each measurement consisted of one measurement inside the structure (an average of 10 readings in 5 seconds) followed immediately by one measurement outside the structure. Percent shade was calculated as described for forest percent shade calculations. The five-number summary, mean and standard deviation were calculated for the percent shade of each shade structure type using JMP statistical software (SAS Institute 2004).

On 30 May 2006, three individuals of each plant species were randomly assigned in a restrictedly randomized design to each of the 12 shade structures. I selected one individual of each species randomly to be harvested for biomass measurements. The remaining individuals were repotted into two-gallon pots and placed in the structures. Individuals were rotated within each enclosure bi-monthly. Plants were watered daily as needed throughout the experiment and were fertilized biweekly, beginning 10 July 2006 with Peter’s 20-10-20 NPK at 200ppm.

Although plants in the ‘90%’ shade treatment often required less water than those in the ‘70%’ shade treatment, species were fertilized equally in both treatments. Species requiring more water were additionally watered with fertilizer-free water. The shade cloth was also occasionally sprayed with water to remove debris that might alter the shade values. Mouse and rat traps were regularly baited in each structure to minimize damage due to rodent foraging.

6. Growth Measurements and Biomass Allocation

Branch number and length of each individual plant were recorded on 6 June 2006,1 July 2006 and 1 August 2006. When the distinction between a branch and an offshoot was not apparent, only shoots off the main stem were counted as branches. This measure, while not absolute, yields consistent results within a species without destructive sampling (Sanford *et al.* 2003). All branches on each individual were summed as an approximation of overall elongation of the species. Relative Growth Rates by Height (RGRHs) were calculated between the June and July, July and August, and overall sampling dates and were expressed in cm cm^{-1} $week^{-1}$ [RGRH $= (\ln H_2 - \ln H_1)/(t_2-t_1)$; where H_1 = earlier recorded height, H_2 = later recorded height and t = time] (Sanford *et al.* 2003).

One individual of each species in each shade structure was randomly selected for destructive sampling on 6 June 2006 and 1 August 2006. Leaves were stripped from each replicate and leaf area was calculated for all 12 individuals of each species with an Li-3000 Portable Area Meter (LI-COR Biosciences, Lincoln, NE USA). Stems were clipped at the soil surface and placed in a paper bag with its detached leaves for drying. All biomass measurements reflect above-ground characteristics only, as roots were discarded. Leaves and stems were oven-dried (70 ^{0}C for 48 hrs) and weighed. Relative growth rates were calculated for above-ground biomass between the June and August destructive sampling dates and were expressed in g g^{-1} $week^{-1}$ [RGR = (ln W_2 – ln W_1)/(t_2-t_1); where W_1 = weight at week 1, W_2 = weight at week 8 and t = time] (Hunt 1990). At the conclusion of the experiment, each plant was compared to the average mass for the species at the beginning of the study to calculate individual RGR. Specific leaf area was also calculated for the 6 June and 1 August 2006 samples and was expressed in cm^2 g^{-1} [SLA = LA/ LW; where LA = leaf area and LW = leaf weight] (Davidson *et al.* 2002).

Growth (RGR and RGRH) characteristics were analyzed using the Wilcoxon/Kruskal-Wallis alternative to the t-test due to concerns that the assumptions for valid use of the parametric procedures were violated due to sample size. Biomass allocation (SLA) was analyzed using ANOVA followed by Tukey's Pairwise Means Comparison Test ($p < 0.05$). JMP statistical software was used for all statistical analyses (SAS Institute 2004).

7. Chlorophyll Analysis

Chlorophyll (Chl) content was measured from one newly-emerged, fully-expanded leaf from each harvested plant on 6 June 2006 and 1 August 2006. Each excised leaf was photographed for analysis of leaf area using digital imaging (ImageJ 1.36b, NIH, USA) and placed into a 20-dram glass vial. The vials were placed in a cool, dark container for transport to the lab within eight hours. Each vial was then filled with 20 ml of 95% ethanol and tightly capped. The vials were stored at room temperature in the dark for seven days and agitated periodically to ensure complete chlorophyll extraction. Chlorophyll extraction was deemed complete when the remaining leaf was colorless. If 20 ml of ethanol was insufficient to completely extract the chlorophyll, the ethanol-Chl solution was decanted and the leaf was treated with 20 ml of fresh ethanol. This process was repeated as necessary to ensure complete extraction of chlorophyll for larger leaves and the ethanol-Chl solution from each extraction for each leaf was combined at the end of the seven days.

Absorbances of the ethanol-Chl solution at 665 and 649 nm were measured spectrophotometrically with a Perkin-Elmer 552A UV/VIS spectrophotometer (PerkinElmer Optoelectronics, Fremont, CA). The following equations were used to determine the chlorophyll a, chlorophyll b and total chlorophyll contents (Wintermans and De Mots 1965):

a. $\mu\text{g Chl a/ml solution} = (13.70 * A_{665\text{ nm}}) - (5.76 * A_{649\text{ nm}})$

b. $\mu\text{g Chl b/ml solution} = (25.80 * A_{649\text{ nm}}) - (7.60 * A_{665\text{ nm}})$

c. $\mu\text{g Chl a+b/ml solution} = (6.10 * A_{665\text{ nm}}) + (20.04 * A_{649\text{ nm}})$

Chlorophyll concentrations were then multiplied by the leaf area of each sample and expressed in $\mu g/cm^2$. Chlorophyll *a*, *b* and total chlorophyll per leaf area were analyzed using ANOVA followed by Tukey's Pairwise Means Comparison Test ($p < 0.05$). JMP statistical software was used for all statistical analyses (SAS Institute 2004).

8. Gas Exchange Measurements

The response of net CO_2 assimilation (A) to Photosynthetic Photon Flux Density (PPFD) was measured through gas exchange early and late in the summer, approximately 6 weeks apart, for *P. lewisii* and *S. japonica*. Gas exchange was measured for *P. lewisii* 6 June 2006 through 8 June 2006 and again on 13 July 2006 through 21 July 2006. Gas exchange was measured for *S. japonica* 16 June 2006 through 19 June 2006. Due to equipment malfunctions and unexpected species' sensitivity to the experimental conditions, no gas exchange data were generated for the other study species or for the late summer *S. japonica* measurement. Gas exchange measurements were made with an Lc*pro*+ portable photosynthesis system on the newest fully-emerged leaf of each replicate (ADC BioScientific Ltd., Herts, England). Before each measurement, the Lc*pro*+ was calibrated and the chemicals were replaced if not fully active. *Philadelphus lewisii* measurements were conducted in the broad leaf cuvette; *S. japonica* measurements were conducted in the conifer cuvette. At 1600 on the day previous to measurement, each plant was placed on a table in the shade for ease of measurement. All measurements were made between 600 and 1400 PDT and each replicate was allowed a 20 min. induction period at 1000 PPFD. After the induction period, PPFD was decreased in a stepwise fashion from 1500 PPFD to 0 PPFD. At each step, the leaves were allowed to equilibrate for 10 minutes before measurements were made. The cuvette was wrapped in black cloth for the dark respiration measurement (0 PPFD). The leaf selected for gas exchange measurement was removed from the plant following the measurement and photographed for analysis of leaf area using digital imaging (ImageJ 1.36b, NIH, USA). Rates of gas exchange were corrected based on the actual area of the leaf in the cuvette. Immediately following measurement, plants were returned to the assigned treatment.

RESULTS

1. Shade Regime in Pacific Northwest Coniferous Forests

Median percent shade in the five habitat types ranged from 84% to 98% shade (table 2). Mean percent shade values ranged from 70% to 93% and were lower than the median values because of sunflecks through gaps in the canopy. Stands in the *Pinus ponderosa/Symphoricarpos albus* habitat type displayed the lowest percent shade. The *Abies grandis/Pachistima myrsinites* habitat type was significantly shadier than the *P. ponderosa/S. albus* habitat type. Stands in the *Tsuga heterophylla/Pachistima myrsinites* habitat type were the shadiest of all the habitat types. Light levels in the *Pseudotsuga menziesii/Physocarpus malvaceus* and *Abies lasiocarpa/Pachistima myrsinites* habitat types were not significantly different from each other and fell in between the *A. grandis/P. myrsinites* and *T. heterophylla/P. myrsinites* habitat types in mean percent shade.

2. Experimental Shade Structures

The '70%' shade structures provided 78.25% ± 3.15% shade, while the '90%' shade structures provided 93.59% ± 1.14% shade (table 3). The nominal '70%' and '90%' shade treatments will be referred to as "78%" and "94%," respectively. The percent shade in the shade structures approximated the lower and upper ranges of the shade regime in the five habitat types included in this study (see table 2)

The rodent barriers in each structure proved sufficient, as there was no rodent damage on any of the plants throughout the course of the experiment. There was no evidence of any parasite or predator damage, and no plants died throughout the experiment.

3. Allium cernuum **and** *Allium tuberosum*

Both the native *Allium cernuum* and the non-native *A. tuberosum* had greater relative growth rates for above-ground biomass (RGR) in the 78% treatment than the 94% treatment (p=0.0453 and p=0.0063, respectively) (fig. 2). However, *A. tuberosum* achieved greater growth rates than the native congener in both treatments (78% p=0.0051, 94% p=0.0050).

Allium cernuum added more leaf length between June and July in the 78% treatment than in the 94% treatment (p=0.0082), but otherwise showed no significant differences in relative growth rates by height (RGRH) between treatments (see Appendix 1) (fig. 3). Leaf elongation in *A. tuberosum* was not significantly different at any time during the study (see Appendix 1). However, the leaves of *A. tuberosum* grew more rapidly than the leaves of the native congener at all times in both shade treatments (see Appendix 1).

Specific leaf area (SLA) was not significantly different in the 78% or 94% shade treatment from the pre-study SLA for *A. cernuum* (see Appendix 2) (fig. 4). However, *A. tuberosum* showed higher SLA in both the 78% and 94% treatment compared to the pre-study SLA (p=0.0053). Moreover, *A. tuberosum* had significantly higher SLA in both the 78% and 94% treatments than the native congener (p=0.0306 and p=0.0051, respectively).

Neither *A. cernuum* nor *A. tuberosum* exhibited significant changes in Chlorophyll *a* content throughout the study (see Appendix 3) (fig. 5a). *Allium cernuum* and *A. tuberosum* did not significantly differ from one another in Chl *a* levels in the 78% or 94% shade treatment (see Appendix 3).

Allium cernuum showed a significant reduction in Chl *b* in both shade treatments compared to the pre-study levels (p=0.0007) while *A. tuberosum* exhibited no significant changes (p=0.4380) (fig. 5b). *Allium cernuum* began the study with significantly higher Chl *b* levels than the non-native congener, but this significant difference was lost when the species were subjected to the shade treatments (see Appendix 3).

Overall, *A. cernuum* had significantly more total Chl before the study than at the conclusion of the study in either shade treatment (p=0.0002) (fig. 5c). Total Chl levels in *A. tuberosum* did not change significantly throughout the study and were not affected significantly by the shade treatments (p=0.2725). Although *A. cernuum* began the study with more total Chl than the non-native congener (p<0.0001), this significant difference did not persist when the species were grown in 78% or 94% shade (see Appendix 3).

The non-native species entered the study with a significantly higher Chl *a:b* ratio than the native species (p=0.0051), but this significant difference was not seen in either of the shade treatments (see Appendix 3) (fig. 6). The Chl *a:b* ratio rose significantly in both shade treatments for the native *A. cernuum* (p=0.0138) but did not change significantly for *A. tuberosum* throughout the study (p=0.2265).

4. Philadelphus lewisii **and** *Philadelphus kansuensis*

The native *Philadelphus lewisii's* growth rate in the higher light treatment was significantly greater than its RGR for above-ground biomass in the higher shade treatment (p=0.0082) (fig. 7). There was no evidence that *P. kansuensis* grew more rapidly in either shade treatment (p=0.1282). There were no significant differences in growth rate between the two species within each shade treatment (see Appendix 1).

There were no significant differences in rate of branch elongation (RGRH) between the 78% and 94% shade treatment for either species (see Appendix 1) (fig. 8). *Philadelphus kansuensis* had a significantly greater RGRH than *P. lewisii* between July and August in the 94%

shade treatment (p=0.0051), but overall, the congeners did not grow at significantly different rates from one another in the 94% shade treatment (p=0.1282). *Philadelphus kansuensis* also had a significantly greater RGRH than *P. lewisii* between July and August in the 78% shade treatment (p=0.0081). This difference led to significantly more rapid growth overall in the 78% shade treatment for the non-native species compared to the native species (p=0.0081).

Philadelphus lewisii exhibited the highest SLA values before the study, intermediate SLA values in the 94% shade treatment and the lowest SLA values in the 78% shade treatment (p=0.0007) (fig. 9). In contrast, *P. kansuensis* exhibited the lowest SLA values before the study, intermediate SLA values in the 78% shade treatment and the highest SLA values in the 94% shade treatment (p=0.0079). The native species had significantly higher pre-study SLA values than the non-native species but concluded the study with significantly lower SLA values than the non-native species in both shade treatments (see Appendix 2).

Both *P. lewisii* and *P. kansuensis* had significantly less Chl *a* before the study than at its conclusion (p=0.0004 and p=0.0271, respectively) (fig. 10a). In *P. kansuensis*, the largest increase in Chl *a* content occurred in the 78% shade treatment, while the increase in the 94% shade treatment was intermediate. The non-native *P. kansuensis* had significantly more Chl *a* than the native *P. lewisii* at the outset of the study (p=0.0304). No significant differences were observed between the two species in the 78% shade treatment (p=0.2980). However, in the 94% shade treatment, the native species had significantly more Chl *a* than the non-native species (p=0.0453).

Similar to Chl *a* content, both *P. lewisii* and *P. kansuensis* had significantly more Chl *b* at the conclusion of the study than at its beginning (p=0.0044 and p=0.0279, respectively) (fig. 10b). In both species, the most Chl *b* occurred in the 94% shade treatment while the levels in the

78% shade treatment were intermediate. No significant differences in levels of Chl *b* were observed between the species in either shade treatment (see Appendix 3).

The patterns observed for total Chl content in *P. lewisii* and *P. kansuensis* were almost identical to the patterns for Chl *a* content (fig. 10c). Total Chl content increased significantly throughout the course of the study in both *P. lewisii* and *P. kansuensis* (p=0.0005 and p=0.0191, respectively). No significant differences in total Chl content between the species were detected before the study or in the 78% shade treatment (see Appendix 3), but the native species had significantly more total Chl than the non-native species in the 94% shade treatment (p=0.0453).

There were no significant differences in *Chl a:b* ratio within species or treatments for *P. lewisii* or *P. kansuensis* (see Appendix 3) (fig. 11).

5. *Spiraea douglasii* and *Spiraea japonica*

The native *Spiraea douglasii* grew significantly more rapidly for above-ground biomass (RGR) in the 78% shade treatment than the 94% shade treatment (p=0.0358) (fig. 12). In contrast, the non-native *S. japonica's* growth rate did not differ significantly between the 94% shade treatment and the 78% shade treatment (p=0.0656). The native species grew significantly more rapidly the non-native species in the 78% shade treatment (p=0.0358) but not in the 94% shade treatment (p=0.5752).

The two shade levels did not affect branch elongation (RGRH) differently for either species as there was no evidence of significantly different growth rates in the 78% and 94% shade treatments (see Appendix 1) (fig. 13). *Spiraea douglasii* elongated significantly more rapidly than *S. japonica* between July and August in the 78% shade treatment (p=0.0306). This difference led to significantly greater RGRH overall in the 78% shade treatment for the native species compared to the non-native species (p=0.0306). No differences in the rate of branch elongation were detected between the two species in the 94% shade treatment.

Specific leaf area decreased significantly in both *S. douglasii* and *S. japonica* during the study (p=0.0094 and p=0.0010, respectively) (fig. 14). Specific leaf area in *S. douglasii* decreased significantly from the pre-study value in both shade treatments. The lowest SLA in *S. japonica* was seen in the 78% shade treatment while the SLA in the 94% shade treatment was intermediate. In all cases, the SLA in the non-native *S. japonica* was significantly higher than the native *S. douglasii* (pre-study p=0.0101, 78% p=0.0137 and 94% p=0.0051).

Chlorophyll *a* content increased through the study in both *S. douglasii* and *S. japonica* (p=0.0346 and p=0.0052, respectively) (fig. 15a). The lowest levels of Chl *a* in *S. douglasii* were observed before the study, the highest levels occurred in the 78% shade treatment and the 94% shade treatment levels were intermediate to the other two values. *Spiraea japonica* exhibited significantly higher levels of Chl *a* in both shade treatments over the pre-study levels. *Spiraea douglasii* had significantly more Chl *a* than *S. japonica* before the study began (p=0.0127), but no significant differences were observed between the species in either shade treatment (see Appendix 3).

Chlorophyll *b* content increased through the study in *S. douglasii* and *S. japonica*, but the difference for *S. douglasii* may not be significant (p=0.1299 and p=0.0030, respectively) (fig. 15b). No significant differences were observed in Chl *b* levels between the species before the study began (p=0.1166). The non-native *S. japonica* had significantly higher Chl *b* levels in the 94% shade treatment than the native *S. douglasii* (p=0.0202). There was no significant difference between the two species in the 78% shade treatment (p=0.5752).

The patterns observed for total Chl content in *S. douglasii* and *S. japonica* were identical to the patterns for Chl *a* content (p=0.0594 and p=0.0054, respectively) (fig. 15c). Total chlorophyll content increased significantly throughout the study for both species as described in the pattern for Chl *a*. *Spiraea douglasii* entered the study with significantly more total Chl than did *S. japonica* (p=0.0247) but this significant difference did not persist in either shade treatment (see Appendix 3).

Finally, the Chl *a:b* ratio for *S. douglasii* did not change signiciantly throughout the study (p=0.4769) but *S. japonica's* Chl *a:b* ratio decreased in the 94% shade treatment (p=0.0022) (fig. 16). Both before and during the study in both treatments, the non-native *S. japonica* had a significantly lower Chl *a:b* ratio than its native congener (pre-study p=0.0321, 78% p=0.0131, 94% p=0.0051).

6. *Spiraea douglasii* and *Spiraea wilsonii*

All within species comparisons for the native *S. douglasii* were stated in the above section and will not be restated here. There was no evidence that *S. wilsonii* grew at a significantly different rate for above-ground biomass (RGR) in the 78% shade treatment than in the 94% shade treatment (p=0.2971) (fig. 17). Neither species grew significantly more quickly than the other in the 94% treatment (p=0.6884), but the native *S. douglasii* had a significantly greater RGR than the non-native *S. wilsonii* in the 78% shade treatment (p=0.0358).

Branch elongation (RGRH) in *S. wilsonii* did not differ significantly in the 78% and 94% shade treatments throughout the study (p=0.1282) (fig. 18). *Spiraea douglasii* and *S. wilsonii* exhibited similar patterns of branch elongation in the 94% shade treatment (p=0.2980). However, the native *S. douglasii* grew more rapidly between July and August in the 78% shade treatment than the non-native *S. wilsonii* (p=0.0453), leading to an overall greater native RGRH in the 78% shade treatment (p=0.0051).

Specific leaf area in *S. wilsonii* was significantly higher before the study and in the 94% shade treatment than in the 78% shade treatment (p=0.0080) (fig. 19). There was no evidence that the species exhibited significantly different SLA values from each other before the study or in either shade treatment (see Appendix 2).

Spiraea douglasii and *S. wilsonii* exhibited approximately the same patterns as each other in Chl *a* content throughout the study (fig. 20a*)*. *Spiraea wilsonii* began the study with the lowest Chl *a* content, exhibited significantly higher Chl *a* content in the 94% shade treatment and the highest Chl *a* content in the 78% shade treatment (p=0.0007). However, at no time during the study did the Chl *a* contents differ significantly between the two species (see Appendix 3).

