Abstract

In order to investigate the effects of light intensity on (1) growth, morphology, and size hierarchy of *Amaranthus retroflexus*, and (2) transmission of far-red (FR) light through leaves lambsquarters (*Chenopodium album*), redroot pigweed (*A. retroflexus*) and bush beans (*Phaseolus vulgaris*), field experiments were conducted using a randomized complete block design with five replications per treatment. Plants were grown under four light intensities (22%, 33%, 55% and 100% of full sunlight) using 3, 2, 1 and 0 layers of mesh screen, respectively. These treatments represented approximately 400, 600, 1,000 and 1,800 µE m⁻² s⁻¹ light intensity on a clear day at noon at the Totem Field at UBC. Size hierarchy for plant height significantly increased with decreasing light intensity. Size hierarchy at 22% light intensity was 67% higher compared to that at 100% sunlight. Size hierarchy of shoot biomass was not affected by light level. The magnitude of several growth/morphological characters decreased with decreasing light intensity. Since light treatments were applied to relatively uniform populations, effect of light intensity on size hierarchy could possibly be due to genetic variability within a pigweed population.

In order to study the effect of light intensity on FR transmission through leaves, plants were subjected to four light intensity treatments as described above. Lambsquarters and bean leaves developed at 22% light intensity transmitted higher FR light, compared to those developed at 100% sunlight. There was a weak negative correlation between specific leaf weight and FR transmission in PW (*R²* = 0.16) compared to bean (*R²* = 0.78) and lambsquarters (*R²* = 0.69) leaves. FR transmission from pigweed leaves was generally higher compared to lambsquarters and bean leaves but there was no consistent and/or significant difference in FR transmission through pigweed leaves developed at different light intensities. The leaf position on plant stem did not influence FR transmission in this study. These results show that light intensity influences FR transmission characteristics of leaves and the three species employed in this study differ in this regard. Leaf optical properties as well as leaf area should therefore be considered while assessing plant-plant interactions in mixed populations.
Preface

This dissertation is original, unpublished, and independent work by the author, Rashmi Gaire. Part of this work (Chapter 2) was presented as a poster entitled “Effect of light intensity on growth, morphology and size hierarchy of redroot pigweed (*Amaranthus retroflexus* L.)” at the 2014 Joint Annual Meeting of Weed Science Society of America and Canadian Weed Science Society in Vancouver, British Columbia, Canada. Another part of this work (Chapter 3) was also presented as a poster entitled “Effect of light intensity on transmission of far-red light through leaves of lambsquarters, redroot pigweed, and bush beans” at the 2014 Joint Annual Conference of Canadian Society of Agronomy and Canadian Society for Horticultural Science in Lethbridge, Alberta, Canada.
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Chapter 1. General Introduction and Literature Review

1.1 General Introduction

Size hierarchy or size inequality, a common feature of natural populations, refers to the presence of individuals with different sizes from large to small in a population (Buston and Cant 2006). Plants within a population differ in their size even when they emerge at the same time and the size differences increase with time. Size inequality has ecological and evolutionary importance. For example, in a population with a larger size hierarchy; smallest plants suffer density dependent mortality (Weiner 1985). Only the larger plants will survive to maturity and pass on their genes to the next generation (Heywood 1986). This reduces the gene pool of the smaller plants and decreases genetic diversity (Weiner 1985).

It is important to study the causes of size hierarchy formation because it is closely related to plant fitness and reproduction. Many factors like seed size, emergence time, competition for resources and genetics are known to influence size inequality (Tilman 1982). Competition for resources is widely regarded as the most dominant factor influencing size hierarchy. Size hierarchy thus reflects the existence of competition amongst individuals within plant population (Buston and Cant 2006), which might be asymmetric (e.g. for light) or symmetric (e.g. for nutrients) (Weiner and Thomas 1986). When the competition is symmetric, individuals use the same amount of resources irrespective of their size, whereas when competition is asymmetric larger individual obtain disproportionate share of the resources (Weiner 1990). Competition for light is usually asymmetric and conventionally is seen as major determinant of the population structure. Larger plants intercept more light thereby shading and suppressing the growth of smaller plants but not vice versa (Schwinning and Weiner 1998).
Lorenz curves and Gini coefficient (G) have been recommended and widely used to evaluate inequalities in economics and ecology (Weiner and Solbrig 1984). The Lorenz curve ranks the individuals by size (from the smallest to the largest). It is a graph of the cumulative percentage of the plants population (x) plotted against the cumulative percentage of the variables (y) whose inequality is to be evaluated. The Lorenz curve with straight diagonal line represents a population with perfect equality where all individuals are of the same size (Weiner and Solbrig 1984; Damgaard and Weiner 2000). Inequality within a population gives a curve below the straight diagonal line. The total amount of inequality can be summarized by the G. G quantifies the area enclosed by the Lorenz curve and the line of perfect equality (Weiner 1985). G ranges from a minimum value of zero, when all individuals are equal (perfect equality), to a theoretical maximum value of one, indicating the sizes of all individuals except one are zero (Weiner and Solbrig 1984).

Light striking the leaf surface is partly absorbed, transmitted or reflected. In the visible light spectrum range, most of the blue and red light is absorbed whereas green and far-red light (FR) is mostly either reflected or transmitted. This is why: the light transmitted through the leaves has a much greater proportions of FR than the light that reaches the leaf surface under unshaded conditions. Therefore, under natural conditions plants growing in shade are not only subjected to a reduced light quantity but also experience an altered light quality (a lower R/FR ratio) due to the selective absorbance and reflectance of different wavelengths by leaves. It is through the use of the R/FR photoreceptor phytochromes that plants are able to detect alterations in the spectral composition of sunlight, recognize the light signal and then react via the shade avoidance response (Ballare et al. 1994; Smith 2000). Holmes and Smith (1977) found a very small variation in R/FR ratio due to climatic and cloud conditions. They reported that
proportions of red and far-red lights (655-665 nm/725-735 nm) in daylight remained nearly constant ($R/FR \approx 1.15 \pm 0.02$), irrespective of the time of the year and weather conditions. The ratio however ranges between 0.1 to 0.7 under a leaf canopy. $R/FR$ ratio is influenced by the proximity, architecture and optical properties of neighbouring plants (Casal and Smith 1989).

Many studies show that leaf optical properties (reflectance, transmittance, or absorptance) are influenced by physiological stresses (Carter and Knapp 2001). These stresses include dehydration, flooding, freezing, ozone, herbicides, competition, disease, insects, and deficiencies in ectomycorrhizal development and N fertilization on wide range of species; from grasses to conifers and deciduous trees (Lee and Graham 1986; Carter and Knapp 2001; Serbin et al. 2012). The optical properties are influenced by stress at the visible wavelength (400-720 nm) and changes in narrower band near 700 nm are more crucial for plant stress detection and estimation of chlorophyll concentration (Carter and Knapp 2001). While changes in leaf optical properties caused by common stressors are similar, the extent of response to a particular stress may vary among species (Carter 1993; Carter and Knapp 2001).