The two species exhibited slightly different patterns in Chl *b* content (fig. 20b). Chlorophyll *b* content in *S. wilsonii* increased significantly in both shade treatments over the pre-study levels (p=0.0002). Although the Chl *b* content was not significantly different in either species before the study or in the 94% shade treatment (see Appendix 3), the non-native *S. wilsonii* contained more Chl *b* in the 78% shade treatment than the native *S. douglasii* (p=0.0306).

Overall, *S. douglasii* and *S. wilsonii* did not differ significantly from each other in levels of total Chl throughout the study (see Appendix 3) (fig. 20c*)*. *Spiraea wilsonii* exhibited significant stepwise differences in total chlorophyll content from the lowest pre-study levels to the intermediate levels in the 94% shade treatment to the highest levels in the 78% shade treatment (p=0.0005).

Chl *a:b* ratios did not differ significantly for *S. douglasii* throughout the study (p=0.4769) (fig 21). In contrast, *S. wilsonii* exhibited reduced Chl *a:b* ratios in both shade treatments compared to the pre-study ratio (p=0.0007). Before the study began, the non-native *S. wilsonii* had a higher Chl *a:b* ratio than the native *S. douglasii* (p=0.0321), but this pattern was reversed in the 94% shade treatment (p=0.0202).

7. Fargesia rufa

No significant differences in relative growth rate for above-ground biomass (RGR) in *F. rufa* were detected between the two shade treatments. However, these data were unreliable because the *F. rufa* culms varied widely in initial size and have been omitted. The shade treatments did not cause significant differences in the rate of branch elongation (RGRH) in this species (see Appendix 1) (fig. 22).

No significant differences in SLA (p=0.0.4144) were detected between the two shade treatments for this species (fig. 23). Chlorophyll *a* in *F. rufa* increased significantly in both the 78% and 94% shade treatments over the pre-study levels (p=0.0056) (fig. 24). Conversely, Chl *b* in *F. rufa* decreased significantly in both shade treatments compared to the pre-study levels (p=0.0391). These differences effectively cancelled each other, and total Chl content in this bamboo did not change significantly throughout the study (p=0.6977). However, Chl *a:b* ratios did change significantly during the study: the Chl *a:b* ratio was higher in both shade treatments compared to the pre-study ratio (p=0.0021) (fig. 25).

DISCUSSION

1. The Role of Light in Thwarting or Facilitating Establishment of Non-native Species

a. Shade in native habitat types and experimental treatments

The habitat types fall out along an environmental gradient from low shade, low elevation, drier sites to higher shade, high elevation, mesic sites: *Pinus ponderosa/Symphoricarpos albus, Pseudotsuga menziesii/Physocarpus malvaceus, Abies grandis/Pachistima myrsinites*, *Tsuga heterophylla/Pachistima myrsinites* and *Abies lasiocarpa/Pachistima myrsinites* (U.S. Department of Commerce 1960, Daubenmire 1966, Daubenmire and Daubenmire 1968). It is not surprising that the shade levels correspond with altitude and moisture levels since the three are inextricably linked. Habitat types at higher altitudes are invariably cooler than those at lower elevations. Since the habitat types at higher elevations are cooler, the amount of precipitation they receive is exaggerated because less moisture is lost to evaporation. In addition, denser tree canopies prevent more evaporation than sparse tree canopies, further exaggerating these differences in moisture retention (Geiger 1965). The resulting differences in effective precipitation create a steep moisture gradient between central Washington and northern Idaho. As a result, many discrete habitat types occur in a relatively small area along this effective precipitation gradient (Daubenmire 1966, Daubenmire and Daubenmire 1968). The interaction of the altitude, moisture, percent shade largely determines the distribution of species in these habitat types.

The median percent shade in the habitat types ranged from 84% to 98%; light availability is limited in these forests. I conclude that any established understory species in these habitats must be tolerant of these levels of shade unless they can persist in canopy gaps. The 78% and

94% experimental shade structure chosen for this experiment loosely approximate the lower and upper ranges of shade in the coniferous forests of eastern Washington and Northern Idaho. Consequently, the results of this study should reliably predict whether the study species could tolerate the shade levels in these forests.

b. Evidence from relative growth rates

Among the most intuitive measures of shade tolerance are survival, growth and reproduction of a plant grown in a shade treatment. No mortality was observed in either shade treatment throughout the course of the study. This result indicates that all of the study species can withstand 78% and 94% shade at least in the short term. However, a closer look at the relative growth rates of each species indicated that this shade tolerance might not persist on a longer time scale for all study species.

Both *Allium cernuum* and *Allium tuberosum* grew more rapidly in the 78% shade treatment than in the 94% shade treatment indicating that the dense shade of the higher altitude habitat types of the Pacific Northwest would be limiting to these species. However, the non-native *A. tuberosum* grew at approximately twice the rate of the native *A. cernuum* in both shade treatments. This result suggests that *A. tuberosum* is a more shade-tolerant species than the native species and might be able to produce more above-ground biomass than the native species in any of the habitat types of the Pacific Northwest.

Philadelphus lewisii and *Philadelphus kansuensis* did not differ significantly from one another the 78% and 94% shade treatment in terms of growth rate. However, the native *P. lewisii* grew more rapidly in the lower shade treatment than in the higher shade treatment, indicating that this species is only partially shade tolerant. In contrast, the non-native *P. kansuensis* grew approximately as rapidly in the 94% shade treatment as in the 78% shade treatment indicating that it is more shade tolerant than its native congener. If the two species occurred in a severely light-limited environment, the non-native species might be able to produce more above-ground biomass than the native species.

The non-native *Spiraea japonica* and *S. wilsonii* do not appear to be as well adapted to these Pacific Northwest forests as the native *S. douglasii*. Although both *S. japonica* and *S. wilsonii* grow more rapidly in the 78% shade treatment than in the 94% shade treatment, they are outstripped in growth rate in the 78% shade treatment by *S. douglasii*. Neither *S. japonica* nor *S. wilsonii* is likely to produce more above-ground biomass than the native species in the less shady habitats of the Pacific Northwest. None of the species grew significantly more rapidly in the 94% shade treatment than the other species, but since *S. douglasii* is rarely found in the shadier habitats (Hitchcock and Cronquist 1973), it is unlikely that either of the non-native species would grow in the more densely shaded habitats of the Pacific Northwest in which they were introduced.

These results are similar to numerous studies of plant growth rates in varying degrees of shade (Pierson *et al.* 1990, Pattison *et al.* 1998, Baruch *et al.* 2000, Naumburg *et al.* 2001 and others). For each species, the trends indicate that less above-ground biomass is produced in the denser shade treatment than in the lighter shade treatment, resulting in slower relative growth rates. The more important evaluation, however, is the relative reduction in growth rate of a species compared to the reduction in growth rate of its closely-related congener. The species that maintain higher relative growth rates than their congeners are more likely to be good competitors. For example, in a similar shade study of a current Hawaiian invasive woody perennial, *Bidens pilosa*, and its native congener, *B. sandwicencis*, the invasive species had relative growth rates approximately three times higher than the native species (Pattison et al. 1998).

In terms of relative growth rate, *A. tuberosum* stands out as the largest threat with growth rates approximately 50% higher than the native species in both shade treatments. *Philadelphus kansuensis* did not differ significantly in growth rate from the native congener, *P. lewisii*, but was not limited in growth rate by the higher shade treatment. Both non-native *Spiraea* species tended to have equal or lower growth rates than the native species so these species are not likely to outcompete their native counterpart.

c. Evidence from relative growth rates by height

Another intuitive measure of the extent of pre-adaptation to environmental conditions is the rate at which the leaves or branches elongate. This measure has the added advantage that it is non-destructive such that the measure can be repeated through time to see if the effects of shade treatment change through time.

Allium tuberosum showed greater rates of leaf elongation than its native counterpart, *A. cernuum*, throughout the summer in both shade treatments. *Allium cernuum* grew more rapidly in the 78% shade treatment than the 94% shade treatment between June and July, but this trend did not continue into August. *Allium cernuum* probably does not tolerate the shadier conditions as well as does the non-native species. *Allium tuberosum*, in contrast, grew as rapidly in the lower shade treatment as in the higher shade treatment and its growth rate was about twice as rapid overall compared to the native species.

Philadelphus kansuensis showed greater overall rates of branch elongation in the 78% shade treatment than its native counterpart. No significant differences in branch elongation rates between the two species were observed between June and July, but a different trend emerged at the end of the summer. Between July and August, the non-native species grew about twice as rapidly as the native species. This result is difficult to interpret, as the difference may simply be a result of the species having different phenolgies. Alternatively, this later growth spurt in *P. kansuensis* may indicate that the species has acclimated to the environment and is now capable of more rapid growth rates. A final explanation could be that the species is so light limited that a switch in biomass allocation occurred. One symptom of a shade-intolerant species under shade stress is rapid branch elongation, which may maximize the likelihood that it will intercept light (Pothier and Prévost 2002). If this is the case, then *P. kansuensis* is not well suited for these habitat types because it is unlikely to scavenge enough light in the understory through rapid branch elongation. Because little is known about the life history of this species (see "Study Species" in this manuscript), it is difficult to determine which of these explanations is most credible.

The branches of *S. douglasii* elongated significantly more rapidly overall in the 78% shade treatment than the branches of *S. japonica* and *S. wilsonii.* The native species growth rate was approximately equal to the non-native species growth rates between June and July but was much higher between July and August. Both of the non-native species grew approximately as well in both shade treatments, indicating that they are approximately as well adapted to all the Pacific Northwest habitat types that I employed here. The overall trend suggests that the non-native species simply do not elongate as quickly as the native species under these shade conditions. These results indicate that both shade treatments may be too shady for the native *S. douglasii*. This species occurs along streams and other moist places, which generally have little overstory and, therefore, little shade. The longer branches and faster elongation of *S. douglasii* resulted in spindly, etiolated branches that are uncharacteristic of this species. In this case, the slower branch elongation seen in *S. japonica* and *S. wilsonii* may indicate that they are better adapted for the levels of shade in these Pacific Northwest habitat types than the native congener.

Finally, *Fargesia rufa* appears to be as well adapted for the 78% shade treatment as the 94% shade treatment. The trend indicates that *F. rufa* elongates more slowly in the 94% shade treatment than in the 78% shade treatment, but this difference is not statistically significant. Because growth rates did not vary much throughout the summer, I have no reason to believe that these shade levels are overly limiting to this species.

These results correlate fairly well to the relative growth rates for each species; species with greater above-ground biomass also tended to elongate more rapidly. These results are difficult to interpret in isolation because faster elongation of branches may indicate light limitation rather than growth due to sufficient acclimation. However, this tendency to produce etiolated branches is more common in sun-adapted species than shade-adapted species (Grime 2001). If a species is shade-tolerant and exhibits high RGRH in shade treatments, it is likely that the species is sufficiently acclimated to the habitat. Thus, if we assume that each of the non-native species in this study is shade tolerant based on the species' description and as part of the "worst case scenario," then the results for RGRH support the conclusions drawn for RGR. The rate of leaf elongation suggests that *A. tuberosum* could outcompete its native counterpart if they occurred in the same habitat. Similarly, if the late summer growth spurt in *P. kansuensis* is an indication of acclimation, then this species also becomes a candidate for spread. The two non-native *Spiraea* species may be better adapted for these shade levels than is the native *Spiraea* species. However, *S. douglasii* does not occur in these shade levels in the Pacific Northwest. This observation suggests that *S. japonica* and *S. wilsonii* would have to be significantly better adapted or better able to acclimate to these shade levels than *S. douglasii* to occur in these shade regimes. There is no evidence for such acclimation in terms of RGRH. Finally, *F. rufa* does not appear to be hindered by the shade treatments and maintains rates of elongation similar to the other species; it may pose a threat to the native plant communities.

d. Evidence from leaf morphology

Shifts in carbon allocation in shaded leaves can be rapid (Larcher 1995). As a plant acclimates to a shady environment, specific leaf area consistently increases. These thin, broad, shade-acclimated leaves have more surface area for light absorption than sun-acclimated leaves, which helps maximize their RGR (Grime 2001, Larcher 1995). However, not all plants exhibit significant shifts in SLA in response to shade, and consequently the relative plasticity of two species can be readily compared (Sanford *et al.* 2003). A species with a high degree of phenotypic plasticity likely has a broader ecological amplitude than a species with less plasticity and may be able to naturalize in a shading regime that is not identical to the shade conditions in its native habitat (Sanford *et al.* 2003). In addition to plasticity in leaf morphology, absolute SLA values may play a role in the potential for invasion. High SLA can be a good indicator of invasive potential, most likely because of the resulting boost in RGR (Baruch and Goldstein 1999, Grotkopp *et al.* 2002, but see Burns 2006). Species with SLA values of 90 cm^2 g^{-1} or more are more likely to become invaders than those with lower specific leaf areas (Rejmánek *et al.* 2005).

The SLA values for *Allium cernuum* and *A. tuberosum* did not differ significantly from one another at the beginning of the study. These values for *A. cernuum* did not change in either shade treatment but SLA significantly increased in *A. tuberosum.* This change in leaf morphology of the non-native species suggests that it is highly plastic in its response to shade and has the potential to acclimate to these shade conditions.

The non-native *Philadelphus kansuensis* entered the study with significantly lower SLA than *P. lewisii*. This pattern of leaf morphology indicates that, although both species were grown in the same light conditions in the greenhouse, the native species is better shade-adapted than the non-native species. However, this pattern was reversed during the shade experiment: *P. kansuensis* exhibited increased SLA in both of the shade treatments compared to the native congener. The non-native species exhibited a greater ability to acclimate to the shade conditions than the native congener.

Spiraea japonica consistently had lower SLA than *S. douglasii*. These differences in leaf morphology most likely reflect inherent differences in the species, but nonetheless indicate that the non-native *S. japonica* is better pre-adapted for shade than the native species. This result is not surprising because, as previously discussed, *S. douglasii* generally occurs in canopy openings in the forests of the Pacific Northwest. Thus, the non-native species is likely better adapted for the selected shade conditions than is the native *S. douglasii*. Neither species displayed much plasticity in response to shade. Specific leaf area values decreased in the shade treatments compared to the pre-study values, making the leaves appear more sun-acclimated than shade-acclimated. This characteristic is more likely to be a fixed trait of the species' phenology than a response to the shade conditions. Consequently, neither species demonstrates an outstanding ability to acclimate to the shade conditions of these Pacific Northwest forests.

Spiraea douglasii and *S. wilsonii* appear to be adapted to approximately the same degree for shade in terms of leaf morphology. The species did not differ significantly from each other in SLA before the study or in any of the treatments. Similar to the first *Spiraea* pair, the changes throughout the experiment are more indicative of sun-acclimated leaves than of shade-acclimated leaves and do not indicate an ability to acclimate to the shade conditions. Since *S. douglasii* does not occur in the more heavily shaded Pacific Northwest habitat types and the two species display similar acclimation in terms of leaf morphology, it is not likely that the non-native species would occur in these habitat types either.

Fargesia rufa displayed an obvious trend towards shade-acclimation. Specific leaf area increased from the pre-study value to the 78% shade treatment and then again in the 94% shade treatment. However, neither of these differences was statistically significant. Whether this species could acclimate to the shade conditions of the Pacific Northwest remains equivocal.

If high specific leaf area alone is a reliable indicator of the potential to invade, then each of the non-native species in this study falls into this high-risk category. However, each of the native species also display high specific leaf area. In fact, since high SLA is a characteristic common in shade-acclimated species, most understory species are likely to have high SLA and would therefore also be at high-risk for invasion. Since not all introductions of understory species have resulted in invasions, the high SLA value of understory species alone is not likely to be a reliable indicator of potential for invasion. However, high SLA values in concert with the ability to acclimate to shade conditions as well as or better than the native congener may provide stronger evidence for a potential invasion. In that case, the leaf morphology results of this study provide support for the other results of this study and indicate that *A. tuberosum* and *P. kansuensis* are species displaying a high risk for invasion in the Pacific Northwest. *Spiraea japonica* and *S. wilsonii* do not appear to pose significant risk to the Pacific Northwest. The results of the leaf morphology study in *F. rufa* are equivocal.

e. Evidence from leaf chlorophyll content

Significant shifts in chlorophyll content, relative Chl *a* and Chl *b* quantities and chloroplast structure are common in shade-acclimated leaves (Björkman 1972, Anderson and

Andersson 1988). Total Chl content may change as a plant acclimates to shade, but the direction and magnitude of this change varies by species. For instance, in a recent study of shade-acclimation in grasses, shade tolerance was positively correlated with total Chl content (Baig *et al*. 2005). In contrast, in a similar study with *Picea abies* total Chl content was lower in shade needles than sun needles (Bertamini *et al*. 2006). In some cases, the total Chl content per leaf area does not change significantly in either direction (Björkman 1972). Such differences may reflect differences in light harvesting strategies and therefore total Chl content may not be useful as an indicator of shade-tolerance in all species.

One reason total Chl content may not change during shade-acclimation is that Chl *a* often decreases while Chl *b* increases, such that the components compensate for each other in the total Chl content (Björkman 1972, Pandey and Kushwaha 2005). In high light, the number of photosynthetic reaction centers of photosystem II per leaf increase to maximize electron transport efficiency (Anderson and Andersson 1988). These reaction centers consist mainly of Chl *a* (Pandey and Kushwaha 2005). However, when the same plant is grown in low light, more energy is invested in the light-harvesting complex II, which contains both Chl *a* and Chl *b* (Anderson and Andersson 1988, Pandey and Kushwaha 2005*)*. Therefore, the Chl *a:b* ratio decreases in shade-grown plants as a result of increased investment in light-harvesting mechanisms and decreased investment in electron transport efficiency, which is not a limiting factor under low-light conditions. Thus, decreased Chl *a:b* ratio should be a reliable indicator of the degree of shade-acclimation in a plant. Moreover, appropriate shifts in Chl content and in Chl *a:b* ratio should maximize the rate of photosynthesis, and therefore the RGR, of the plant.

At the outset of the investigation, the native *Allium cernuum* contained significantly more Chl per leaf area than it contained in either of the shade treatments. The Chl *a:b* ratio in *Allium* *cernuum* significantly increased in both shade treatments. In contrast, *A. tuberosum* entered the study with significantly less total Chl and significantly higher Chl *a:b* ratio than did *A. cernuum* but these levels did not change throughout the study. Thus the native species appears to enter the study better shade-acclimated than the non-native species but it loses this advantage in the shade treatments. Neither species appears to be better adapted for the shade conditions and, in fact, they acclimate very similarly to the shade treatments.

Philadelphus lewisii and *P. kansuensis* both increased in total Chl content in both shade treatments compared to their initial Chl contents. However, there are no significant differences within or between species in Chl *a:b* ratio. Thus, the two species reacted similarly to the shade conditions of the experiment, and neither species appears better adapted to the shade conditions of these Pacific Northwest habitat types.

The non-native *Spiraea japonica* entered the study with significantly less total Chl content per leaf area than *S. douglasii*. However, total Chl content increased in both species in the shade treatments and their final Chl contents were not significantly different from each other. Thus the two species exhibit similar changes in total Chl content in response to shading. In contrast, the total Chl *a:b* ratio in *S. japonica* was significantly lower than in the native species before the study and in both shade treatments. *Spiraea japonica* may be better adapted for these shade conditions than the native congener because the non-native species exhibited a lower Chl *a:b* ratio.

Spiraea douglasii and *S. wilsonii* exhibited similar changes in total Chl content throughout the study. The species did not differ significantly from each other in terms of total Chl at the beginning of the study and these values increased in both shade treatments. Thus, this *Spiraea* pair also exhibits similar changes in total Chl content in response to shading. However, the Chl *a:b* ratios suggest differences in ability to acclimate to shading. The non-native species entered the study with a significantly higher Chl *a:b* ratio than did the native species. The ratios are approximately equal in the 78% shade treatment but the non-native species has a significantly lower Chl *a:b* ratio than the native species in the 94% shade treatment. Thus, although the native species enters the study better shade-acclimated than the native species, the reverse is true in the highest shade treatment. This result suggests that, in terms of photosynthetic pigments, the non-native species is more plastic in its response to shading than is the native species.