Plant competition for light is common in natural as well as agricultural systems. Variation in light environments influences competition as well as survival in plant populations (Smith 2000). Weeds under a crop canopy receive light with lower $R/FR$ ratio due to the higher transmission of FR through the leaves. Light environment affects the growth of neighbouring plants and/or of plants growing under a canopy, which influences the size of plants in a population. $R/FR$ ratio serves as an initial signal for competition and triggers morphological and physiological changes in plant population (Page et al. 2010). Individuals within a population may experience different $R/FR$ ratio due to the difference in optical properties of leaves at different age and at different position in a plant stem. Under low $R/FR$ ratio plants express shade-
avoidance responses which favour stem elongation. Differences in height among individuals within a population lead to the development of size inequality within the population (Franco and Harper 1988; Weiner 1990). There are not many studies on effects of light intensity on the size hierarchy or the effect of leaf age or leaf position on the optical properties in weedy species. The overall goal of this research was to increase our understanding of effects of light intensity on development of size inequality in weed population and transmission of FR light through plant leaves. This study is expected to improve our understanding of plant-plant interaction and the dynamics of size distribution within plant populations under different light intensities.

The specific objectives of this research were to determine:

1) the effect of light intensity on growth, morphology and size hierarchy of *Amaranthus retroflexus*,

2) the effect of light intensity during leaf development on transmission of FR light through leaves of *Phaseolus vulgaris, Amaranthus retroflexus* and *Chenopodium album*, and

3) if the transmission of FR light varies with leaf position on *C. album* stems.

This thesis is presented in a manuscript format with specific introduction, materials and methods, results and discussion for each chapter. Chapter 1 provides a general introduction and literature review relevant to this study. Chapter 2 investigates the effect of light intensity on growth, morphology and size hierarchy of *A. retroflexus* and *C. album* (Objective 1). The effect of light intensity on the transmission of FR light through leaves of *P. vulgaris, A. retroflexus* and *C. album* leaves is reported in Chapter 3 (Objective 2). General discussion and conclusions from this research are presented in Chapter 4.
1.2 Literature Review

This section briefly reviews relevant literature on the plant species used in this study, some general concepts concerning the optical properties of leaves, changes and the role of R/FR ratio in leaf canopy, and the size hierarchy and its importance in plant fitness.

1.2.1 Plant materials used in this study

1.2.1.1 Lambsquarters (*Chenopodium album* L.)

*C. album*, commonly known as lambsquarters, fat-hen, and white goosefoot is a broad-leaved summer annual weed of the family Chenopodiaceae. It has alternate, petiolated leaves which are oval or triangular with irregular margins. The upper surface of the older (lower) leaves is greenish and glabrous whereas the lower surface may be glabrous or covered with white powder with tiny white hairs. The upper (younger) leaves are similar in appearance to the lower leaves, except that they are smaller, narrower, and whiter due to the presence of tiny white glands present on both surfaces of leaves. It is primarily self-pollinated, although some wind mediated cross-pollination can occur (Bassett and Crompton 1978).

Lambsquarters is one of the worst weeds of the world. It is highly competitive weed in many cropping systems (Yerka et al. 2012). It releases allelochemicals into the soil which may inhibit or stimulate the germination and the growth of the neighbouring plants (Majeed et al. 2012). It is native to Europe and Asia and is found in cultivated or disturbed soil in every province of Canada (Bassett and Crompton 1978). It ranks amongst the 10 most important agricultural weeds in Saskatchewan (Thomas 1977; Beckie et al. 2008). It reproduces only from seeds (Bassett and Crompton 1978), which can remain viable in soil for over 20 years (Lewis
1973). So, frequently the best strategy to control lambsquarters is to destroy plants before they seed.

In recent years, lambsquarters has gained an increasing attention because of its nutritional value. Its grain is the source of vitamins B, C, E and Ca, Mg, K, Fe and proteins (Adedapo et al. 2011; Gqaza et al. 2013). It has been reported to be poisonous to sheep and swine when consumed in large quantities over a sufficient period of time (Bassett and Crompton 1978). *C. album* was chosen for this study because of its upright growth habit, competitive ability and prevalence in almost every cropping system.

1.2.1.2 Redroot pigweed (*Amaranthus retroflexus* L.)

Redroot pigweed (Family - Amaranthaceae) is a summer annual herb which reproduces only by seeds. It is also known as amarante a racine rouge, green amaranth, pigweed, redroot, rough pigweed, tall pigweed, amarante reflechie, and armarante pied rouge (OMAFRA 2003). Its stem is erect (0.5 to 2 m high), simple or branched, greenish to slightly reddish but usually red near the roots. The lower part of the stem is thick and smooth whereas the upper part is often rough with dense short hair (Burki et al. 1997). Leaves are alternate, long-stalked, ovate with usually indented or notched at the tip and smooth margins (Costea et al. 2004). The inflorescence is short, dense and branched (Costea et al. 2004). It bears unisexual flowers which are numerous, small, green and densely crowded into small finger like spikes forming 5 to 20 cm long panicles (Mitich 1997; Costea et al. 2004). It is mostly wind-pollinated but insect pollination may also occur under certain circumstances (Costea et al. 2004).
Native to North America, redroot pigweed was first collected in Canada from various sites in Quebec between the 17th and 18th century (Costea et al. 2004). It is listed as a noxious weed in Quebec and Manitoba and has now successfully spread to most provinces of Canada (Holm et al. 1991). It can survive a broad range of soil types, texture and pH levels but prefers a warm climate and fertile soils. It is among the world’s most troublesome agricultural weed found in 70 countries in 60 crops (Holm et al. 1991). Redroot pigweed grows rapidly, produces a large number of viable seeds and is reported to be more competitive than C. album (C3 species) because of its C4 photosynthetic pathway (Costea et al. 2004). The vigorous growth habit and allelopathic effects of pigweed helps this species strongly compete with other crops/plants leading to the loss of yield and quality (Murphy et al. 1996). Besides yield reduction, pigweed has been documented to have high levels of nitrates and oxalates that might be poisonous, potentially fatal to livestock if ingested in large quantities (Kerr and Kelch 1998).

*A. retroflexus* is used as a vegetable, forage, grain crop, ornamental plant and has some medicinal value (Costea et al. 2004). Stems and leaves can be a good source of Ca, protein and carbohydrates (Sleugh et al. 2001; Costea et al. 2004). *A. retroflexus* was selected for this study because of its world-wide economic importance in agricultural ecosystems.

### 1.2.1.3 Bush beans (*Phaseolus vulgaris* L.)

*P. vulgaris*, also known as common bean, string bean, field beans, flageolet bean, French bean, garden bean, haricot bean, pop bean or snap bean, is an annual herbaceous plant. It is a member of the Leguminosae family and is an important legume worldwide for human consumption. It is grown for its edible fruit; dry seeds or unripe fruits. There are many cultivated varieties which
are classified as bush beans or pole beans depending on their growth habit. Pole beans (climbers) are commonly cultivated in association with maize (*Zea mays*) whereas bush beans are mostly grown in monoculture (Gebeyehu et al. 2006).

Native to Latin America, *P. vulgaris* is now grown widely in temperate regions of both the old and the new world and in Africa (Francis et al. 1982; Santalla et al. 1995; Graham and Ranalli 1997). *P. vulgaris* is documented to occupy 85% of the area sown to different *Phaseolus* spp. in the world (Singh 2001). Dry seeds are rich in calories with average protein content of 22% (Santalla et al. 1995).