Total Chl content in *Fargesia rufa* did not change throughout the study. However, the relative shifts in Chl *a* and Chl *b* reflect those typical of a sun-acclimated species: the Chl a fraction increased while the Chl b fraction decreased. As a result, the Chl a:b ratio increased in both of the shade treatments compared to the pre-study values. These results have alternative explanations. It is possible that the solar radiation received in the shade treatments was greater than in the greenhouse early in the year. Alternatively, the shade regime in the shade treatments may represent a sunnier habitat than the species' native habitat. In either case, *F. rufa* demonstrated acclimation potential in response to shading. Whether this acclimation is beneficial to the species is difficult to determine from this characteristic alone.

In terms of Chl *a:b* ratio, *S. japonica* and *S. wilsonii* appear better adapted for the shade conditions of the Pacific Northwest than their native congener. The two *Allium* species and the two *Philadelphus* species appear similarly adapted to shade, indicating that the non-native species could persist in the shade conditions of the Pacific Northwest as well as do their native congeners. The results of the Chl analysis for *F. rufa* are again equivocal. Thus, these results indicate that at least 4 of the 5 non-native species could acclimate to the light conditions of the Pacific Northwest forests.

f. Extent of gas exchange studies

Characterizing the photosynthetic ability of a plant can help complete the picture of its state of acclimation. In addition to the acclimatory responses discussed in earlier sections, plants may exhibit shifts in photosynthetic capacity to improve light utilization in response to shade (Nemali and van Iersel 2004). For instance, a plant grown in low light typically exhibits lower rates of photosynthesis and respiration than one grown in high light (Taiz and Zeiger 2002). These acclimations allow a plant to maximize carbon gain (photosynthesis) while minimizing carbon expenditure (respiration) and therefore maximize RGR. In general, shade-adapted species do not show large changes in photosynthetic capacity when exposed to varying levels of shade (Boardman 1977). Thus, large reductions in photosynthetic capacity in the shade-adapted species of this study could indicate that a species is stressed and not able to meet its carbon demands. Alternatively, small changes or increases in photosynthetic capacities of these species could indicate that a species is well-adapted or had sufficiently acclimated to these conditions to maintain its RGR (Bazzaz and Carlson 1982, Sims and Pearcy 1989, Naumburg *et al.* 2001 and others).

Unfortunately, the photosynthetic results of this study are unreliable. First, time constraints imposed by the number of species, replicates and the two hours required for each measurement placed sever restrictions of collecting an adequate sample size of measurements. As a result, gas exchange was measured in the field from 0600 to 1400. During those eight hours, environmental conditions such as ambient temperature, humidity and water availability changed drastically. For instance, air temperatures frequently varied 15^0C or more during the day. Changes in leaf age, temperature and water availability can significantly affect photosynthetic rates independent of the light availability (Cornic 2000, Dreyer *et al.* 2001, Grassi and Magnani 2005 and others). Thus, the photosynthetic characteristics of individual plants varied widely, irrespective of their shade treatments.

Furthermore, of the eight species studied, only two, *Spiraea japonica* and *Philadelphus lewisii*, maintained normal rates of photosynthesis while in the gas exchange cuvette. The other species were more sensitive to the conditions in the cuvette and exhibited erratic stomatal closure, such that photosynthetic rates could not be measured. Third, the Lc*pro*+ portable photosynthesis system was unreliable and inoperative during half the summer measurement period. Even when fully functioning, this instrument is not practical for use in a large field study. One would need to use multiple instruments simultaneously. A similar study in the forest would be even more difficult because the unit has a short battery life and requires a reliable electricity supply. In short, the goal of a reliable, broadly applicable and rapid method of screening potential invasive species in the field cannot be achieved with this instrument.

Instead, I suggest two possible alternatives to estimate rates of photosynthesis. Growth chamber experiments where the environmental conditions are carefully controlled and manipulated may be more practical for evaluation of non-native species. In growth chambers, photoperiods can be staggered so that each replicate can be measured under the same conditions. However, a faster and easier method is needed for land managers in the field. Porometers are a less expensive alternative to gas exchange systems and can quickly estimate photosynthetic capacity (Decagon Devices 2006). Neither method is without problems (McDermitt 1990), but porometers are more practical than gas exchange systems for rapid field assessment.

g. Utility of shade experiments in invasive species prediction

Shade experiments provide a rapid and inexpensive method to determine a species' ability to acclimate to shade levels in the potential introduced range. The changes in leaf physiology, morphology and growth rates responded rapidly to these treatments. These results indicate that light levels play an important role in determining a species' growth and potential survival in a new habitat.

However, I suggest one addition to this experimental design for future studies. The results of this experiment would have been stronger if a third treatment of full sunlight had been included. Although the survival of these species in full sunlight is not directly of interest in this study, the performance of these species in full sunlight would have provided a basis for comparison with the two levels of experimental shade. A study could easily test multiple shade regimes simultaneously and thereby determine the entire potential range of a non-native species. Nevertheless, with only two shade levels, this study provided valuable information about the role of light in thwarting or facilitating the growth of non-native species.

2. The Role of Congeners in Predicting Invasive Species

a. *Allium cernuum* and *Allium tuberosum* comparisons

Allium cernuum and *Allium tuberosum* are similar not only in morphology and habit but also in adaptation to the shade levels of the Pacific Northwest forests. For instance, although the species entered the study with different Chl *a:b* ratios, they acclimated similarly for the shade treatments such that their Chl *a:b* ratios became approximately equal. However, whereas no significant changes in leaf morphology were seen in the native species, the *A. tuberosum* leaves showed significant shade acclimation. As a result, *A. tuberosum* grew more rapidly than its native congener. Because *A. tuberosum* demonstrated more plasticity and higher growth rates than its native congener, I conclude that this species could naturalize in the light regimes in the Pacific Northwest forests I investigated here. This conclusion provides evidence for the theory that the presence of a native congener in a habitat may indicate potential for establishment of a non-native species.

b. *Philadelphus lewisii* and *Philadelphus kansuensis* comparisons

Philadelphus lewisii and *Philadelphus kansuensis* also have similar morphology and habit. The two species exhibited similar patterns of chlorophyll content and photosynthetic pigment ratios in the shade treatments, indicating that the two species acclimate similarly to shade. However, the non-native species demonstrated significantly more plasticity in terms of leaf morphology acclimation. As a result, by the end of the experiment, *P. kansuensis* branches grew significantly faster than *P. lewisii* treatments in both treatments. *Philadelphus kansuensis* grew slightly faster overall than *P. lewisii*, though this trend is not significant. Although the data are not as conclusive as for the *Allium* species, I conclude that *P. kansuensis* may be able to naturalize in the light regime of the Pacific Northwest forests. This pair also provides support for the theory that closely-related congeners may be more likely to establish in reciprocal habitats than unrelated species.

c. *Spiraea douglasii*, *Spiraea japonica* and *Spiraea wilsonii* comparisons

The three *Spiraea* species in this study were not as similar in habit as the other congener pairs. For instance, *S. japonica* had broad, thin leaves, while *S. wilsonii* had small, delicate leaves and *S. douglasii* had intermediate-sized, thick, velvety leaves. These species also displayed significant differences in adaptation and acclimation. Although each species acclimated similarly in total chlorophyll content to the shade treatments, the non-native species displayed greater ability to acclimate to shade than did the native species in terms of Chl *a:b* ratio. *Spiraea japonica* exhibited a lower Chl *a:b* ratio than *S. douglasii* throughout the experiment. *Spiraea wilsonii* demonstrated more plasticity than either of the other two species in decreased Chl *a:b* ratio in response to more shade. However, neither of the non-native species demonstrated much ability to acclimate to the shade conditions of the Pacific Northwest in terms of leaf morphology. As a result, *S. japonica* and *S. wilsonii* had lower growth rates in the 78% shade treatment than the native species; these results seem to indicate that *S. douglasii* is better adapted for these habitat types than the non-native species. However, in this case I believe the raw numbers are misleading.

These pairings may be the proverbial exception that proves the congener rule. Although *S. douglasii* is native to the Pacific Northwest, it rarely occurs in shade levels as dense as the shade levels in this experiment. Thus, it is not surprising that *S. douglasii* exhibited lower growth rates in the 94% shade treatment than in the 78% shade treatment. Since neither non-native *Spiraea* species' growth rate was more inhibited in the 94% shade than in the 78% shade, I conclude that the non-native species are better adapted for shady conditions than the native congener. Therefore, these congeneric pairings are somewhat mismatched. This mismatch is evident even in the differences in leaf and plant morphology. To better evaluate the potential of the non-native species to naturalize in Pacific Northwest forests, a native congener more typical of these habitat types should be chosen. Thus, it is not sufficient to make a comparison solely on the basis of genus. A more ideal pairing would take into account the fine-scale ecology and distribution of the species. Since there are no native *Spiraea* species in the denser forests of the Pacific Northwest, no such valid pairing exists for this species.

Despite this shortcoming in the experiment's design, I conclude that *S. japonica* and *S. wilsonii* are not likely to naturalize in the light regime of the Pacific Northwest forests. Since *S. douglasii* grew as rapidly as or more rapidly than the non-native species in the shade levels from which it is generally excluded, *S. japonica* and *S. wilsonii* are not likely to occur in these habitat types either.

d. *Fargesia rufa*

The inclusion of *Fargesia rufa*, a bamboo, in this study in the absence of a congener provides a good test for the utility of congeners in predicting invasive species. Because there is no congener for comparison, it is difficult to determine whether *F. rufa* has characteristics that would allow this species to establish in Pacific Northwest forests. For instance, there was no change in overall chlorophyll content throughout the study but the Chl *a:b* ratio suggests adaptation to a sunny environment. If there were a native bamboo species in the Pacific Northwest flora, one could determine whether this was a characteristic of the species or if it indicates acclimation to a low shade environment. The evidence from leaf morphology suggests that the species may have acclimated to shady environments through changes in leaf surface area, although this trend is not statistically significant. The inclusion of a congener could resolve this apparent contradiction. *Fargesia rufa* tended to grow more rapidly in the lower shade treatment than in the higher shade treatment, though this difference was not statistically significant. Overall branch elongation was on par with the growth rates of the other species in this experiment but, since I cannot make a direct comparison, I cannot conclude whether this growth rate is sufficient for a bamboo to survive in these shade levels. However, because this species survived and grew in the shade treatments, I conclude that *F. rufa* could at least establish in the light regime in these Pacific Northwest forests.

e. Utility of congeners in invasive species prediction

This study provides support for the contention that closely-related congeners are useful in prediction of future invasive species. The congeners most similar in ecology (*Allium* and

Philadelphus species) were similarly adapted for the shade treatments. Congeneric pairs that were not as similar in ecology (*Spiraea* species) were not as similarly adapted for the shade treatments. Less information was gleaned for *Fargesia rufa* because there was no native congener for comparison.

Perhaps more informative than the similarities between native and non-native congeners are the differences that may confer a competitive advantage (Mack 1996). In a study of current invasive and non-invasive congeners, Burns (2006) found that SLA and RGR was higher for invasive species than non-native species. Studies with current invasive and non-invasive congeners are useful because the results of such studies can be applied to studies of congeners before an invasion occurs. The current study found that *Allium tuberosum* and *Philadelphus kansuensis* had higher SLA and RGR while *Spiraea japonica* and *S. wilsonii* had lower SLA and RGR than their native congeners. Thus, I predict that *A. tuberosum* and *P. kansuensis* are more likely to become invasive than are *S. japonica* and *S. wilsonii.*

A limitation in congeneric species comparison for predicting invasive ability is that not all invasive species have native congeners in the invasive range (Mack 1996). The lack of a native congener to *F. rufa* in the Pacific Northwest flora, limits the predictive power of this study for this species. Other information may have helped compensate for this shortcoming. For instance, if the light levels in the greenhouse were known, I would be able to interpret the contradicting chlorophyll and leaf morphology data for this species. Alternatively, a third treatment of full sunlight would provide more evidence in case of such ambiguities.

Another limitation in this study is the short duration. During the eight-week shade experiment, some species showed signs of poor acclimation, but all of the species survived. Therefore, I cannot predict the effects of subtle acclimation or lack thereof on the reproduction and long-term survival of the species. Only *A. cernuum* and *S. douglasii* flowered during the study. None of the species produced seed, so it is unclear whether any of the species could persist in these light conditions. A multiple-year evaluation would be ideal for evaluating these claims, which could be a serious limitation in a rapid screening protocol.

3. China as a Source of Future Plant Invaders in the United States

The number of Chinese plants being introduced into the U.S. is certain to continue to increase (National Research Council 2002). Historical patterns indicate that, amongst the many beneficial introductions, a few invasive species are likely to emerge (Pimentel *et al*. 2005). The striking ecological and floristic similarities between the biotas of China and the U.S. may elevate the likelihood of pre-adapted species becoming established in our native forests (National Research Council 2002). Direct studies of the species entering the U.S. such as this study can help determine which of these introduced species is well adapted for our forests. This study demonstrated that all five of the Chinese understory species at least tolerate the shade conditions of the Pacific Northwest habitat types I studied. Amongst these species, *Allium tuberosum* and *Philadelphus kansuensis* appear to be not only well adapted for the light regime of these Pacific Northwest forests but are perhaps better adapted than the native congener. The similarities in adaptation to these light levels amongst the few species selected for this study indicate that other Chinese understory species may pose a similar threat. Therefore, Chinese importations should be carefully evaluated before they are introduced as China is a potential source of future plant invasions.

4. The Role of Field-based Trials in the Prediction of Future Plant Invasions

While much progress has been made in building models for prediction of future invasions, these models must be tested and strengthened through experimentation (Richardson and Pysek 2006). Mack (1996) proposed that manipulation of species, especially congeneric species, in field studies may be the best method to demonstrate the potential for the naturalization of a non-native species. Growth chamber studies such as those of Patterson and his colleagues (Patterson *et al.* 1990, Hall and Patterson 1992, Patterson 1994, Patterson 1997 and others) have demonstrated the utility of isolating one or two environmental factors and determining the roles of these environmental conditions in a species' range expansion and limitations. However, the direct sowing of non-native species in their potential range could be an even more powerful tool because the species would be simultaneously subjected to all of the biotic and abiotic barriers of the environment (Mack 1996). Although direct introduction of non-native species into the habitat type in question would be the most informative method, it is also risky and sometimes impractical. The trials would need to be carefully monitored to prevent escape and all non-native plant material, including seeds and underground vegetative material, would need to be destroyed upon completion of the experiment. Such experiments would also require dedicated, secure sites within forests.

I contend that a multi-step field trial would be a practical and accurate alternative to direct sowing experiments (see examples National Research Council 2002). The current study has demonstrated the ease and utility of shade experiments in evaluation of the potential for establishment of non-native species. A species that cannot tolerate the shade regime of the Pacific Northwest forests cannot become established, regardless of other environmental factors (e.g. Gray and Spies 1997, Caplan and Yeakley 2006). However, shade tolerance is not the only important factor in species' establishment or exclusion; a species that can tolerate the shade regime of the Pacific Northwest forests will not necessarily become established. Thus, I envision a multi-step sieve to identify the fate of each species at several important junctures in a species' survival: dispersal, seed or propagule survival, germination and young seedling growth. If a species fails to overcome the barriers to establishment at any of these stages, it can be classified as a species with low risk of invasion.

Consequently, one could design an effective triage system for prioritizing the risk of invasion (National Research Council 2002). Every horticultural introduction would be subjected to these potential barriers to establishment and their responses carefully monitored (Mack 2005). As with prediction models, species would fall into one of three categories; reject, further analysis/monitoring needed or accept. In depth field-based research will serve to narrow the middle range of uncertainty more than currently possible with existing predictive models (Mack 1996). A more precise triage system would allow researchers, policy-makers and conservationists to focus energy and resources where it can be most effective (National Research Council 2002). Species identified at elevated or mixed risk for naturalization could be recommended for careful monitoring or exclusion, or both, from the horticultural trade (Mack 2005). Similar methods could be implemented throughout the country in all ecosystems to aid the U.S. Department of Agriculture's Animal and Plant Health Inspection Service (USDA-APHIS) and other organizations in preventing serious ecological and economic damage (National Research Council 2002).

5. Conclusions and Directions for Future Study

The results of this study indicate that *Allium tuberosum, Fargesia rufa, Philadelphus kansuensis, Spiraea japonica* and *Spiraea wilsonii* all tolerate the shade levels of an array of Pacific Northwest forests. *Allium tuberosum* and *P. kansuensis* displayed abilities to acclimate to these conditions that exceed even those of their native congeners. Thus, in the proposed triage system, *A. tuberosum* and *P. kansuensis* would be potentially denied entry to the U.S. (subject to evaluation of their fate under other environmental constraints), while the other three species would be recommended for further monitoring.

The responses of these species to other environmental factors should be studied to better predict the likelihood of establishment. For instance, studies of seed dispersal, seed predation, seedling emergence and seedling growth in the presence of predators, parasites and seasonal weather patterns would likely identify other environmental factors that would thwart the establishment of these species (Harper 1977, George and Bazzaz 1999, Baskin and Baskin 2001, Howe and Brown 2001, Schafer and Kotanen 2003, Garcia and Houle 2005, Messaoud and Houle 2006). Entry to the U.S. of such species would be authorized while those that were able to survive and reproduce in all conditions would be rejected.

In conclusion, field-based studies that employ congeners for comparison can be useful tools in future invasive species prediction. Further, this study indicates that horticulture is a potential vector for future invasive species and that the flora of China harbors some of these species. Studies of Chinese ornamental species before they are introduced into the U.S. may help prevent serious economic and ecological damage to Pacific Northwest forests.

H.t.	**Stand**	**Location**	**GPS Coordinates**	**Slope**	**Aspect**
Pinus ponderosa / Symphoricarpos albus	Smoot Hill	Hudson Reserve (WSU)	N46^0 49.670’ W117^0 13.367’	~22^0	N
	Lyle Grove	Lyle Reserve (WSU)	N46^0 44.347’ W117^0 19.896’	~21^0	N
Pseudotsuga menziesii / Physocarpus malvaceus	Douglas fir 1	University of Idaho Experimental Forest (UI)	N46^0 50.572’ W116^0 47.091’	~14^0	N
	Douglas fir 2		N46^0 50.410’ W116^0 47.221’	~13^0	NE
Abies grandis / Pachistima myrsinites	Grand fir 1	University of Idaho Experimental Forest (UI)	N46^0 51.151’ W116^0 45.052’	~9^0	S
	Grand fir 2		N46^0 50.422’ W116^0 45.237’	~7^0	NW
Tsuga heterophylla / Pachistima myrsinites	Hemlock 1	Priest River Experimental Forests (USFS)	N48^0 20.400’ W116^0 48.000’	~16^0	NW
	Hemlock 2		N48^0 21.600’ W116^0 48.000’	~17^0	NW
Abies lasiocarpa / Pachistima myrsinites	Subalpine fir 1	Priest River Experimental Forests (USFS)	N48^0 21.658’ W116^0 44.349’	~4^0	Knob sloping all directions
	Subalpine fir 2		N48^0 20.700’ W116^0 46.027’	~9^0	NW

Table 1. Physical characteristics of the 10 stands (5 habitat types) included in this study.

Figure 1. Shade experiments on the Washington State University campus. Shade structures were spaced so as to prevent shading by a nearby structure.

Habitat Type	**Percent Shade Summary**					**Mean**	**Mean Standard deviation**	**n**	**Months Surveyed**
	Minimum	1st quartile	Median	3rd quartile	Maximum				
Pinus ponderosa / Symphoricarpos albus	-3.92%	57.68%	**84.14%**	93.15%	98.29%	70.24%a	30.20%	11 months	July-Sep 2005, May-Aug 2006
Pseudotsuga menziesii / Physocarpus malvaceus	-0.24%	67.47%	**88.74%**	95.63%	98.79%	76.88%c	26.16%	10 months	July-Aug 2005, April-Aug 2006
Abies grandis / Pachistima myrsinites	-6.41%	83.62%	**94.01%**	97.70%	99.70%	84.92%b	21.71%	12 months	Aug-Sep 2005, April-Aug 2006
Tsuga heterophylla / Pachistima myrsinites	3.63%	93.30%	**97.87%**	99.09%	99.82%	92.95%d	14.77%	6 months	Sep 2005, June-Aug 2006
Abies lasiocarpa / Pachistima myrsinites	-3.06%	78.98%	**96.83%**	98.63%	99.80%	79.90%c	32.08%	6 months	June-Aug 2006

Table 2. Percent shade of late seral habitat types during peak growing season 2005/2006. The habitat types were determined to be late seral by inspection only. The median value is more accurate than the mean because canopy gaps cause severe left skews in the data. Median and mean percent shade values increase with the increase of average elevation and effective precipitation in the habitat types with the exception of the *Abies lasiocarpa / Pachistima myrsinites* habitat type. Bold letters indicate significant differences in mean percent shade from a Tukey grouping ($p<0.05$). Each month (n) represents 100 data points along a transect inside a forest stand.

Shade Structure Type	**Percent Shade Summary**					**Mean**	**Mean Standard deviation**	**n**
	Minimum	1st quartile	Median	3rd quartile	Maximum			
‘70%’	73.73%	75.55%	77.69%	80.42%	88.42%	**78.25%**	3.15%	4 days
‘90%’	91.88%	92.74%	93.29%	94.39%	96.17%	**93.59%**	1.14%	4 days

Table 3. Percent shade in shade structures during shade experiments in June and July 2006. Here the mean is an appropriate measure because the lack of canopy gaps results in more uniform data in the structures than the forest habitat types. Each day (n) represents 6 hourly measurements in each of 6 replicate structures for a total of 36 shade measurements. Shade treatment types will be referred to as ‘78%’ and ‘94%’ for ease.

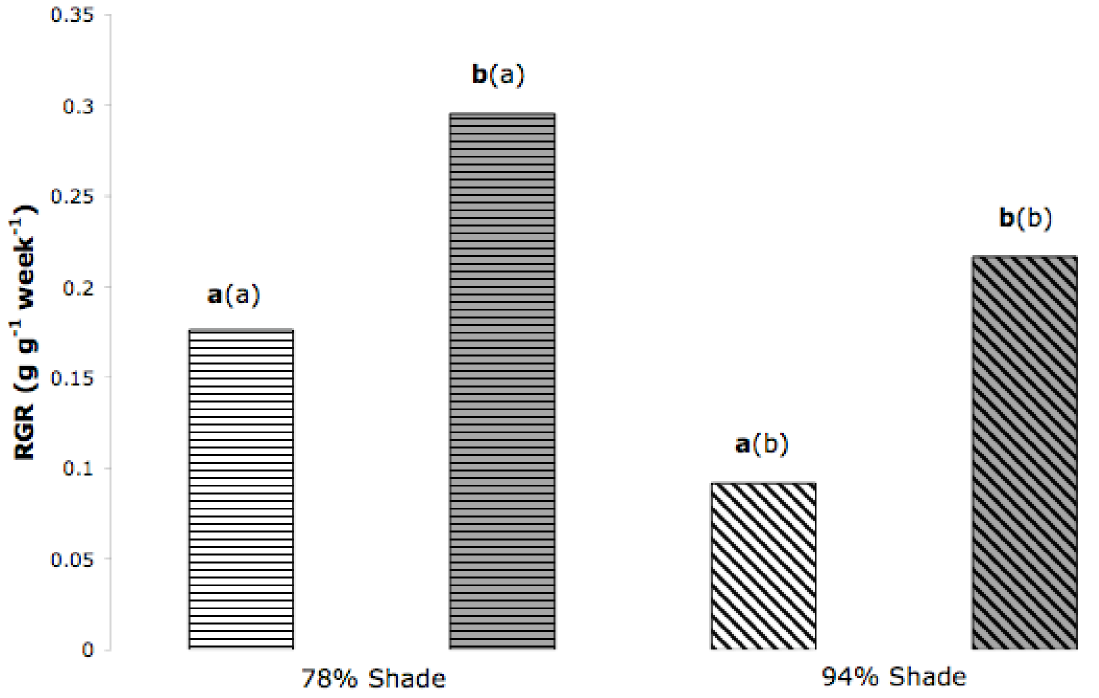

Figure 2. Relative growth rates for above-ground biomass (RGR) of *Allium cernuum* (white bars) and *Allium tuberosum* (gray bars) in the 78% (horizontal bars) and 94% (diagonal bars) shade treatments (n = 6 for each bar). Letters indicate significant differences from a Wilcoxon/Kruskal Wallis normal approximation test ($p < 0.05$). Bold letters are for comparisons between species within a shade treatment and letters in parentheses are for comparisons between shade treatments within a species.

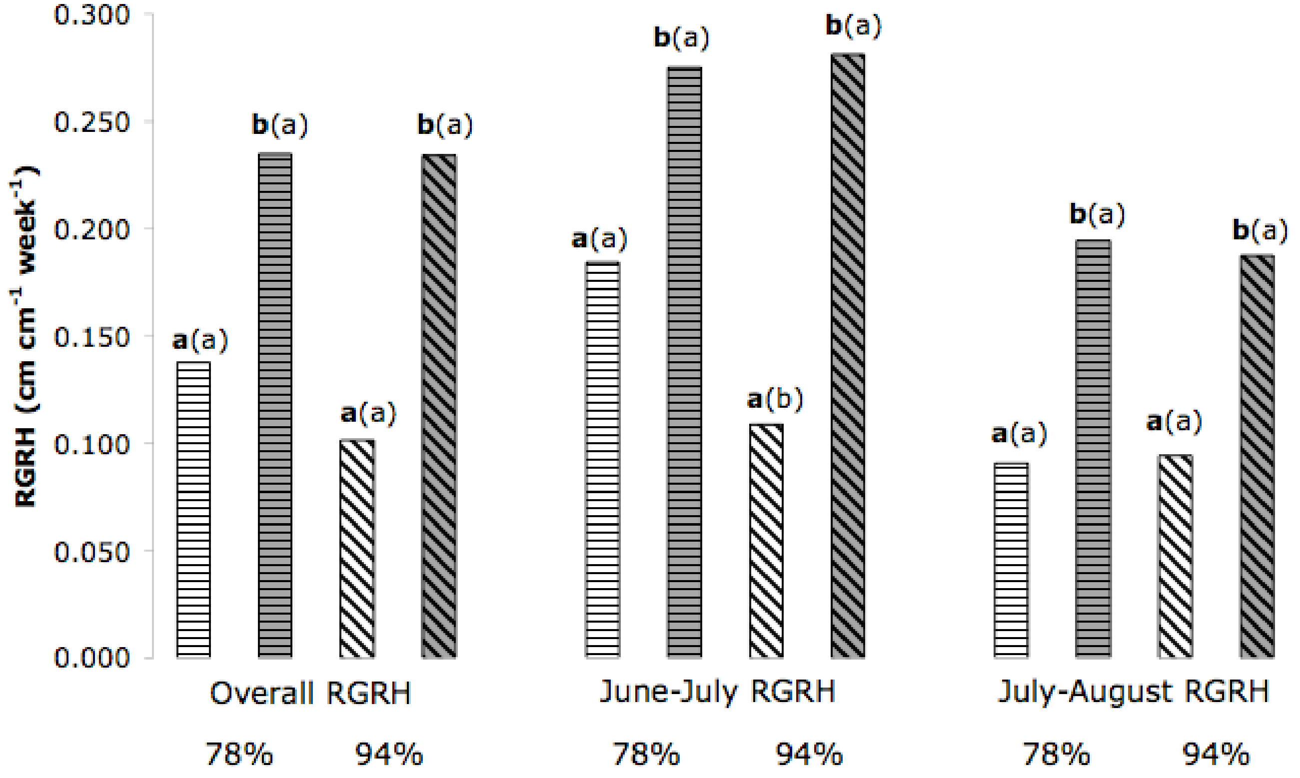

Figure 3. Relative growth rates by height (RGRH) of *Allium cernuum* (white bars) and *Allium tuberosum* (gray bars) in the 78% (horizontal bars) and 94% (diagonal bars) shade treatments (n = 6 for each bar). Letters indicate significant differences from a Wilcoxon/Kruskal Wallis normal approximation test ($p < 0.05$). Bold letters are for comparisons between species within a shade treatment and letters in parentheses are for comparisons between shade treatments within a species.

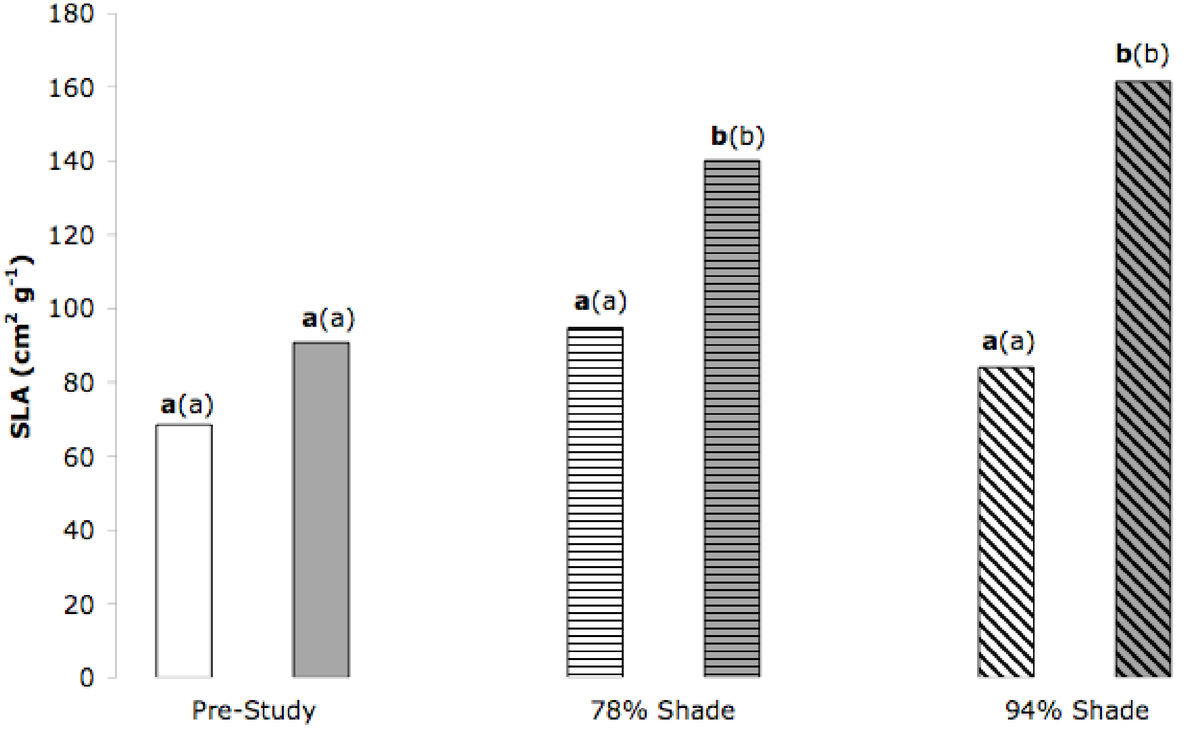

Figure 4. Specific leaf area (SLA) of *Allium cernuum* (white bars) and *Allium tuberosum* (gray bars) before the study (open bars, n = 10 for each bar), in the 78% shade treatment (horizontal bars, n = 6 for each bar) and in the 94% shade treatment (diagonal bars, n = 6 for each bar). Bold letters indicate significant differences from a Wilcoxon/Kruskal Wallis normal approximation test ($p < 0.05$) between species within a shade treatment. Letters in parentheses indicate significant differences from a Tukey grouping ($p < 0.05$) between shade treatments within a species.

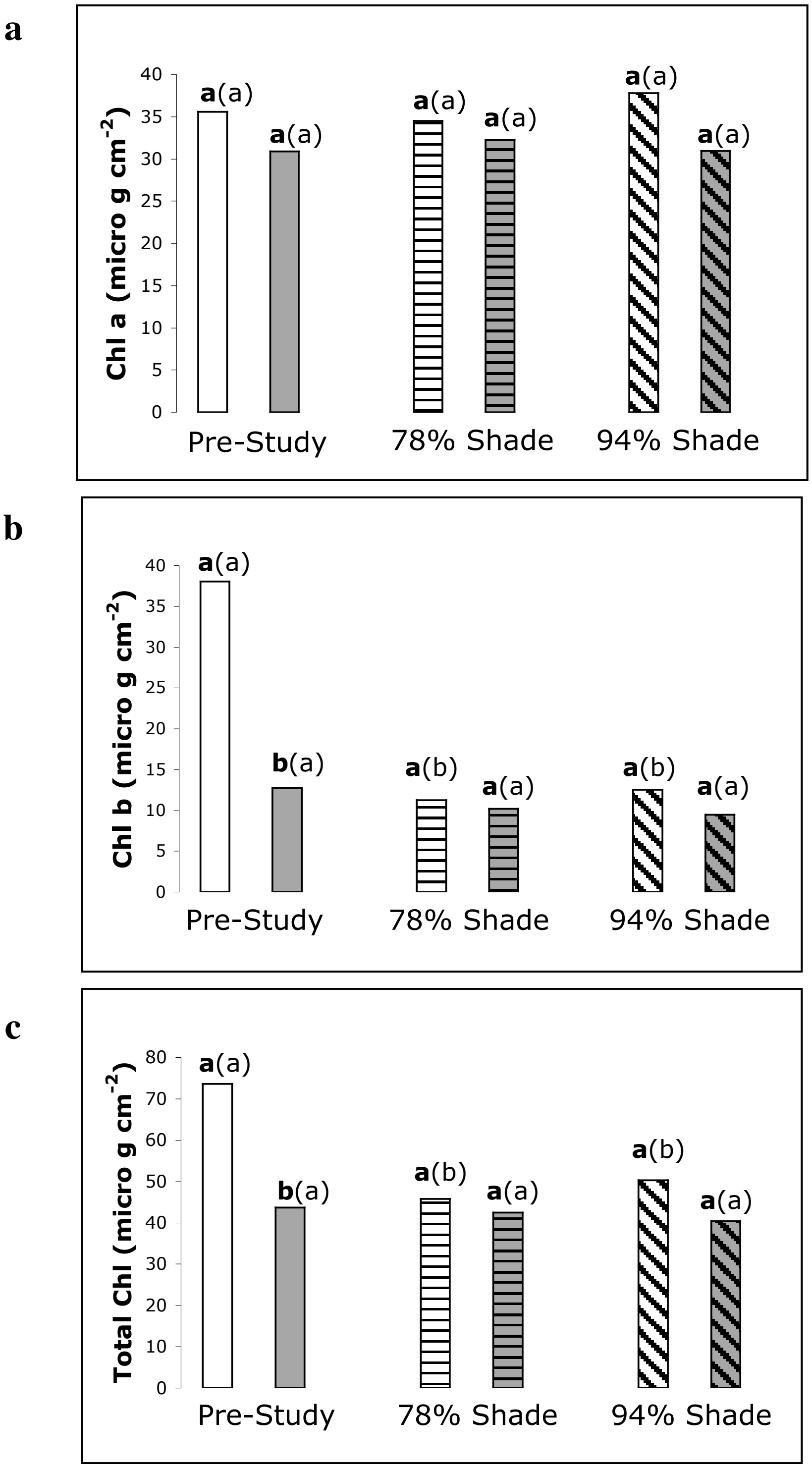

Figure 5. Chlorophyll *a*, *b* and total Chl levels in *Allium cernuum* (white bars) and *Allium tuberosum* (gray bars) before the study (open bars, n = 10 for each bar), in the 78% shade treatment (horizontal bars, n = 6 for each bar) and in the 94% shade treatment (diagonal bars, n = 6 for each bar). Bold letters indicate significant differences from a Wilcoxon/Kruskal Wallis normal approximation test ($p < 0.05$) between species within a treatment. Letters in parentheses indicate significant differences from a Tukey grouping ($p < 0.05$) between treatments within a species.

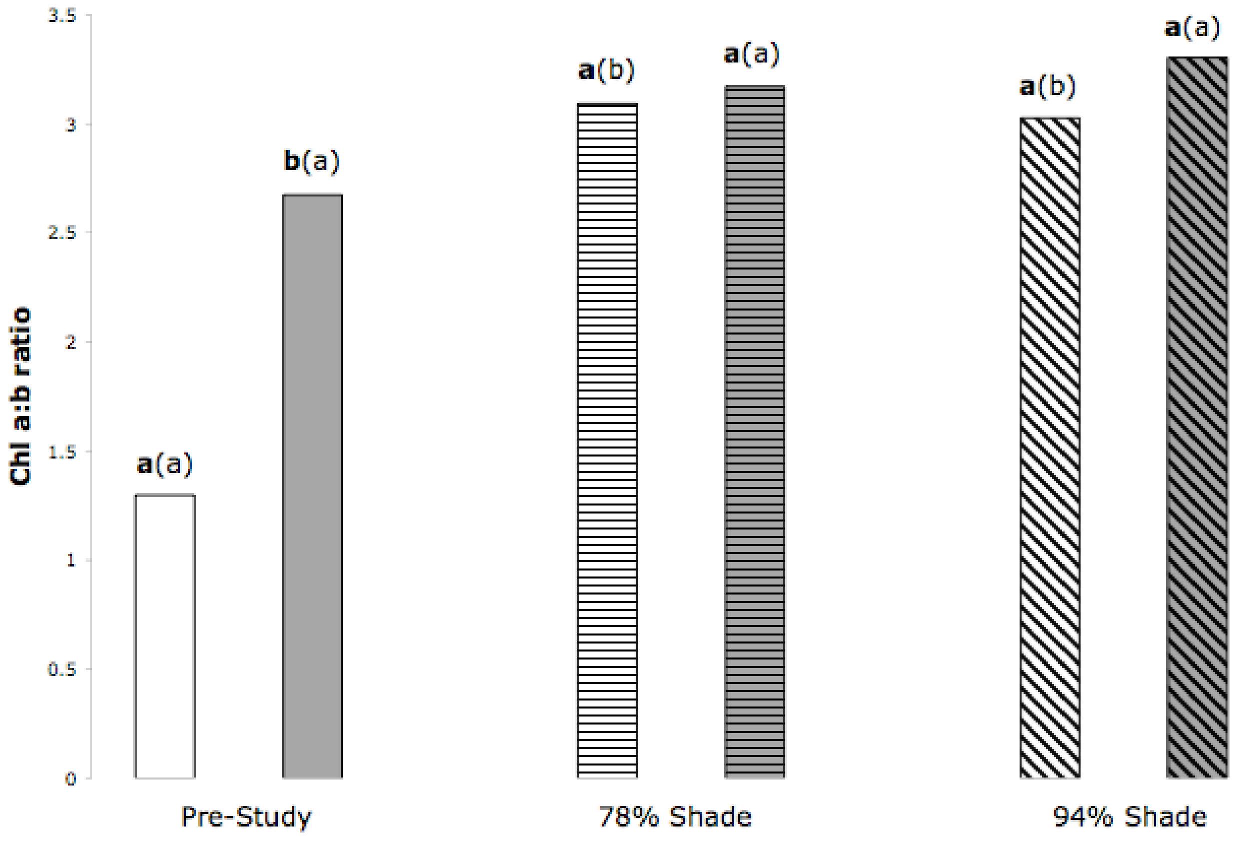

Figure 6. Chlorophyll *a:b* ratios of *Allium cernuum* (white bars) and *Allium tuberosum* (gray bars) before the study (open bars, n = 10 for each bar), in the 78% shade treatment (horizontal bars, n = 6 for each bar) and in the 94% shade treatment (diagonal bars, n = 6 for each bar). Bold letters indicate significant differences from a Wilcoxon/Kruskal Wallis normal approximation test ($p < 0.05$) between species within a shade treatment. Letters in parentheses indicate significant differences from a Tukey grouping ($p < 0.05$) between shade treatments within a species.