The roots of bean plant are mostly fibrous, with a single main root (Duke 1981). It has 3 to 7 trifoliate broad leaves on the main stem. Flowers are monoecious and thus predominantly self-pollinated. The color of flowers may be white, pink or purple. Flowering initiates 28 to 42 days after planting, with physiological maturity occurring in 60 to 65 days after planting (Graham and Ranalli 1997). *P. vulgaris* grows well under temperate climate (Gepts 2001). Bush bean varieties have a shorter stem which makes it unsuitable to grow under shaded communities. Weed infestation can reduce *P. vulgaris* yield by over 50% (Ngouajio et al. 1997) due to direct competition for light, moisture, and nutrients, as well as by harboring insects and diseases. Bush bean was used in this study because of its growth habit, economic importance, widespread occurrence and susceptibility to shading.

### 1.2.2 Leaf optical properties

Reflectance and transmission characteristics of leaf are functions of both the quantity and the quality of pigments (e.g. chlorophylls, carotenoids) and other biochemical contents (e.g. water,
cellulose, lignin, starch, proteins), foliar anatomy (e.g. epicuticular wax, leaf thickness, trichomes and cellular structure), and the physiological status such as water content (Mohammed et al. 2000). The decrease in absorption and increase in reflectance/transmittance are significant even with a very little reduction in chlorophyll concentration in FR wavelengths (Carter and Knapp 2001). Leaf aging and environmental stressors influences leaf optical properties by decreasing chlorophyll content (Leblon 1997). The variation in reflectance, transmittance and absorptance in 400-500 nm, 670-680 nm and in near-infrared spectra generally appears to be low for stressed compared to unstressed leaves (Carter and Knapp 2001). The concentration of carotenoids and other accessory pigments are high enough in stressed leaves to compensate for the reduced concentration of chlorophyll pigments, due to which absorption in the 400 to 500 nm waveband does not change significantly (Merzlyak et al. 1999). Meanwhile relatively large amounts of chlorophyll must be lost from leaves for the significant optical difference to occur in 670 to 680 nm wavebands (Carter and Knapp 2001). However, in the near infrared region, beyond 730 nm, the change in optical properties is not strongly related to the chlorophyll absorptivity; it is more related to change in leaf anatomy or water content in response to stress (Sinclair et al. 1973).

1.2.3 R/FR ratio under foliar canopy

Due to the optical properties of leaves, plant growing under the leaf canopy experiences not only different quantity but also different quality of light compared to the plants grown in full sunlight (Kasperbauer 1987; Schmitt and Wulff 1993). Light quality is the spectral distribution of the light that plants receive under a canopy or when growing close to or under the neighboring plants (Schmitt and Wulff 1993; Ballare and Scopel 1997). One aspect of the spectral properties of light
that changes as it passes through a leafy canopy is its R/FR ratio (Schmitt and Wulff 1993; Smith 2000). R/FR ratio under the foliar canopy is lower compared to the R/FR ratio above the canopy (Rajcan and Swanton 2001). Variables that are known to alter the R/FR ratio include solar angle, leaf orientation, plant density, and distance from the vegetative canopy (Ballare et al. 1987; Kasperbauer 1987; Smith et al. 1990; Ballare et al. 1994). A reduction in R/FR ratio serves as a signal for the detection of potential competitors. It is important to study the factors that affect R/FR ratio because this signal can influence plant fitness and increase plant to plant variability (Page et al. 2010). Seed germination is inhibited under crop canopies with less R/FR ratio (Gorski et al. 2013). Plants react to low R/FR ratio by triggering the shade-avoidance response in order to optimize their chance for survival. Shade avoidance syndrome includes internodal elongation, increased plant height, low root-to-shoot weight ratio, thinner leaves, and low leaf to stem weight ratio (Ballare et al. 1987; Ballare and Casal 2000). These responses are used as an attempt to outcompete neighboring plants by growing above them and capturing more R light. Corn plants, which experienced shade-avoidance early in their development due to a low R/FR ratio, partitioned less biomass in the developing ear and set fewer kernels per plant (Page et al. 2010). Corn seedlings in low R/FR environment showed shade avoidance syndrome and, by the time weeds were removed, had on average 1.1 fewer leaves, 11% less leaf area, 12% less leaf biomass and 10% less total biomass, compared to those grown under higher R/FR ratio.

1.2.4 Size hierarchy and plant fitness

Plants are plastic in their growth and display considerable size variation within populations. Plant populations have numerous small individuals and a few large ones that comprise most of a population’s biomass (Weiner 1985). Several approaches have been used to analyze variation in
plant populations. Size inequality has been traditionally derived using statistical measures of size distribution such as standard deviation, coefficient of variation and skewness. In recent years Lorenz curve and Gini coefficient (G) have been popularly employed in plant population studies to measure inequality (Damgaard and Weiner 2000). Lorenz curve and G have been used together to estimate size hierarchy because G alone does not contain all the information in the Lorenz curve; different Lorenz curves can have the same G (Weiner and Solbrig 1984). A comparison of G for different population is appropriate only if they have similar Lorenz curves. In order to get an unbiased evaluation of size inequality, unbiased G is achieved when multiplied by n/(n-1).

Size inequality in plant monocultures is strongly influenced by plant density. Weiner and Thomas (1986) found increased size inequality with increase in density in 88% of the experiments they surveyed. A large size hierarchy in the dense population is due to competition. Within a population where the competition for the aboveground resources (i.e., light) dominates, size hierarchy increases with density and with time within density treatments (Weiner and Thomas 1986). On the other hand if the competition for belowground resources (i.e., soil nutrients) dominates, size hierarchy either decreases or remains the same with increasing density and with time within density treatments (Weiner and Thomas 1986).

Size distribution/hierarchy is important to understand the structure and stability of a population. Plant fitness is strongly related to their size. Small plants not only bear the majority of the size dependent mortality in crowded population but also produce fewer seeds if they survive, than larger plants. Thus, size has a major influence on the fecundity of individual plants. Samson and Werk (1986) examined the relationship between plant size and the biomass of reproductive parts. They found that fecundity per unit plant weight in perennials often increase
with plant size. Larger plants produce more seeds per unit biomass than smaller ones (Samson and Werk 1986). They also reported that the variation in the number of seeds produced per unit biomass is more unequal than the variation in plant size.
Chapter 2. Effect of Light Intensity on Growth, Morphology and Size Hierarchy of Redroot Pigweed

2.1 Introduction

Plant size varies within a population. The majority of plants in most populations are relatively small and a few are large; the few large individuals contribute most to population biomass. Such a size distribution within a plant population is termed as size hierarchy or size inequality (Weiner and Solbrig 1984). Since size hierarchy has evolutionary, ecological and agricultural significance (Weiner 1985; Du et al. 2006), it is important to understand factors that lead to its development. Weiner (1985) reported that size hierarchy is influenced by age and genetic differences, environmental factors and competition for resources. Weiner (1986) concluded that under natural field conditions, environment is a more important factor in determining the size hierarchy than genetic differences.

Competition (symmetric or asymmetric) among plants within a population for resources has been considered a major determinant of population structure (Schiwinning and Weiner 1998). Competition for light, which commonly occurs in natural and agricultural ecosystems (Pierik et al. 2004), is a major factor in the development of size inequality within plant populations (Weiner 1990). It is typically asymmetric; some plants obtain a disproportionate share of the light. Larger plants shade smaller plants but smaller plants have little or no effect on the light availability to larger plants (Weiner 1986; Schiwinning and Weiner 1998). As a result size inequality increases with an increase in competition for light (Jurik 1991; Schiwinning and Weiner 1998).

Size hierarchy influences competitive interactions and plant fitness within a population (Weiner 1986). Due to crop breeding and intensive management (e.g. genetically uniform seed
size, fertilization, and irrigation) and a more controlled environmental conditions, size hierarchies in crop population is generally less compared to weeds, which often grow under crop canopy and are exposed to environmental stresses. Knowledge of the effects of environmental factors on size hierarchy is important to understand their effects on competitive interactions and the persistence of weedy species. The size hierarchy in monospecific plant populations has been investigated extensively in agricultural and forest crops (Benjamin and Hardwick 1986; Weiner and Thomas 1986; Du et al. 2006). However, there are very few studies on development of size hierarchy in weed populations (Jensen 1991; Jurik 1991; Brophy et al. 2008). Thus the objective of the research described in this chapter was to investigate the effect of light intensity on growth, morphology and size hierarchy of *Amaranthus retroflexus*. *A. retroflexus* was chosen for this study because of its upright growth habit and economic importance in cropping system (Bassett and Crompton 1978; Holm et al. 1991).

### 2.2 Materials and Methods

Field experiments were carried out at the Totem Field Laboratory of the University of British Columbia. The first experiment was carried out between May to July, and the second experiment between July to August in the year of 2013. The field had a cover crop of vetch (*Vicia* species) in year 2012 which was plowed and rototilled and no fertilizer was added. *A. retroflexus* (pigweed) seeds collected from the Totem Field Laboratory in 2010 were used for this study. Pigweed seeds were sown 1 cm deep in sandy loam soil (80% sand, 15% silt, 4% clay, and 7% organic matter). Plants were grown in monocultures in 1 m x 1 m plots at a density of 100 plants per plot. An equidistance stand was established using a 1 m x 1 m template with 100 holes at a distance of 1 cm for sowing seeds. Plots were kept weed free by manual weeding. Safeer Insecticidal Soap
(300 ml per 15 L of water) was applied in all plots in experiment 2 at 24 days after sowing to control aphid infestation.

2.2.1 Light intensity treatments

Pigweed plants were grown under four light intensities (22, 33, 55 and 100% of full sunlight) using 3, 2, 1 and 0 (control) layers of 18 x 16 (openings per inch) charcoal fibreglass insect screens (Phifer Inc., Tuscaloosa, AL), respectively to cover both the top and the sides of 1 m x 1 m x 1 m high frames using 0.5” polyvinyl carbonate pipes. These treatments represent 400, 600, 1,000 and 1,800 μE m⁻² s⁻¹ light intensity on a clear day at noon. Henceforth these treatments will be referred to as 22, 33, 55 and 100% light intensity treatments in this thesis. Light intensity was measured using a LI-185B photometer (LI-COR Inc., Lincoln, NE).

Light intensity treatments were applied to 2 week-old seedlings. For the measurement of plant height size hierarchy, 75 plants were randomly sampled from each plot and their height was measured. First observation was taken seven days after the start of light intensity treatment (DAT) in experiment 1 followed by four additional observations at 5-days intervals. In experiment 2, 85 plants per plot were sampled and the first observation was taken at 5 DAT followed by four additional observations at weekly intervals. The size hierarchy of the above-ground biomass was assessed at 23 DAT and 33 DAT in experiment 1 and 2, respectively. Plants were harvested, oven-dried at 60°C for 72 h and weighed. Ten plants per plot were randomly taken at harvest (23 DAT and 33 DAT in experiment 1 and 2, respectively) and the observations on plant height, above-ground biomass, branch number, branch length of lower three branches,
Figure 2.1. Field setup to study the effect of light intensity on size hierarchy of pigweed.
inflorescence length, inflorescence biomass and Spadmeter (SPAD-502) reading were taken. The number of branches in the main stem with length greater than 3 cm was recorded. The length of the lower three branches greater than 3 cm were measured. Length of the terminal inflorescence was measured and the inflorescence was weighed. Spadmeter readings were taken from the fully expanded upper leaves. Spadmeter reading is the measure of leaf greenness which correlates with the chlorophyll content of a leaf (Dwyer et al. 1991).

2.3 Statistical Analysis

Experiments were conducted using a randomized complete block design with five blocks (replications) per light treatment. Data for time-course of average plant height and size hierarchy for height (Gini coefficient) were analyzed using two-way analysis of variance (ANOVA), with time and treatment as fixed factors. Data for growth parameters were analysed using one-way ANOVA. Data were subjected to a generalized linear model procedure (PROC GLM) using SAS (ver. 9.3, SAS Institute Inc., Cary, NC). The experiment was repeated. The residuals were evaluated for equality of variance and for normality. The significance of the regression for each experiment was checked using an F-test at ($\alpha = 0.05$). If the regression was significant, a t-test was used to compare treatment means. The $\alpha$ values for mean comparisons were corrected using the Bonferroni correction method (Holm 1979).

The degree of size hierarchy was estimated by comparing Gini coefficient (G) (Weiner and Thomas 1986). G was calculated using the software “Lorenz curve graphing tool and Gini coefficient calculator” (http://www.peterrosenmai.com/lorenz-curve-graphing-tool-and-gini-coefficient-calculator). Calculated G values were multiplied by $n/(n-1)$ to give unbiased values
(G’). Higher G indicates higher size hierarchy within a population. G ranges from a minimum value of zero, when all individuals are equal (perfect equality), to a theoretical maximum value of one, indicating the sizes of all individuals except one are zero (Weiner and Solbrig 1984).

2.4 Results

2.4.1 Effect of light intensity on size hierarchy (Gini coefficient)

There was no significant (P ≤ 0.05) interaction between the effect of light intensity treatments and days after the start of light intensity treatments (DAT) in experiment 1. Both light intensity treatments and DAT significantly (P ≤ 0.05) affected the Gini coefficient (Fig. 2.2). Size hierarchy for plant height in pigweed (PW) population increased with decreasing light intensity (Fig. 2.2A). The size hierarchy in the population was significantly higher in 33 (G = 17.96) and 22% (G = 19.80) light intensity treatments compared to 100% (G = 14.70) sunlight. The plant height size hierarchy of PW population developed at 22% light intensity was 35% higher compared to those developed at 100% sunlight. The size hierarchy for plant height was significantly (P ≤ 0.05) higher at 7 DAT compared to that at 12, 18 and 23 DAT (Fig. 2.2B). However there was no significant (P ≤ 0.05) difference among G values at 12, 18 and 23 DAT. The size hierarchy at 7 DAT (G = 19.94) was 24% greater compared to that at 23 DAT (G = 15.09).

The light intensity treatments x DAT interaction was significant (P ≤ 0.05) in experiment 2. There was no significant (P ≤ 0.05) difference in the size hierarchy for plant height at different DAT in all four treatments (Table 2.1). However there was a significant (P ≤ 0.05) difference
Figure 2.2. (A) Influence of light intensity treatments on size hierarchy (G) of pigweed in experiment 1. The values are the means ± SE (5 replicates of 75 plants each) for 7, 12, 18 and 23 days after the start of light intensity treatments. Different lowercase letters above the histograms represent significantly (P ≤ 0.05) different means.