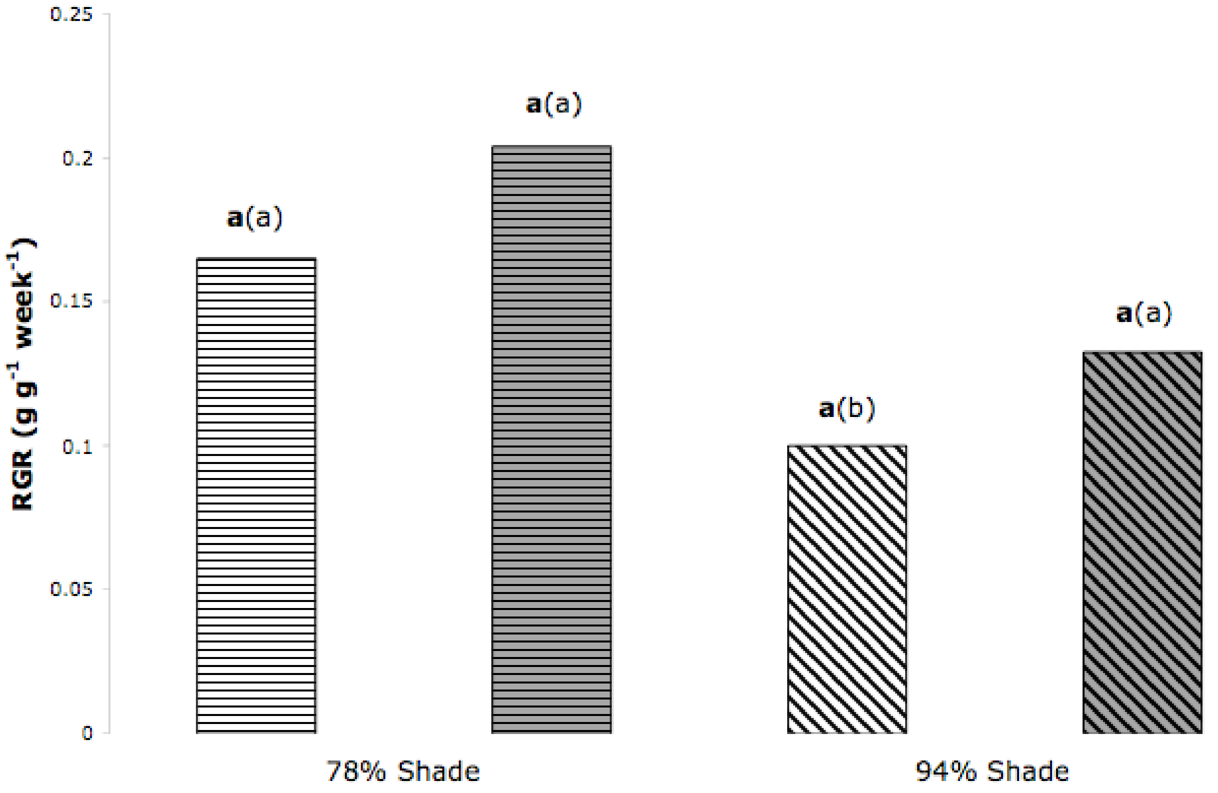

Figure 7. Relative growth rates for above-ground biomass (RGR) of *Philadelphus lewisii* (white bars) and *Philadelphus kansuensis* (gray bars) in the 78% (horizontal bars) and 94% (diagonal bars) shade treatments (n = 6 for each bar). Letters indicate significant differences from a Wilcoxon/Kruskal Wallis normal approximation test ($p < 0.05$). Bold letters are for comparisons between species within a shade treatment and letters in parentheses are for comparisons between shade treatments within a species.

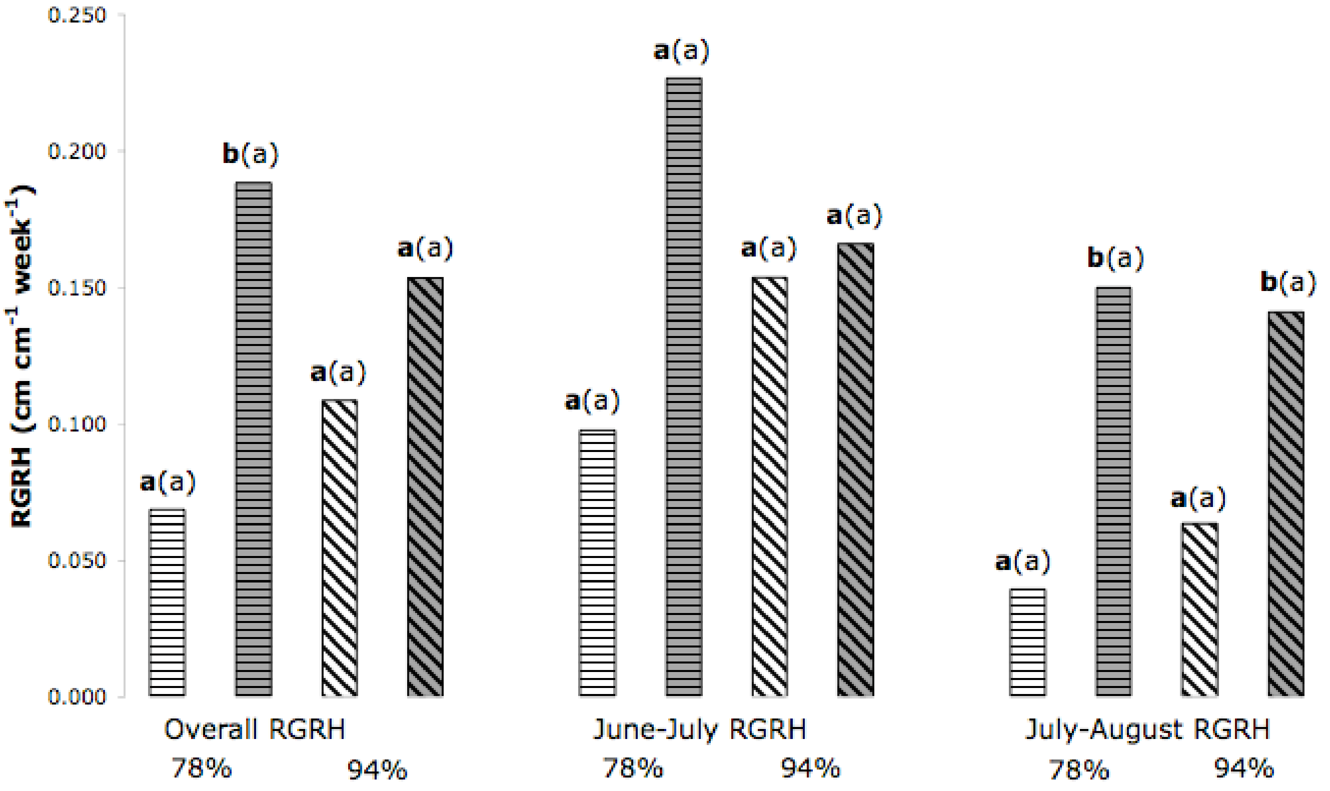

Figure 8. Relative growth rates by height (RGRH) of *Philadelphus lewisii* (white bars) and *Philadelphus kansuensis* (gray bars) in the 78% (horizontal bars) and 94% (diagonal bars) shade treatments (n = 6 for each bar). Letters indicate significant differences from a Wilcoxon/Kruskal Wallis normal approximation test ($p < 0.05$). Bold letters are for comparisons between species within a shade treatment and letters in parentheses are for comparisons between shade treatments within a species.

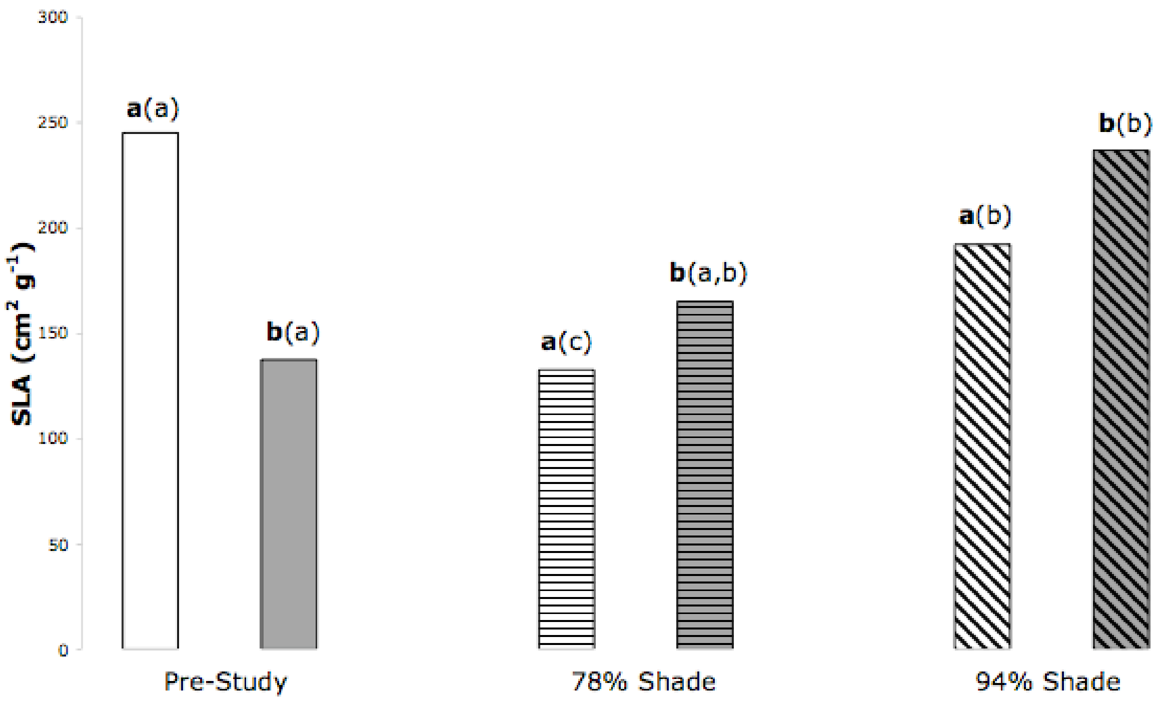

Figure 9. Specific leaf area (SLA) of *Philadelphus lewisii* (white bars) and *Philadelphus kansuensis* (gray bars) before the study (open bars, n = 10 for each bar), in the 78% shade treatment (horizontal bars, n = 6 for each bar) and in the 94% shade treatment (diagonal bars, n = 6 for each bar). Bold letters indicate significant differences from a Wilcoxon/Kruskal Wallis normal approximation test ($p < 0.05$) between species within a shade treatment. Letters in parentheses indicate significant differences from a Tukey grouping ($p < 0.05$) between shade treatments within a species.

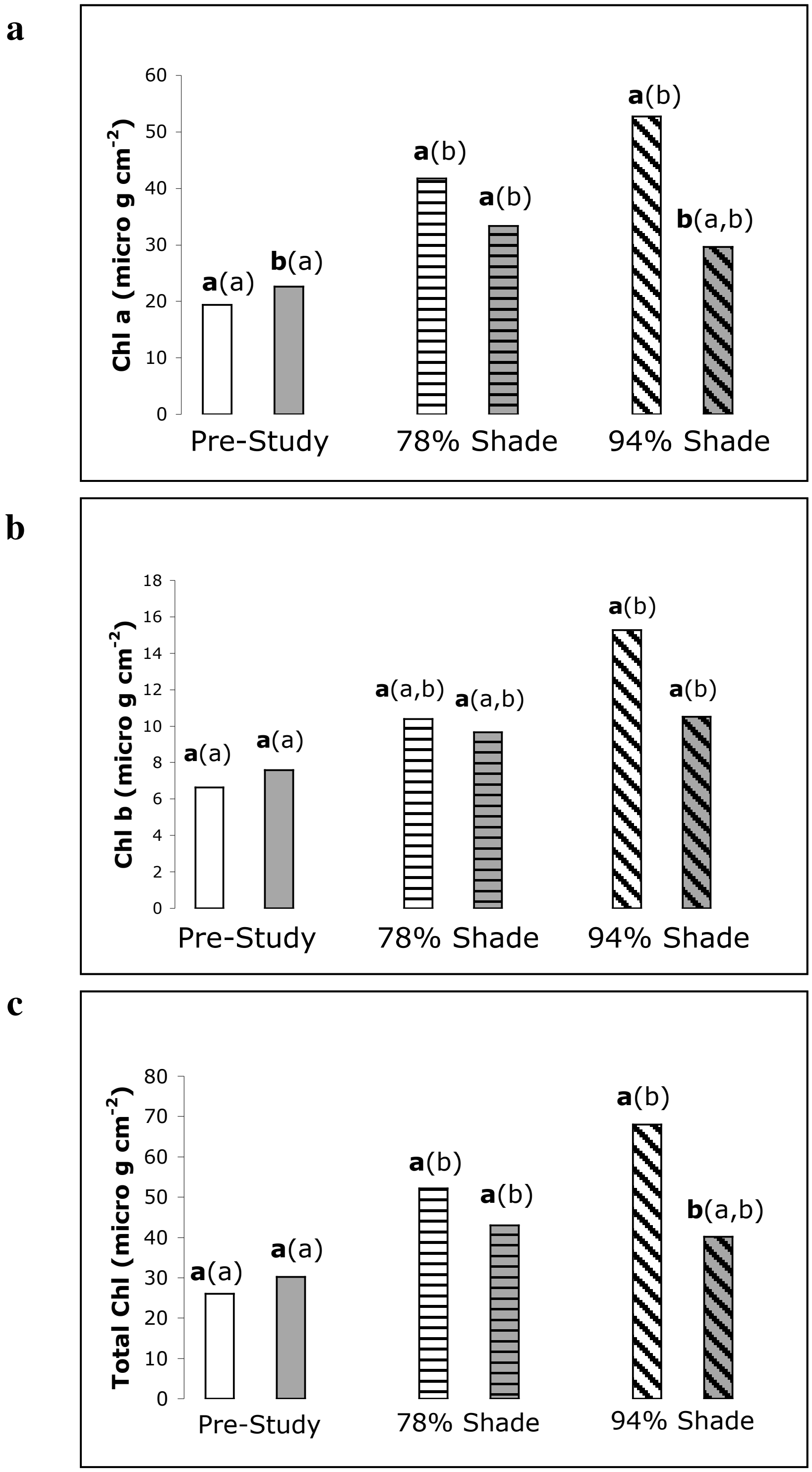

Figure 10. Chlorophyll *a*, *b* and total Chl levels in *Philadelphus lewisii* (white bars) and *Philadelphus kansuensis* (gray bars) before the study (open bars, n = 10 for each bar), in the 78% shade treatment (horizontal bars, n = 6 for each bar) and in the 94% shade treatment (diagonal bars, n = 6 for each bar). Bold letters indicate significant differences from a Wilcoxon/Kruskal Wallis normal approximation test ($p < 0.05$) between species within a treatment. Letters in parentheses indicate significant differences from a Tukey grouping ($p < 0.05$) between treatments within a species.

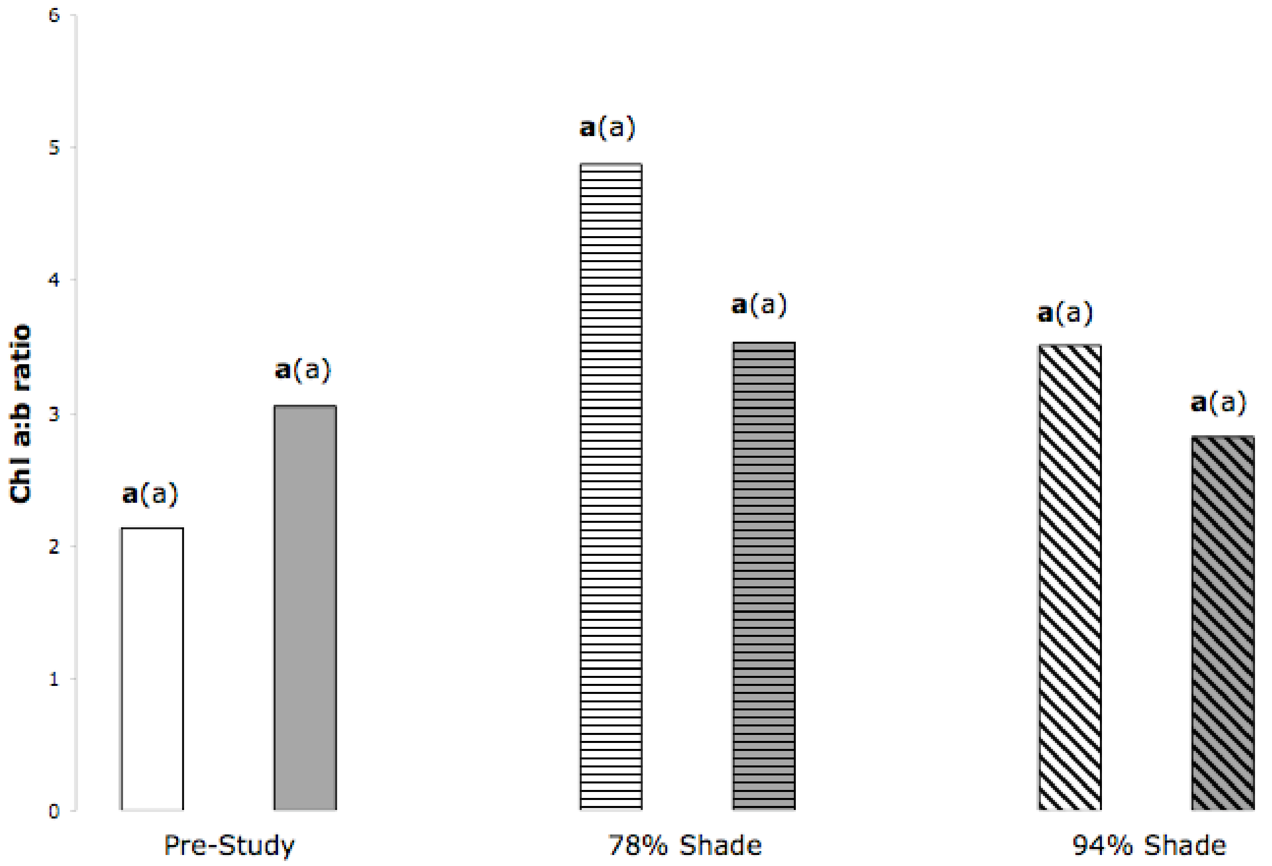

Figure 11. Chlorophyll *a:b* ratios of *Philadelphus lewisii* (white bars) and *Philadelphus kansuensis* (gray bars) before the study (open bars, n = 10 for each bar), in the 78% shade treatment (horizontal bars, n = 6 for each bar) and in the 94% shade treatment (diagonal bars, n = 6 for each bar). Bold letters indicate significant differences from a Wilcoxon/Kruskal Wallis normal approximation test ($p < 0.05$) between species within a shade treatment. Letters in parentheses indicate significant differences from a Tukey grouping ($p < 0.05$) between shade treatments within a species.