(B) Time course of effect of light intensity treatments on size hierarchy (G) of pigweed in experiment 1. The values are the means ± SE (5 replicates of 75 plants each) for four light intensity treatments. Different lowercase letters above the histograms represent significantly (P ≤ 0.05) different means.
<table>
<thead>
<tr>
<th>Percent of full sunlight</th>
<th>Days after treatment</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>5</td>
</tr>
<tr>
<td>100</td>
<td>10.5 ± 0.99 A,a*</td>
</tr>
<tr>
<td>55</td>
<td>13.2 ± 0.99 AB,a</td>
</tr>
<tr>
<td>33</td>
<td>13.6 ± 0.99 AB,a</td>
</tr>
<tr>
<td>22</td>
<td>15.8 ± 0.99 B,a</td>
</tr>
</tbody>
</table>

Light intensity treatment x days after treatment was significant ($P \leq 0.05$). The values are the means ± SE of five replicates of 85 plants each.

*Values followed by the same uppercase letter within a column and the same lower case letter within a row are not significantly ($P \leq 0.05$) different.
among treatments at different DAT (Table 2.1). The Gini coefficient was significantly (P ≤ 0.05) higher at 22% light intensity at all DAT compared to 100% sunlight. The size hierarchy of PW population developed at 22% light intensity was 50 and 203% greater compared to that at 100% at 5 DAT and 33 DAT, respectively. Generally, there was no significant (P ≤ 0.05) difference among 55, 33 and 22% light intensity treatments. But at 19 DAT and 26 DAT, size hierarchy was significantly higher at 22% compared to 55% light intensity treatments. There was no significant difference in the size hierarchy of PW above-ground biomass in both the experiments (Table 2.2).

2.4.2 Effect of light intensity on growth and morphology

The light intensity treatments x DAT interaction was significant (P ≤ 0.05) for height of PW plants in both experiments. Plant height significantly (P ≤ 0.05) differed with DAT in all light intensity treatments (Table 2.3). There was no significant (P ≤ 0.05) effect of light intensity on height of PW plants among different treatments up to 12 DAT in both experiments. At later stages of plant growth, plant height was significantly affected by light intensity. The plant height in 100% and 55% light intensity treatments did not differ significantly (P ≤ 0.05) in experiment 2 at all times. The height was generally 60% higher in 100% light intensity compared to 22% light intensity at 19 DAT, 26 DAT and 33 DAT in experiment 2. The increase in plant height from 7 to 23 DAT in experiment 1 was 421 and 234% in 100 and 22% of light intensity treatments, respectively. The increase in plant height from 5 DAT to 33 DAT was 1635% and 311% in 100% and 22% of light intensity treatments, respectively in experiment 2 (Table 2.3). Several growth and development parameters of PW decreased with decreasing light intensity (Table 2.4).
Table 2.2. Effect of light intensity treatments on size hierarchy (Gini coefficient) for above-ground biomass of pigweed at 23 (experiment 1) and 33 (experiment 2) days after the start of light intensity treatments.

<table>
<thead>
<tr>
<th>Percent of full sunlight</th>
<th>Gini coefficient</th>
<th>Experiment 1</th>
<th>Experiment 2</th>
</tr>
</thead>
<tbody>
<tr>
<td>100</td>
<td>45.77 ± 6.26 $a^*$</td>
<td>31.50 ± 7.15 $a$</td>
<td></td>
</tr>
<tr>
<td>55</td>
<td>48.69 ± 2.82 $a$</td>
<td>28.44 ± 2.69 $a$</td>
<td></td>
</tr>
<tr>
<td>33</td>
<td>45.81 ± 8.25 $a$</td>
<td>31.63 ± 1.16 $a$</td>
<td></td>
</tr>
<tr>
<td>22</td>
<td>47.40 ± 2.67 $a$</td>
<td>35.52 ± 5.84 $a$</td>
<td></td>
</tr>
</tbody>
</table>

The values are the means ± SE of five replicates of 75 and 85 plants each in experiment 1 and experiment 2, respectively.

*Values followed by the same letter within a row are not significantly (P ≤ 0.05) different.
Table 2.3. Time-course of effect of light intensity on plant height (cm) of pigweed.

<table>
<thead>
<tr>
<th>Percent of full sunlight</th>
<th>Days after treatment</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>7</td>
</tr>
<tr>
<td>100</td>
<td>11.2 ± 2.4 A,a*</td>
</tr>
<tr>
<td>55</td>
<td>15.8 ± 2.4 A,a</td>
</tr>
<tr>
<td>33</td>
<td>16.4 ± 2.4 A,a</td>
</tr>
<tr>
<td>22</td>
<td>14.1 ± 2.4 A,a</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Percent of full sunlight</th>
<th>Days after treatment</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>5</td>
</tr>
<tr>
<td>100</td>
<td>4.8 ± 2.1 A,a*</td>
</tr>
<tr>
<td>55</td>
<td>5.9 ± 2.1 A,a</td>
</tr>
<tr>
<td>33</td>
<td>6.1 ± 2.1 A,a</td>
</tr>
<tr>
<td>22</td>
<td>5.9 ± 2.1 A,a</td>
</tr>
</tbody>
</table>

The values are the means ± SE of five replicates of 75 and 85 plants each in experiment 1 and experiment 2, respectively.

*Values followed by the same uppercase letter within a column and the same lowercase letter and within a row are not significantly (P ≤ 0.05) different.
Table 2.4. Effect of light intensity on pigweed growth parameters.

<table>
<thead>
<tr>
<th>Growth parameters</th>
<th>Light intensity treatments (Percent of full sunlight)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>100</td>
</tr>
<tr>
<td><strong>Experiment 1</strong></td>
<td></td>
</tr>
<tr>
<td>Plant height (cm)</td>
<td>81.43 ± 7.53</td>
</tr>
<tr>
<td>Above-ground biomass (gm)</td>
<td>9.57 ± 2.52</td>
</tr>
<tr>
<td>Inflorescence length (cm)</td>
<td>6.27 ± 0.54</td>
</tr>
<tr>
<td>Inflorescence biomass (gm)</td>
<td>0.28 ± 0.01</td>
</tr>
<tr>
<td>Branch number</td>
<td>8.92 ± 0.68</td>
</tr>
<tr>
<td>Branch length (cm)</td>
<td>6.89 ± 1.59</td>
</tr>
<tr>
<td>Spadimeter reading</td>
<td>38.57 ± 2.50</td>
</tr>
<tr>
<td><strong>Experiment 2</strong></td>
<td></td>
</tr>
<tr>
<td>Plant height (cm)</td>
<td>96.86 ± 5.09</td>
</tr>
<tr>
<td>Above-ground biomass (gm)</td>
<td>5.39 ± 0.84</td>
</tr>
<tr>
<td>Inflorescence length (cm)</td>
<td>5.95 ± 0.47</td>
</tr>
<tr>
<td>Inflorescence biomass (gm)</td>
<td>0.23 ± 0.02</td>
</tr>
<tr>
<td>Branch number</td>
<td>8.03 ± 0.67</td>
</tr>
<tr>
<td>Branch length (cm)</td>
<td>8.64 ± 3.36</td>
</tr>
<tr>
<td>Spadimeter reading</td>
<td>44.37 ± 1.61</td>
</tr>
</tbody>
</table>

The values are the means ± SE of five replicates of 10 plants each. The observations were taken at 23 and 33 days after the start of light intensity treatments in experiment 1 and experiment 2, respectively.