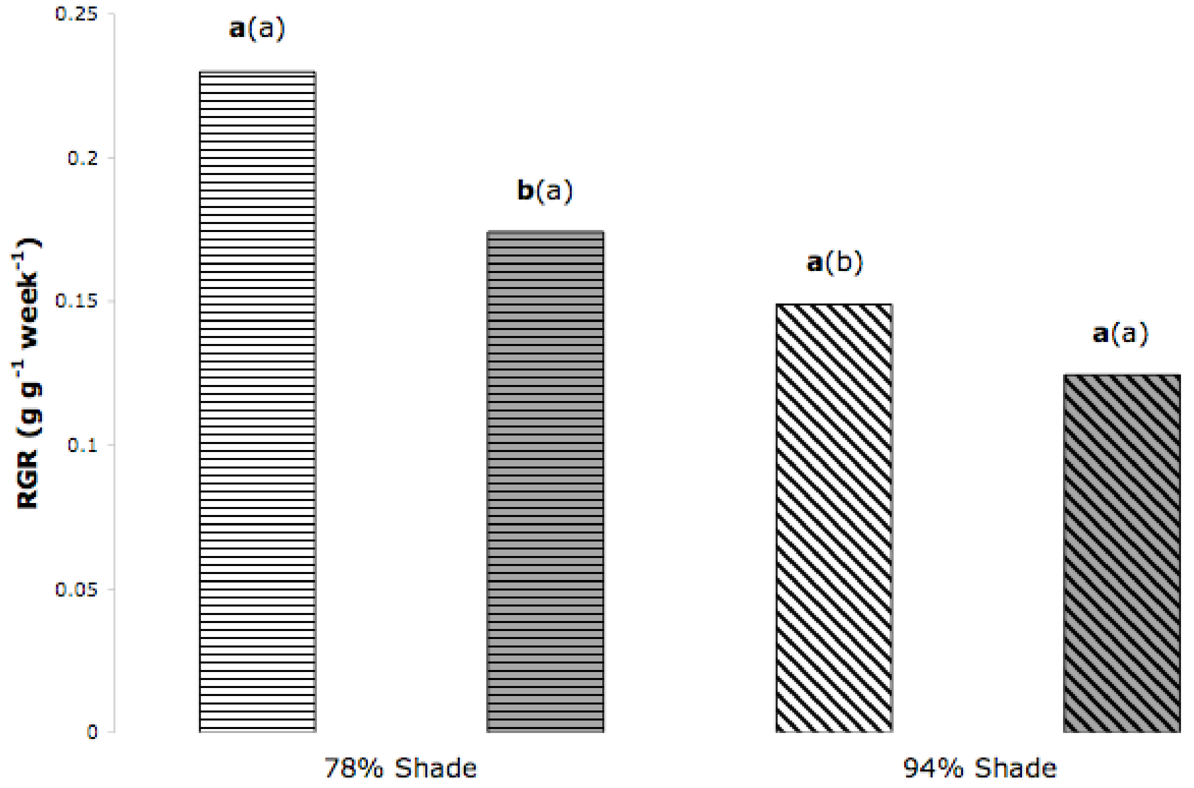

Figure 12. Relative growth rates for above-ground biomass (RGR) of *Spiraea douglasii* (white bars) and *Spiraea japonica* (gray bars) in the 78% (horizontal bars) and 94% (diagonal bars) shade treatments (n = 6 for each bar). Letters indicate significant differences from a Wilcoxon/Kruskal Wallis normal approximation test ($p < 0.05$). Bold letters are for comparisons between species within a shade treatment and letters in parentheses are for comparisons between shade treatments within a species.

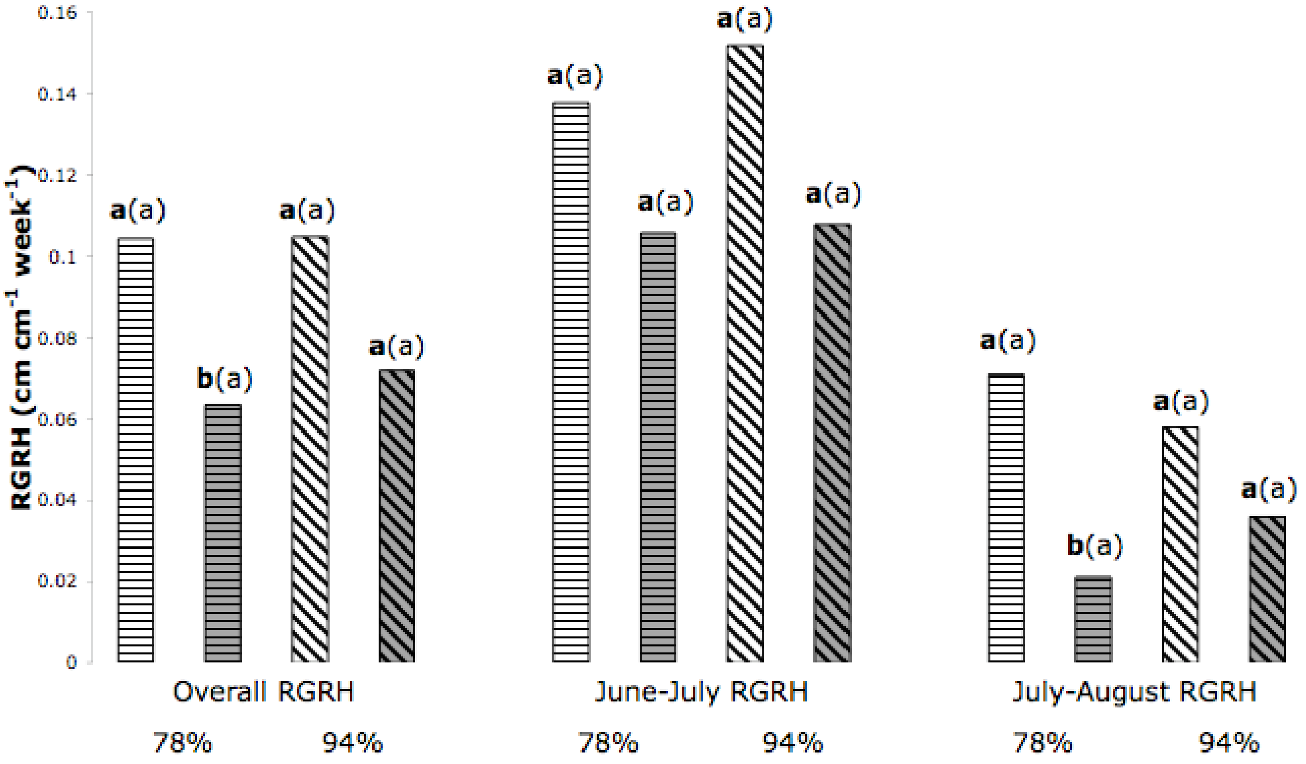

Figure 13. Relative growth rates by height (RGRH) of *Spiraea douglasii* (white bars) and *Spiraea japonica* (gray bars) in the 78% (horizontal bars) and 94% (diagonal bars) shade treatments (n = 6 for each bar). Letters indicate significant differences from a Wilcoxon/Kruskal Wallis normal approximation test ($p < 0.05$). Bold letters are for comparisons between species within a shade treatment and letters in parentheses are for comparisons between shade treatments within a species.

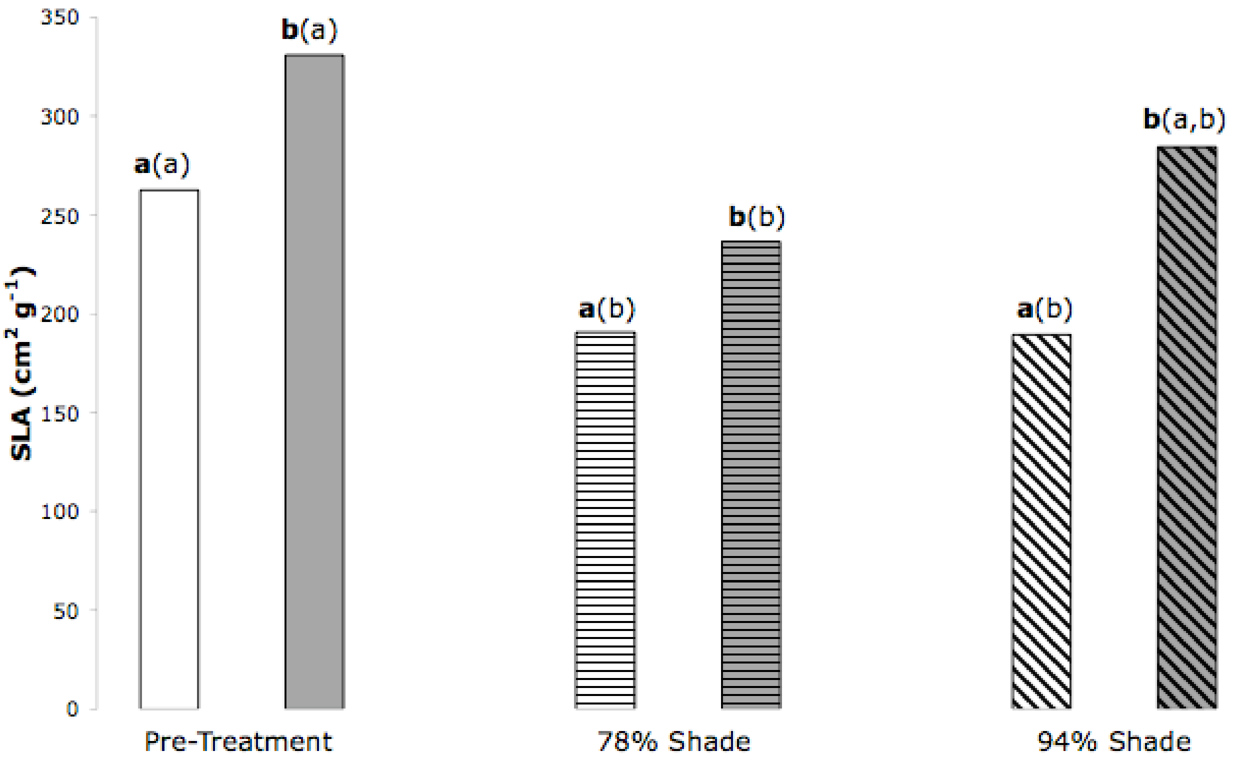

Figure 14. Specific leaf area (SLA) of *Spiraea douglasii* (white bars) and *Spiraea japonica* (gray bars) before the study (open bars, n = 10 for each bar), in the 78% shade treatment (horizontal bars, n = 6 for each bar) and in the 94% shade treatment (diagonal bars, n = 6 for each bar). Bold letters indicate significant differences from a Wilcoxon/Kruskal Wallis normal approximation test ($p < 0.05$) between species within a shade treatment. Letters in parentheses indicate significant differences from a Tukey grouping ($p < 0.05$) between shade treatments within a species.

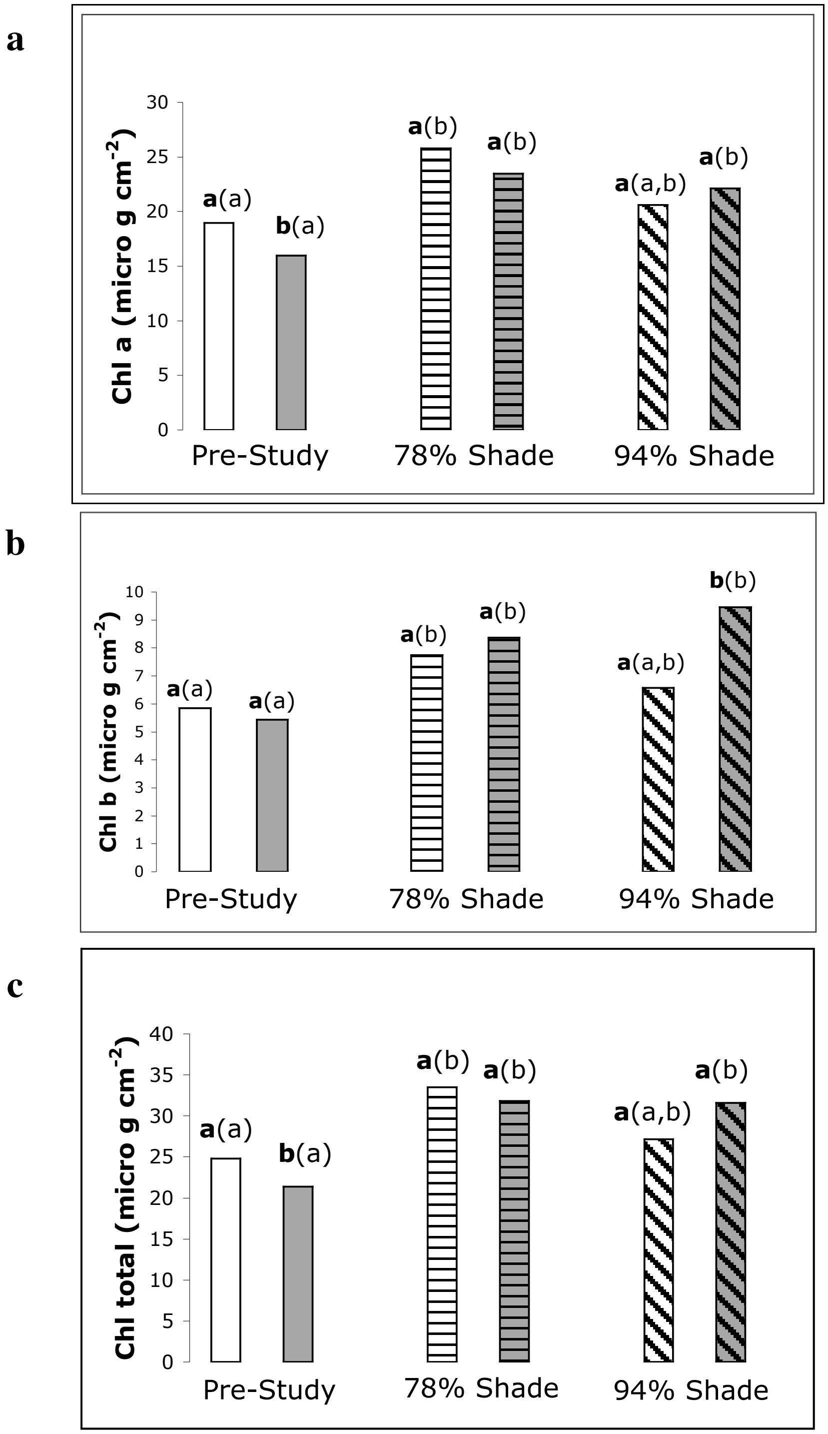

Figure 15. Chlorophyll *a*, *b* and total Chl levels in *Spiraea douglasii* (white bars) and *Spiraea japonica* (gray bars) before the study (open bars, n = 10 for each bar), in the 78% shade treatment (horizontal bars, n = 6 for each bar) and in the 94% shade treatment (diagonal bars, n = 6 for each bar). Bold letters indicate significant differences from a Wilcoxon/Kruskal Wallis normal approximation test ($p < 0.05$) between species within a treatment. Letters in parentheses indicate significant differences from a Tukey grouping ($p < 0.05$) between treatments within a species.

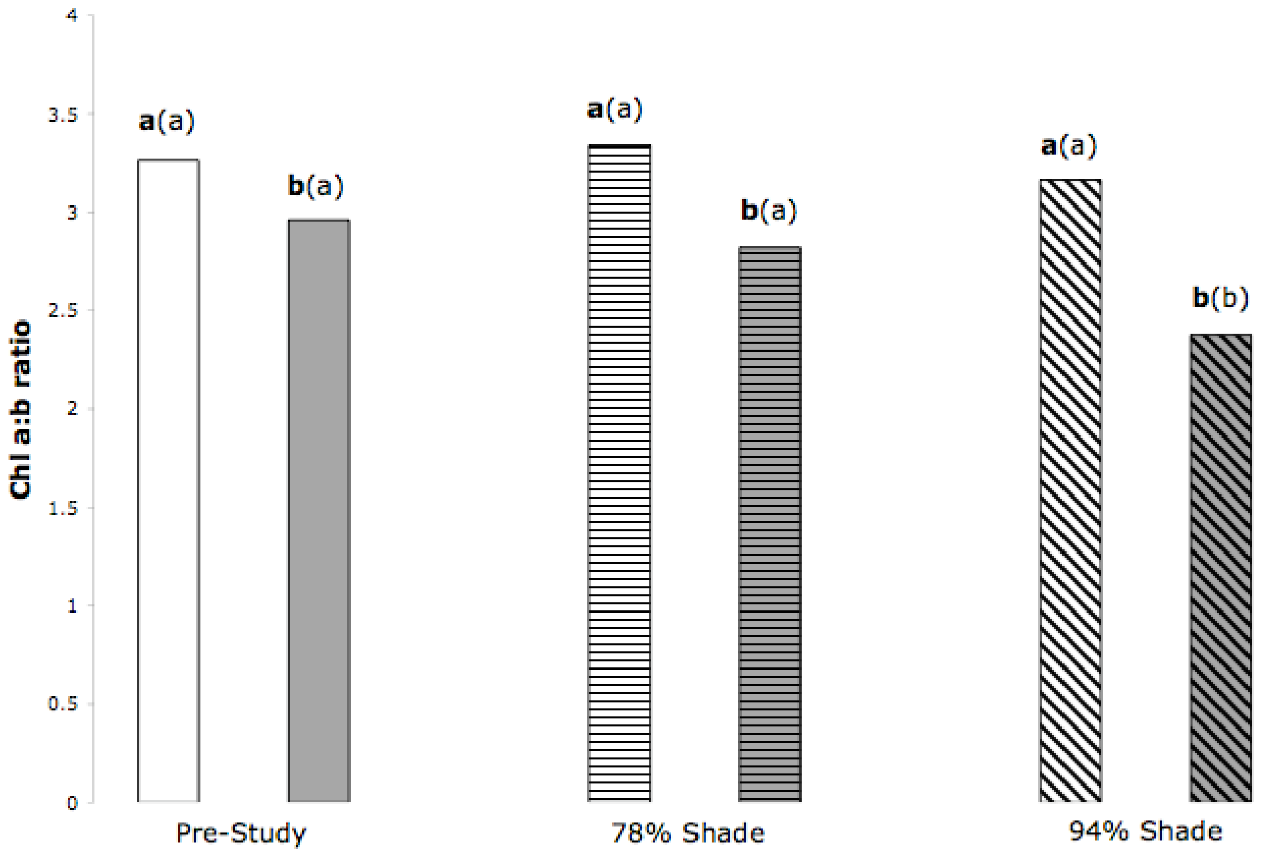

Figure 16. Chlorophyll *a:b* ratios of *Spiraea douglasii* (white bars) and *Spiraea japonica* (gray bars) before the study (open bars, $n = 10$ for each bar), in the 78% shade treatment (horizontal bars, $n = 6$ for each bar) and in the 94% shade treatment (diagonal bars, $n = 6$ for each bar). Bold letters indicate significant differences from a Wilcoxon/Kruskal Wallis normal approximation test ($p < 0.05$) between species within a shade treatment. Letters in parentheses indicate significant differences from a Tukey grouping ($p < 0.05$) between shade treatments within a species.

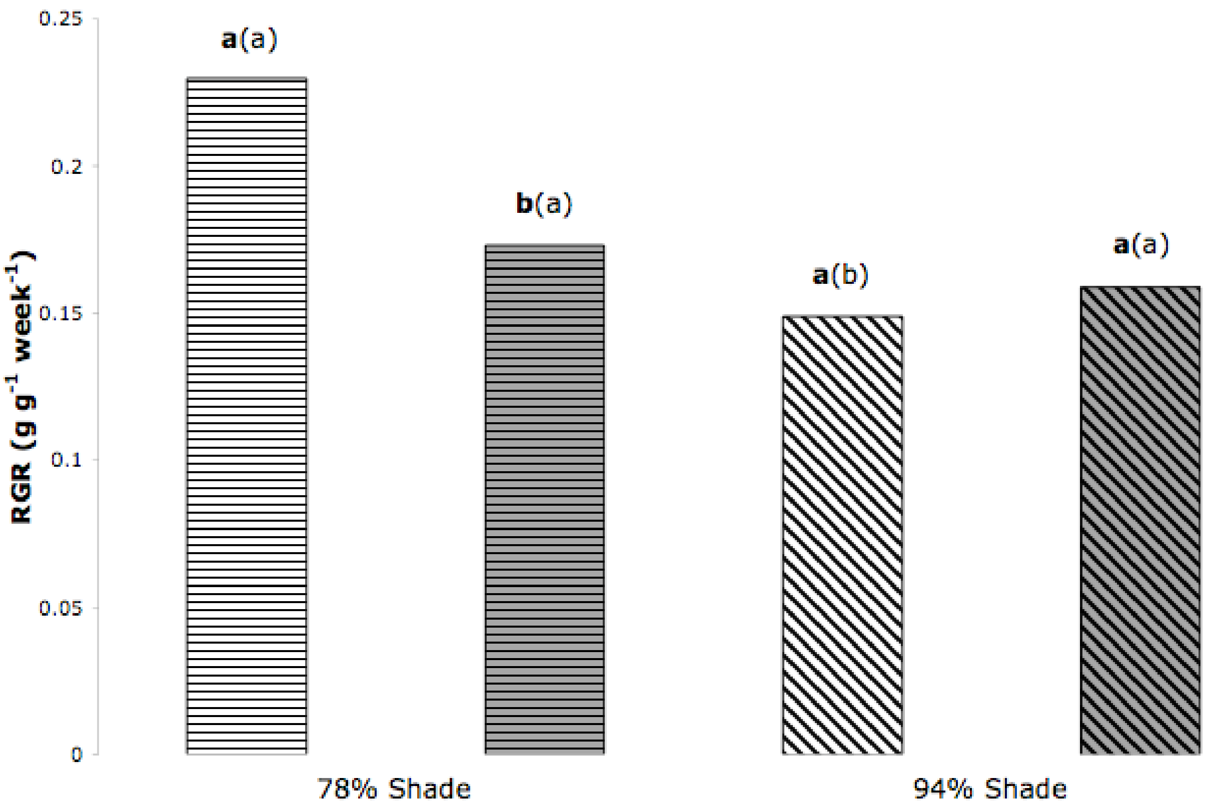

Figure 17. Relative growth rates for above-ground biomass (RGR) of *Spiraea douglasii* (white bars) and *Spiraea wilsonii* (gray bars) in the 78% (horizontal bars) and 94% (diagonal bars) shade treatments (n = 6 for each bar). Letters indicate significant differences from a Wilcoxon/Kruskal Wallis normal approximation test ($p < 0.05$). Bold letters are for comparisons between species within a shade treatment and letters in parentheses are for comparisons between shade treatments within a species.

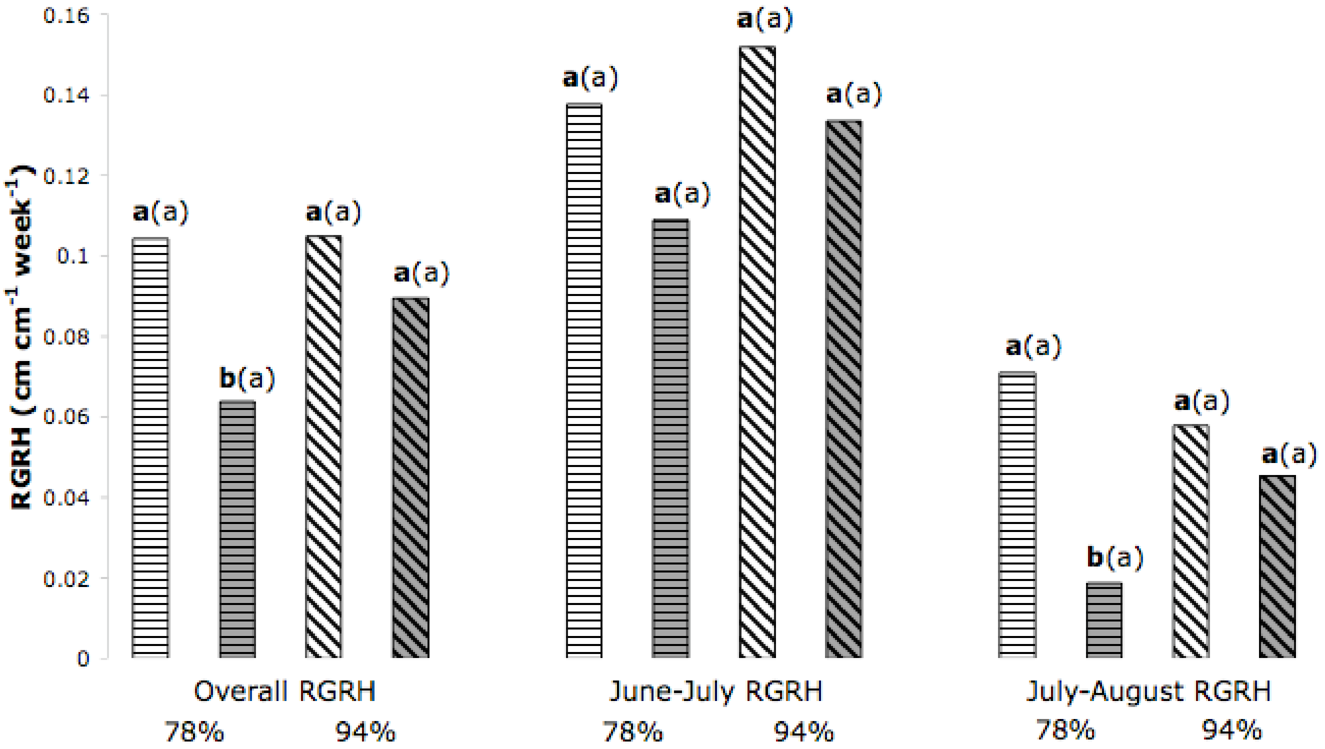

Figure 18. Relative growth rates by height (RGRH) of *Spiraea douglasii* (white bars) and *Spiraea wilsonii* (gray bars) in the 78% (horizontal bars) and 94% (diagonal bars) shade treatments (n = 6 for each bar). Letters indicate significant differences from a Wilcoxon/Kruskal Wallis normal approximation test ($p < 0.05$). Bold letters are for comparisons between species within a shade treatment and letters in parentheses are for comparisons between shade treatments within a species.

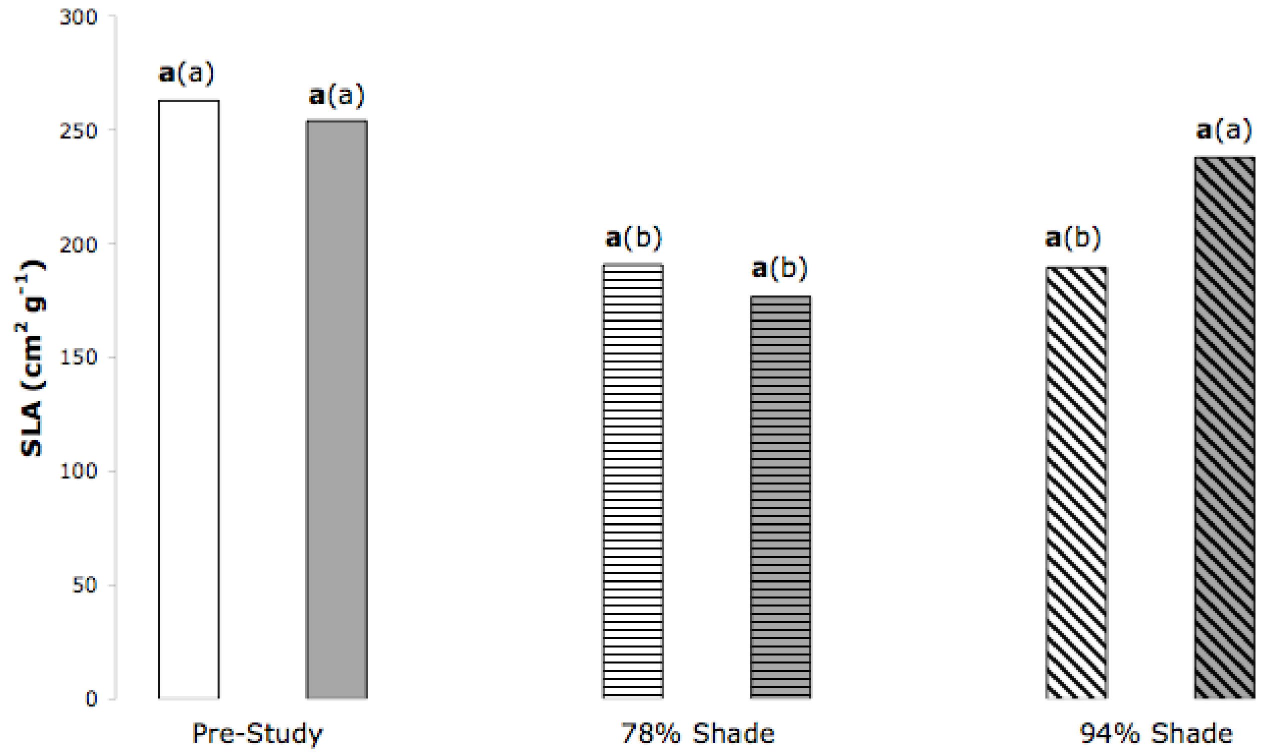

Figure 19. Specific leaf area (SLA) of *Spiraea douglasii* (white bars) and *Spiraea wilsonii* (gray bars) before the study (open bars, n = 10 for each bar), in the 78% shade treatment (horizontal bars, n = 6 for each bar) and in the 94% shade treatment (diagonal bars, n = 6 for each bar). Bold letters indicate significant differences from a Wilcoxon/Kruskal Wallis normal approximation test ($p < 0.05$) between species within a shade treatment. Letters in parentheses indicate significant differences from a Tukey grouping ($p < 0.05$) between shade treatments within a species.

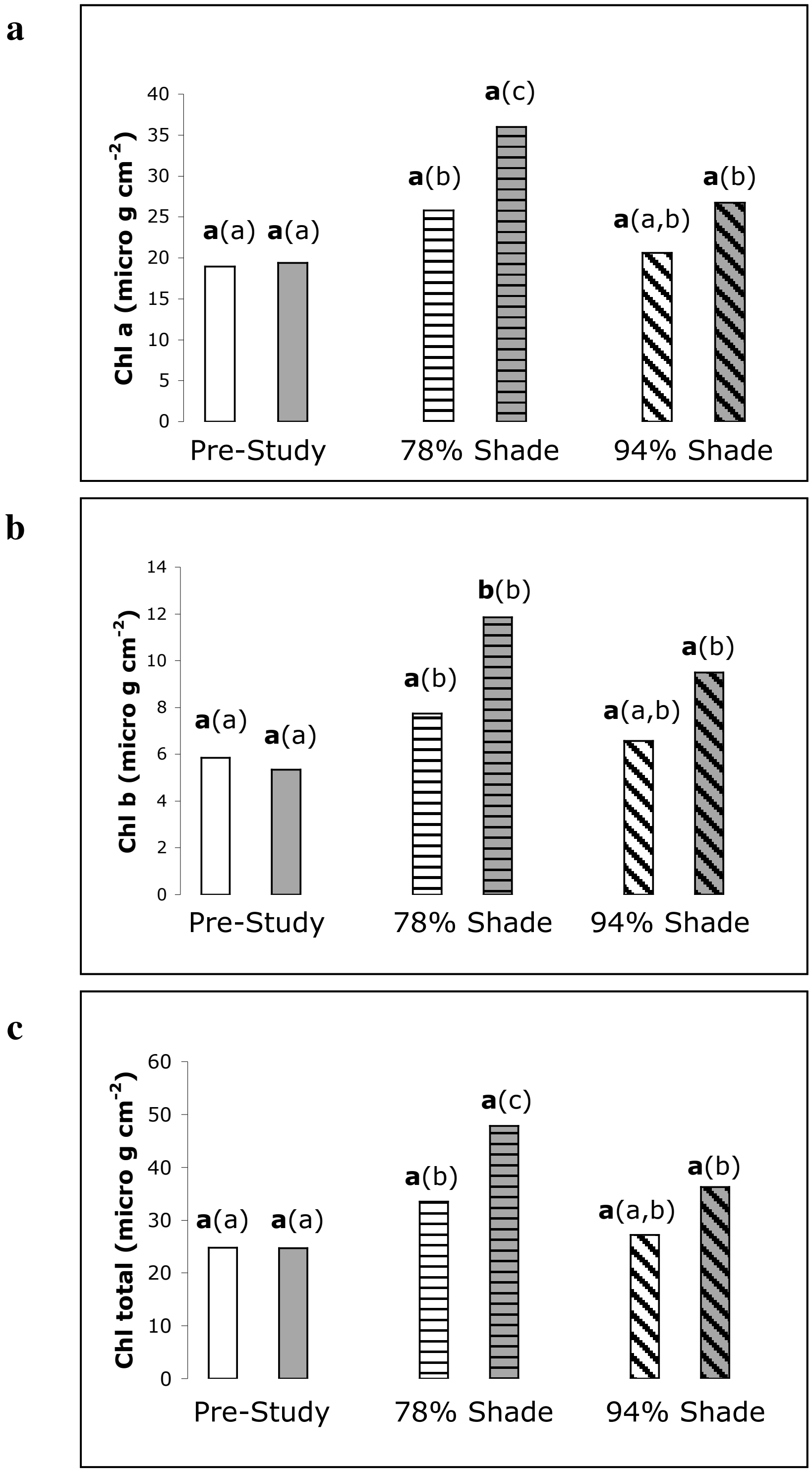

Figure 20. Chlorophyll *a*, *b* and total Chl levels in *Spiraea douglasii* (white bars) and *Spiraea wilsonii* (gray bars) before the study (open bars, n = 10 for each bar), in the 78% shade treatment (horizontal bars, n = 6 for each bar) and in the 94% shade treatment (diagonal bars, n = 6 for each bar). Bold letters indicate significant differences from a Wilcoxon/Kruskal Wallis normal approximation test ($p < 0.05$) between species within a treatment. Letters in parentheses indicate significant differences from a Tukey grouping ($p < 0.05$) between treatments within a species.

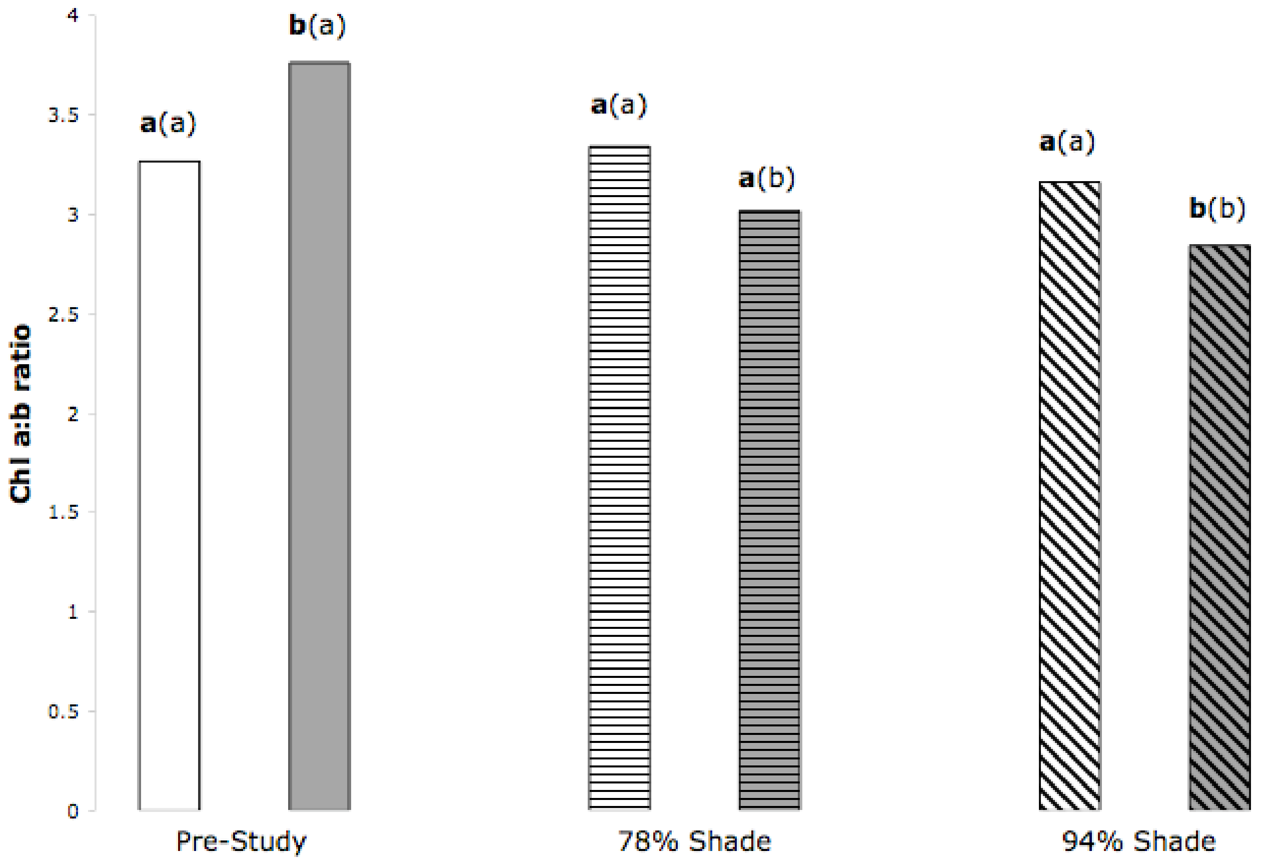

Figure 21. Chlorophyll *a:b* ratios of *Spiraea douglasii* (white bars) and *Spiraea wilsonii* (gray bars) before the study (open bars, n = 10 for each bar), in the 78% shade treatment (horizontal bars, n = 6 for each bar) and in the 94% shade treatment (diagonal bars, n = 6 for each bar). Bold letters indicate significant differences from a Wilcoxon/Kruskal Wallis normal approximation test ($p < 0.05$) between species within a shade treatment. Letters in parentheses indicate significant differences from a Tukey grouping ($p < 0.05$) between shade treatments within a species.

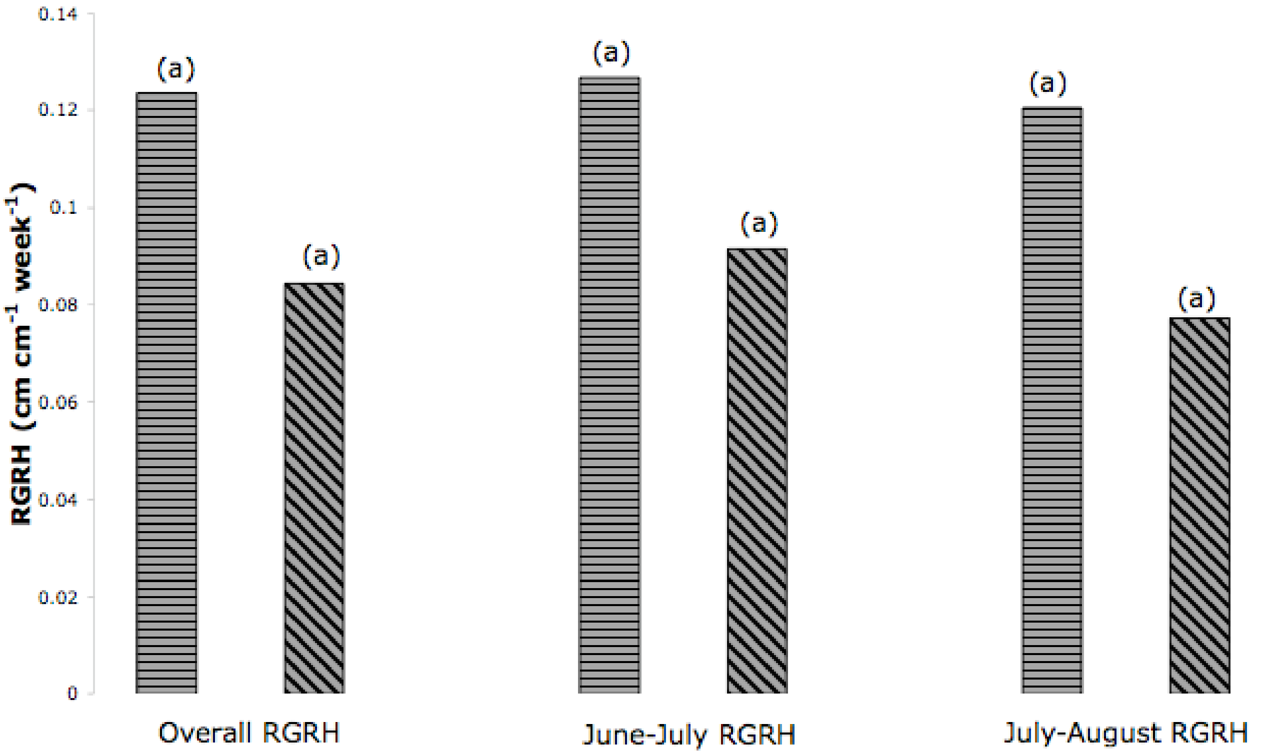

Figure 22. Relative growth rates by height (RGRH) of *Fargesia rufa* in the 78% (horizontal bars) shade treatment and 94% (diagonal bars) shade treatment (n = 6 for each bar). Letters in parentheses indicate significant differences between shade treatments from a Wilcoxon/Kruskal Wallis normal approximation test ($p < 0.05$).