*Values followed by the same letter within a row are not significantly (P ≤ 0.05) different.
All the parameters (except plant height, branch number and spadometer reading in experiment 1) peaked at 100% light intensity in both experiments. Values for these three remaining parameters were highest at 55% light intensity treatment. The lowest values were recorded at 22% light intensity treatment in both experiments. Except for branch number in experiment 1, all treatment effects were significant (Table 2.4). Plant height, above-ground biomass, inflorescence length, inflorescence biomass, and branch length at 100% light intensity was significantly greater compared to that at 33 and 22% light intensity treatments in both experiments (Table 2.4). Plants grown under 100% sunlight had 91, 69, 68 and 54% greater inflorescence biomass, aboveground biomass, branch length and branch number, respectively compared to those grown under 22% light intensity treatment in experiment 2. There was no consistent and/or significant difference in any of the growth parameters between 100 and 55% light intensity treatments.

2.5 Discussion

The results of this study show that (i) PW populations develop higher size hierarchy for plant height under lower light intensity, (ii) there was no influence of light intensity on size hierarchy for above-ground plant biomass, (iii) the size hierarchy for plant height decreased as plants grew, and (iv) the magnitude of several growth/morphological characters decreased with decreasing light intensity.

Higher size hierarchy (higher Gini coefficient) for plant height was observed at 7 DAT compared to 12, 18 and 23 DAT. However, the hierarchies at 12, 18 and 23 DAT did not differ significantly ($P \leq 0.05$) in experiment 1. Similarly, in experiment 2, there was no significant ($P \leq 0.05$) change in Gini coefficient in all four treatments at all DAT. Similar results have been
reported by Ellison and Rbinowitz (1989) in their study of effect of density on size hierarchy. Ellison (1987) also reported no change in size hierarchy in *Salicornia europaea* (pickleweed) in different growing seasons under different densities. Wilson (1988) in a study involving *Festuca ovina* competing for nutrients showed that size differences decreased with time because smaller plants had a higher growth rate compared to larger plants.

The results presented in this chapter show that the exposure of PW population to low light intensities increased the size hierarchy for plant height but the above-ground biomass allocation inequality within the population was not influenced. This might be because under full sunlight all plants in the population receive enough sunlight for photosynthesis and biomass production, thus all plants grow equally fast. By contrast, at lower light intensity the competition for light is high, thus size hierarchy for plant height increases, but the plants in the population do not get enough sunlight and all plants grow equally slowly. This was in agreement with Chu et al. (2009), who suggested that under intense competition and harsh environmental conditions all individuals in a population grow slowly resulting in substantially limited size divergence within plant population.

Several studies indicate that variations in height growth and size hierarchy for plant height are common features within plant populations (Weiner and Fishman 1994; Nasgashima and Terashima 1995; Nagashima et al. 1995; Nagashima 1999). When there is competition for light, height growth (shade-avoidance syndrome) will help individual plants to acquire more of the light resource. The results presented in this chapter (Table 2.3) show similar average plant height at earlier stages under all light intensities but in later stages of plant growth, average plant height was greater with higher light intensity. These results might demonstrate that the shade-avoidance syndrome in response to light competition occurred at earlier stages of plant growth.
However, as the competition for light increases further, an individual plant’s growth rate becomes very low, and therefore the mean height of plants decreases with decreasing light intensity at later stages of plant growth. It has been reported that once the shade-avoidance is expressed, the plants’ ability to utilise the same resources at the later stage of growth and development might be reduced which might decrease plant biomass and other growth parameters (Weing and Delph 2001). In this study plant biomass was lower at lower light intensities, presumably due to reduced light availability for carbon assimilation. Several researchers have reported higher above and below-ground biomass for unshaded than shaded plants (Kolb and Steiner 1990; Messier 1992; Begna et al. 2002).

The study presented in this chapter shows an increase in size hierarchy and reduction in mean biomass, height, number and length of branches, length and dry weight of inflorescence at lower light intensities. This suggests that intraspecific competition in PW populations could become more severe under environmental stresses. This is in agreement with many earlier studies (Weiner; 1985; Weiner 1990; Du et al. 2006) showing that size hierarchy can serve as an index of a population’s competitive status under environmental stress. The reduction in inflorescence length and weight with increase in size hierarchy suggested a negative correlation between levels of size hierarchy and reproductive allocation. This indicates lower plant fitness under low light intensity. Competition for light (asymmetric competition) has an important influence on the outcome of plant population dynamics during growth. Asymmetric competition can increase the initial small difference in the seedling size due to shade avoidance. Thus asymmetric competition can generate a size hierarchy resulting in large differences in the fate of individual plant (Thomas and Bazzaz 1993). Plants with small size, late germination or slow growth would be excluded faster with the increasing intensity of asymmetric competition.
(Weiner and Thomas 1986). Thus time of emergence and seedling growth rate may be important in determining the reproductive success of individuals within a population (Solbrig 1981; Thomas and Bazzaz 1993). Fecundity has been documented to decrease with increase in plant size variation in a population (Gottlieb 1977; Heywood 1986) and decrease in plant size (Aarssen and Taylor 1992). This study suggests that while PW survives wide range of light intensities (100 to 22% of full sunlight), its competitiveness and its reproductive potential might decrease at lower light intensity. As a result, PW might be less problematic in cropping system where the crop canopy is closed.
Chapter 3. Effect of Light Intensity on Transmission of Far-Red Light through Leaves of Redroot Pigweed, Lambsquaters, and Bush Beans

3.1 Introduction

Plant leaves allow more far red (690–720 nm) than red (660–680 nm) light to pass through thus altering the red:far-red ratio (R/FR) of the transmitted light. Because of the selective filtering of light through leaves, plants under extreme shade have a different light environment than those exposed to the full sunlight (Lee and Graham 1986). Leaf optical property influences the availability of photosynthetically active radiation at cellular level. Leaf optical characteristics (reflectance, transmittance, and absorption), particularly for the FR (690-720 nm wavelength) radiation are important in detecting plant stress (Carter and Knapp 2001). Reflectance of the FR light increases in response to environmental stresses (Carter and Knapp 2001). Unfavorable growing conditions result in morphological, physiological and/or biochemical changes that impact the manner with which plants interact with light. Reflectance characteristics of leaf in the 400-700 nm range are primarily influenced by the cellular level of colored pigments like chlorophyll, anthocyanins and carotenoids (Liew et al 2008). In turn the reflectance patterns of leaf have been employed to measure leaf chlorophyll content (Carter and Spiering 2002), N status (Tarpley 2000), xanthophylls and carotenoid pigment levels (Gamon 1997). Therefore, transmission, reflection and/or absorption of light by leaves can provide a thorough understanding of physiological responses to growth conditions and plant adaptations to the environment. Many researchers have pursued studies on remote sensing of biochemical and physiological traits of plant leaves and canopies based on their optical properties (Smith et al. 2002; Baltzer and Thomas 2005; Serbin et al. 2012). Souza and Valio (2003) reported that species differ with regard to effects of shading on leaf optical properties and chlorophyll content.
Leaf optical properties are affected by a wide range of biotic and abiotic stresses. The focus of most of the studies have been on the response of leaf optical characteristics to stressors such as gaseous pollutants (Carter et al. 1992), high temperature and CO₂ (Carter et al. 2000), UV-B radiation (Bornman and Vogelmann 1991), drought and nutrient deficiency (Carter 1993). Many studies on response of leaf optical properties to light have been conducted with tree species. Very few studies have addressed the changes in leaf optical properties of weedy species in response to light intensity. Effects of leaf position and leaf age on transmission of FR light through leaves of weedy species have not been investigated. Since weeds emerging after weed control often grow under crop canopy, they receive reduced irradiance and reduced R/FR ratio. The lower R/FR ratio is a critical environmental signal in plant-plant interactions. Reduction in R/FR ratio enables plants to sense the competition from neighbouring plants and respond to its neighbour by promoting stem elongation. Similarly, weeds emerging earlier may reduce the intensity and quality of radiation reaching the crops by direct interception and/or reflection of light. Changes in optical properties represent significant adaptations of plants to their environment. Adjustments to low light intensity may lead to alterations in leaf thickness, and chlorophyll and carotenoid contents per unit weight (Evans and Poorter 2001, Souza and Valio 2003). These changes in turn might affect the leaf optical properties (Lee et al. 1990, Vogelmann 1993). Study of transmission of FR light through leaves of weedy species and its modification by the environment may improve our understanding of adaptive strategies of weedy species under different environmental conditions. Light is an important environmental factor affecting growth and survival. The specific objective of the research described in this chapter was to investigate the effect of light intensity during leaf development on FR transmission through leaves of selected species (Phaseolus vulgaris, Amaranthus retroflexus and Chenopodium album).
3.2 Materials and Methods