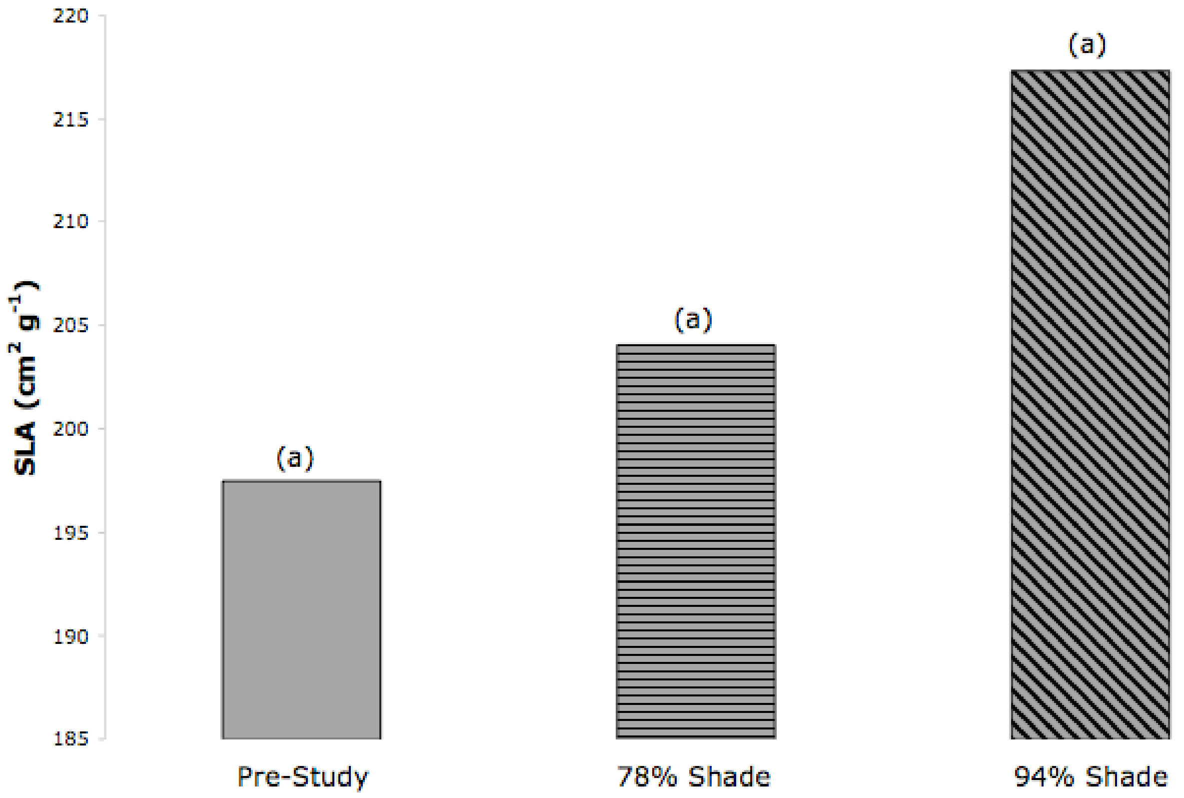

Figure 23. Specific leaf area (SLA) of *Fargesia rufa* before the study (open bars, n= 10 for each bar), in the 78% (horizontal bars, n = 6 for each bar) shade treatment and in the 94% (diagonal bars, n = 6 for each bar) shade treatment. Letters in parentheses indicate significant differences between shade treatments from a Tukey grouping ($p < 0.05$).

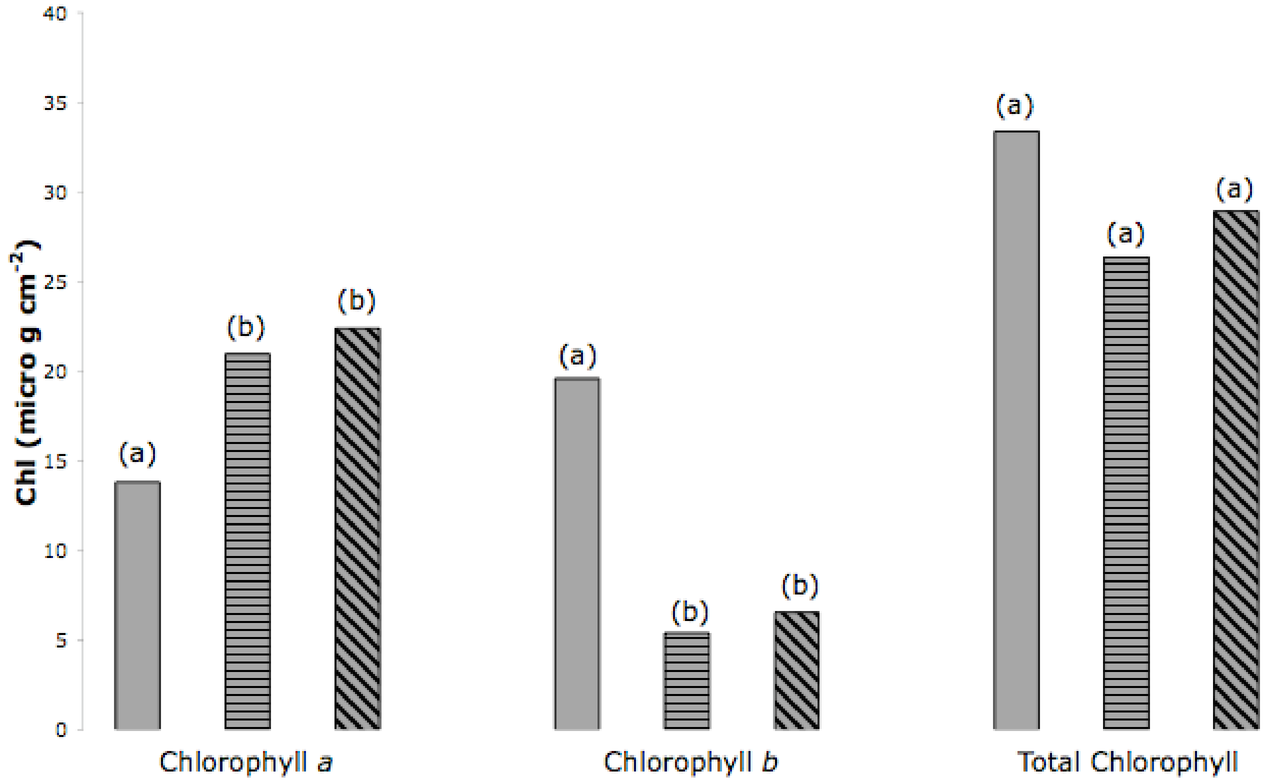

Figure 24. Chlorophyll *a*, *b* and total Chl levels in *Fargesia rufa* before the study (open bars, n= 10 for each bar), in the 78% (horizontal bars, n = 6 for each bar) shade treatment and in the 94% (diagonal bars, n = 6 for each bar) shade treatment. Letters in parentheses indicate significant differences between treatments from a Tukey grouping ($p < 0.05$).

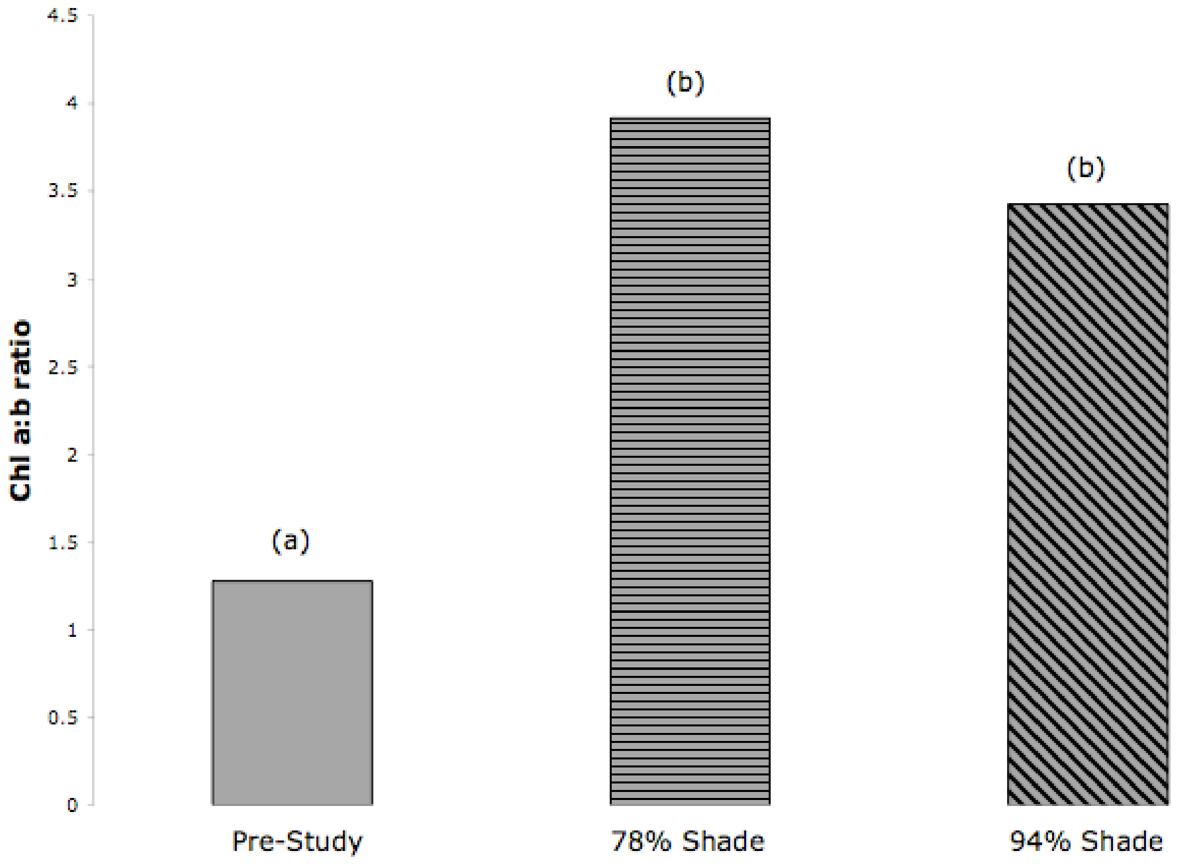

Figure 25. Chlorophyll *a:b* ratios of *Fargesia rufa* before the study (open bars, n = 10 for each bar), in the 78% shade treatment (horizontal bars, n = 6 for each bar) and in the 94% shade treatment (diagonal bars, n = 6 for each bar). Letters in parentheses indicate significant differences from a Tukey grouping ($p < 0.05$) between shade treatments.

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APPENDICES

	78%	94%	p-values within species	p-values between native and non-native congener within 78% shade treatment	p-values between native and non-native congener within 94% shade treatment
RGR (g g^{-1} week^{-1})					
A. cernuum	0.1761	0.0916	0.0453		
A. tuberosum	0.2952	0.2164	0.0063	0.0051	0.0050
F. rufa	-	-	-	NA	NA
P. lewisii	0.1649	0.0999	0.0082		
P. kansuensis	0.2037	0.1323	0.1282	0.0656	0.4712
S. douglasii	0.2298	0.1488	0.0358		
S. japonica	0.1740	0.1243	0.0656	0.0358	0.5752
S. wilsonii	0.1731	0.1587	0.2971	0.0358	0.6884
RGRH Overall (cm cm^{-1} week^{-1})					
A. cernuum	0.1375	0.1013	0.4712		
A. tuberosum	0.2347	0.2341	0.3785	0.0051	0.0051
F. rufa	0.1235	0.0843	0.2703	NA	NA
P. lewisii	0.0685	0.1085	0.2353		
P. kansuensis	0.1882	0.1534	0.1282	0.0081	0.1282
S. douglasii	0.1042	0.1048	0.6889		
S. japonica	0.0633	0.0718	0.9362	0.0306	0.1735
S. wilsonii	0.0637	0.0894	0.1282	0.0051	0.2980
RGRH June-July (cm cm^{-1} week^{-1})					
A. cernuum	0.1843	0.1086	0.0082		
A. tuberosum	0.2751	0.2809	0.9362	0.0082	0.0051
F. rufa	0.1267	0.0914	0.2703	NA	NA
P. lewisii	0.0976	0.1535	0.4113		
P. kansuensis	0.2266	0.1658	0.1735	0.0552	1.0000
S. douglasii	0.1376	0.1517	0.5752		
S. japonica	0.1056	0.1077	0.9362	0.1282	0.2298
S. wilsonii	0.1088	0.1334	0.4712	0.3785	0.2980
RGRH July-August (cm cm^{-1} week^{-1})					
A. cernuum	0.0907	0.0940	1.0000		
A. tuberosum	0.1943	0.1872	0.3785	0.0202	0.0082
F. rufa	0.1204	0.0772	0.5403	NA	NA
P. lewisii	0.0393	0.0634	0.1207		
P. kansuensis	0.1498	0.1409	0.5752	0.0081	0.0051
S. douglasii	0.0708	0.0578	0.5752		
S. japonica	0.0211	0.0359	0.5752	0.0306	0.3785
S. wilsonii	0.0186	0.0453	0.2970	0.0453	1.0000

Appendix 1. Above-ground relative growth rates and relative growth rates by height for each species in the 78% and 94% shade treatments. All p-values indicate level of significance from a Wilcoxon/Kruskal-Wallis normal approximation test. Levels of significance are indicated within species between each treatment and between species within each treatment.

	Pre-Study	78%	94%	p-values within species	p-values between native and non-native congener within Pre-Study treatment	p-values between native and non-native congener within 78% shade treatment	p-values between native and non-native congener within 94% shade treatment
SLA (cm^2 g^{-1})							
A. cernuum	68.43a	94.68a	83.99a	0.0832			
A. tuberosum	90.71a	140.02b	161.47b	0.0053	0.1620	0.0306	0.0051
F. rufa	197.46a	204.04a	217.28a	0.4144	NA	NA	NA
P. lewisii	245.15a	132.54c	192.06b	0.0007			
P. kansuensis	137.43a	165.13ab	236.72b	0.0079	0.0036	0.0131	0.0306
S. douglasii	262.60a	190.52b	189.38b	0.0094			
S. japonica	330.80a	236.67b	284.21ab	0.0010	0.0101	0.0137	0.0051
S. wilsonii	253.84a	176.64b	237.73a	0.0080	0.8197	0.5228	0.0927

Appendix 2. Specific leaf area for each species before the study, in the 78% shade treatment and in the 94% shade treatment. All p-values indicate levels of significance from a Wilcoxon/Kruskal-Wallis normal approximation test. Levels of significance are indicated for each species among pre-study, 78% and 94% treatments and between species within each treatment. Letters indicate significant differences within each species among the pre-study, 78% and 94% treatments from a Tukey grouping ($p<0.05$).

	Pre-Study	78%	94%	p-values within species	p-values between native and non-native congener within Pre-Study treatment	p-values between native and non-native congener within 78% shade treatment	p-values between native and non-native congener within 94% shade treatment
Chlorophyll a ($\mu g\ cm^{-2}$)							
A. cernuum	35.56a	34.50a	37.78a	0.6065			
A. tuberosum	30.90a	32.22a	30.95a	0.6402	0.3722	0.4712	0.1735
F. rufa	13.79a	20.95b	22.37b	0.0056	NA	NA	NA
P. lewisii	19.37a	41.74b	52.76b	0.0004			
P. kansuensis	22.58a	33.38b	29.65ab	0.0271	0.0304	0.2980	0.0453
S. douglasii	18.96a	25.78b	20.59ab	0.0346			
S. japonica	15.95a	23.47b	22.11b	0.0052	0.0127	0.6889	0.4712
S. wilsonii	19.37a	35.98c	26.75b	0.0007	0.7281	0.1735	0.1282
Chlorophyll b ($\mu g\ cm^{-2}$)							
A. cernuum	38.06a	11.25b	12.53b	0.0007			
A. tuberosum	12.77a	10.21a	9.47a	0.4380	0.0006	0.4712	0.0927
F. rufa	19.55a	5.37b	6.53b	0.0391	NA	NA	NA
P. lewisii	6.64a	10.39ab	15.27b	0.0044			
P. kansuensis	7.59a	9.66ab	10.51b	0.0279	0.5067	0.8102	0.0656
S. douglasii	5.85a	7.74b	6.57ab	0.1299			
S. japonica	5.44a	8.36b	9.46b	0.0030	0.1166	0.5752	0.0202
S. wilsonii	5.35a	11.85b	9.51b	0.0002	0.3538	0.0306	0.0656
Total Chlorophyll ($\mu g\ cm^{-2}$)							
A. cernuum	73.62a	50.30b	45.75b	0.0002			
A. tuberosum	43.67a	42.43a	40.42a	0.2725	<0.0001	0.4712	0.1282
F. rufa	33.34a	26.32a	28.90a	0.6977	NA	NA	NA
P. lewisii	26.01a	52.13b	68.03b	0.0005			
P. kansuensis	30.17a	43.05b	40.17ab	0.0191	0.0783	0.2980	0.0453
S. douglasii	24.81a	33.52b	27.16ab	0.0594			
S. japonica	21.39a	31.83b	31.57b	0.0054	0.0247	0.9362	0.2298
S. wilsonii	24.72a	47.84c	36.26b	0.0005	0.7721	0.0656	0.0927
Chlorophyll a:b							
A. cernuum	1.296a	3.091b	3.027b	0.0138			
A. tuberosum	2.673a	3.171a	3.304a	0.2265	0.0051	0.8102	0.2980
F. rufa	1.274a	3.912b	3.421b	0.0021	NA	NA	NA
P. lewisii	2.930a	4.877a	3.506a	0.2698			
P. kansuensis	3.048a	3.530a	2.817a	0.1180	0.4025	0.9362	0.1735
S. douglasii	3.264a	3.339a	3.163a	0.4769			
S. japonica	2.958a	2.819a	2.375b	0.0022	0.0062	0.0131	0.0051
S. wilsonii	3.762a	3.017b	2.842b	0.0007	0.0321	0.0927	0.0202

Appendix 3. Chlorophyll *a*, *b*, total chlorophyll and chlorophyll *a:b* ratio for each species before the study, in the 78% shade treatment and in the 94% shade treatment. All p-values indicate levels of significance from a Wilcoxon/Kruskal-Wallis normal approximation test. Levels of significance are indicated for each species among pre-study, 78% and 94% treatments and between species within each treatment. Letters indicate significant differences within each species among the pre-study, 78% and 94% treatments from a Tukey grouping ($p<0.05$).