Field experiments were carried out at the Totem Field of the University of British Columbia. The first experiment was carried out between May to July, and the second experiment between July to August in the year of 2013. *A. retroflexus* (pigweed), *C. album* (lambsquarters) and *P. vulgaris* (bush bean) seeds were sown in pots (4” wide and 4.5” deep). A single plant was grown in each pot containing sandy loam soil (77% sand, 15% silt, 7.5% clay, and 4.1% organic matter). Pigweed and lambsquarters seeds used in this experiment were collected from the Totem Field Laboratory of UBC in 2010. Bean seeds (Festina, BN119) were purchased from West Coast Seeds Ltd. Delta, BC, Canada. Pigweed and lambsquarters were chosen for this study because of their growth habit, widespread occurrence, and economic importance in cropping systems and are major weeds of bean. Bean, a broad leaved crop, can easily shade weeds growing under its canopy. Because of its short stature, it can also be easily shaded from weeds emerging earlier than it.

3.2.1 Light intensity treatments

Plants were grown under four light intensities (22, 33, 55 and 100% of full sunlight) using 3, 2, 1 and 0 (control) layers of 18 x 16 (openings per inch) charcoal fibreglass insect screens (Phifer Inc., Tuscaloosa, AL), respectively to cover both the top and the sides of 1 m x 1 m x 40 cm high frames made of 0.5” polyvinyl carbonate pipes. These treatments represent 400, 600, 1,000 and 1,800 µE m⁻² s⁻¹ light intensity on a clear day at noon at UBC’s Totem Field Laboratory. Henceforth these treatments will be referred to as 22, 33, 55 and 100% light intensity treatments in this thesis. Light intensity was measured using a LI-185B photometer (LI-COR Inc., Lincoln, NE).
FR transmission from leaves was measured using SKR 110 (660/730 nm) sensor and a SKR 100 meter (SKY Instruments Ltd. Llandrindod Wells, Powys, UK). For each leaf, the upper surface of the leaf was irradiated with a beam of light from Lumigrow FR bulb (740 nm peak; ECC – FR, Lumigrow, Inc. Novato, CA) mounted on a stand (Fig. 3.1). The FR bulb was mounted at a distance of 10 cm from the diffuser and the leaf sample was placed below the diffuser. The diffuser was used to scatter the light equally in all directions; it does not absorb any light, and thus passes 100% of the light it receives uniformly to the leaf sample placed below it.

Light intensity treatments were given to 2 week-old seedlings of the three species employed in this study. Time-course of effect of light intensity treatments and leaf position on transmission of FR light in lambsquarters was studied. Four observations (three in experiment 2) at weekly intervals starting from one week after the start of light intensity treatments were taken. Fully expanded 6th true-leaf was used to measure changes in FR transmission with time. To study the effect of leaf position, FR transmission through leaves at different positions on the plant was measured at four weeks after the start of light intensity treatments (three weeks in experiment 2).

Transmission of FR light through leaves of pigweed, lambsquarters and bean developed at different light intensities was compared. FR transmission through the leaves of these species was measured 3 week after the start of light intensity treatments. Fully expanded 6th true-leaves of pigweed and lambsquarters, and the third trifoliate leaves of bean were used for measurement. The transmission from all three leaflets of bean leaf was measured and the average calculated. Leaf dry weight and leaf area was measured and the specific leaf weight (mg cm$^{-2}$) of leaves developed at different light intensities was calculated. Specific leaf weight was used as a measure of leaf thickness (Liu and Stutzel 2004; Vile et al. 2005). Experiments were terminated three or four weeks after treatment as specified in the results section.
Figure 3.1. Setup for the measurement of far-red transmission through leaves.
3.3 Statistical Analysis

All experiments were conducted using a randomized complete block design with five replications per light treatment and were repeated. Statistical analyses were conducted using the SAS statistical package version 9.3, PROC GLM with a Type I error rate of $\alpha = 0.05$. The residuals were evaluated for equality of variance and for normality. The analysis of FR transmissions with time (weeks after treatment) and the effect of leaf position on transmission of FR light were tested using two-way ANOVA. The transmission of FR light through leaves of different species developed at different light intensity treatments was also tested using two-way ANOVA, with light intensity treatments and species as fixed effects. Data for two experiments were analysed separately because the results were not similar. The significance of the regression for each experiment was checked using the F-test ($\alpha = 0.05$). If the regression was significant, a t-test was used to compare treatment means. The $\alpha$ values for individual comparisons of means were corrected using the Bonferroni correction method (Holm 1979).

3.4 Results

3.4.1 Effect of light intensity on transmission of FR light through bush bean, lambsquarters (LQ) and redroot pigweed (PW) leaves.

3.4.1.1 Effect of light intensity on transmission of FR light

The interaction between light intensity treatments and species was significant ($P \leq 0.05$) in influencing the transmission of FR light through leaves. FR transmission generally increased with decreasing light intensity in LQ and bean in both experiments (Table 3.1). But in PW, there was no consistent and/or significant ($P \leq 0.05$) difference in the FR transmission through leaves.
developed at different light intensities (Table 3.1). Both bean and LQ transmitted significantly (P ≤ 0.05) higher FR light from leaves developed at 22% compared to those developed at 100% light intensity; the increase was higher in case of LQ in both experiments. The FR transmission was 22 and 12% higher in LQ and bean leaf developed at 22% light intensity, respectively compared to those developed at 100% sunlight (Table 3.1). Generally, there was no significant (P ≤ 0.05) difference between 55 and 33% light intensity treatments in any of the three species except for LQ in experiment 1.

FR transmission from PW leaf was generally higher compared to LQ and bean leaves at all light intensity treatments (Table 3.1). PW leaves at higher (100 and 55%) light intensities transmitted significantly (P ≤ 0.05) higher FR light compared to bean and LQ leaves in experiment 2 but not in experiment 1. FR transmission from PW leaves (10.86 µmol m⁻² s⁻¹) developed at 100% sunlight was 19 and 12% higher than LQ (8.78 µmol m⁻² s⁻¹) and bean (9.55 µmol m⁻² s⁻¹) leaves, respectively. Similarly, PW leaves developed under 55% light intensity transmitted 10 and 9% greater FR light than LQ (9.76 µmol m⁻² s⁻¹) and bean (10.11 µmol m⁻² s⁻¹) leaves, respectively (Table 3.1). However, the three species did not differ significantly (P ≤ 0.05) in FR transmission at lower (33 and 22%) light intensities.

3.4.1.2 Effect of light intensity on specific leaf weight (SLW)

Neither light intensity nor species influenced SLW in experiment 1 (Figure 3.2). However, in experiment 2, there was a significant (P ≤ 0.05) effect of light intensity treatments as well as of species on SLW (Fig. 3.3). SLW of bean was 19% higher than the PW leaves (Fig. 3.3A). SLW was significantly (P ≤ 0.05) higher for the leaves developed at higher light intensity compared to
those developed at lower light intensity (Fig. 3.3B). Specific leaf weight was significantly (P ≤ 0.05) higher in 100% compared to all other light intensity treatments. The leaves developed at 100% (6.1 mg cm\(^{-2}\)) had 46% higher (P ≤ 0.05) SLW than those at 22% (3.3 mg cm\(^{-2}\)) light intensity. There was no significant (P ≤ 0.05) difference in SLW among leaves developed at 55 (5.0 mg cm\(^{-2}\)) and 33% (4.3 mg cm\(^{-2}\)) light intensity treatments.

### 3.4.1.3 Relationship between transmission of FR light and SLW

A negative correlation between FR transmission and SLW was observed but R\(^2\) values were different for the three species (Fig. 3.4A,B,C). Generally, a strong negative correlation between SLW and FR transmission in bean (R\(^2\) = 0.78) and LQ (R\(^2\) = 0.69) but a relatively weak correlation (R\(^2\) = 0.16) in PW (Fig. 3.4B) was observed. R\(^2\) for both experiments as well as the average of the two experiments are given in Fig. 3.4A,B,C.

### 3.4.2 Effect of light intensity and leaf position on transmission of FR light through lambsquarters leaves

FR transmission through LQ leaves generally differed significantly (P ≤ 0.05) both with light intensity treatments during leaf development (Table 3.2) and weeks after the start of light intensity treatments (Table 3.3). However, the interaction between light intensity treatments and weeks (wk) after start of the treatment was not significant (P ≤ 0.05). Leaves developed at 100% light intensity transmitted significantly (P ≤ 0.05) lower FR light compared to those developed at 33 and 22% light intensity in both experiments. There was no significant (P ≤ 0.05) difference in FR transmission through LQ leaves developed under 55 and 33% light intensity treatments (Table 3.2).
Table 3.1. Effect of light intensity during leaf development on FR transmission through leaves of lambsquarters, pigweed and bean.

<table>
<thead>
<tr>
<th>Species</th>
<th>FR transmission (µmol m⁻² s⁻¹)</th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>100</td>
<td>55</td>
<td>33</td>
<td>22*</td>
</tr>
<tr>
<td><strong>Experiment 1</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lambsquarters</td>
<td>9.50 ± 0.23 a,A**</td>
<td>9.82 ± 0.20 a,A</td>
<td>11.16 ± 0.20 b,AB</td>
<td>11.46 ± 0.20 b,A</td>
</tr>
<tr>
<td>Pigweed</td>
<td>10.88 ± 0.20 a,B</td>
<td>11.18 ± 0.20 ab,B</td>
<td>12.10 ± 0.23 b,A</td>
<td>11.45 ± 0.23 ab,A</td>
</tr>
<tr>
<td>Bean</td>
<td>10.12 ± 0.20 a,AB</td>
<td>10.37 ± 0.20 ab,AB</td>
<td>10.63 ± 0.20 ab,B</td>
<td>11.33 ± 0.20 b,A</td>
</tr>
<tr>
<td><strong>Experiment 2</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lambsquarters</td>
<td>8.78 ± 0.14 a,A</td>
<td>9.76 ± 0.14 b,A</td>
<td>10.29 ± 0.14 bc,A</td>
<td>10.87 ± 0.14 c,A</td>
</tr>
<tr>
<td>Pigweed</td>
<td>10.86 ± 0.14 a,B</td>
<td>10.88 ± 0.14 a,B</td>
<td>10.60 ± 0.14 a,A</td>
<td>11.18 ± 0.14 a,A</td>
</tr>
<tr>
<td>Bean</td>
<td>9.55 ± 0.14 a,C</td>
<td>10.11 ± 0.14 ab,C</td>
<td>10.20 ± 0.14 ab,A</td>
<td>10.72 ± 0.14 b,A</td>
</tr>
</tbody>
</table>

Values are means ± SE of five replicates of one plant each.

*Percent of full sunlight.

**Values followed by the same uppercase letter within a column and the same lowercase letter within a row are not significantly (P ≤ 0.05) different.
Figure 3.2. (A) Specific leaf weight of lambsquarters, pigweed and bean in experiment 1. Values are means ± SE of the four light intensities (22, 33, 55 and 100% of full sunlight) with five replicates of one plant each per light intensity treatments. Different letters above the histograms represent significantly (P ≤ 0.05) different means.

(B) Effect of light intensity during leaf development on the specific leaf weight in experiment 1. Values are means ± SE of three species (lambsquarters, pigweed and bean) with five replicates of one plant each per species. Different letters above the histograms represent significantly (P ≤ 0.05) different means.
Figure 3.3. (A) Specific leaf weight of lambsquarters, pigweed and bean in experiment 2. Values are means ± SE of the four light intensities (22, 33, 55 and 100% of full sunlight) with five replicates of one plant each per light intensity treatments. Different letters above the histograms represent significantly (P ≤ 0.05) different means.

(B) Effect of light intensity during leaf development on the specific leaf weight in experiment 2. Values are means ± SE of three species (lambsquarters, pigweed and bean) with five replicates of one plant each per species. Different letters above the histograms represent significantly (P ≤ 0.05) different means.
Figure 3.4. Correlation between specific leaf weight and FR transmission through leaves of lambsquarters (A), pigweed (B) and bean (C). Values are for fully expanded 6th true leaf of lambsquarters and pigweed and the average of 3 leaflets of the 3rd true leaf of bean.
<table>
<thead>
<tr>
<th>Treatment (Percent of full sunlight)</th>
<th>FR transmission (µmol m(^{-2}) s(^{-1}))</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Experiment 1</strong></td>
<td></td>
</tr>
<tr>
<td>100</td>
<td>10.16 ± 0.10 ( a^* )</td>
</tr>
<tr>
<td>55</td>
<td>10.42 ± 0.10 ( ab )</td>
</tr>
<tr>
<td>33</td>
<td>10.78 ± 0.10 ( bc )</td>
</tr>
<tr>
<td>22</td>
<td>11.11 ± 0.10 ( c )</td>
</tr>
<tr>
<td><strong>Experiment 2</strong></td>
<td></td>
</tr>
<tr>
<td>100</td>
<td>9.48 ± 0.11 ( a^* )</td>
</tr>
<tr>
<td>55</td>
<td>10.04 ± 0.11 ( b )</td>
</tr>
<tr>
<td>33</td>
<td>10.38 ± 0.11 ( b )</td>
</tr>
<tr>
<td>22</td>
<td>10.95 ± 0.11 ( c )</td>
</tr>
</tbody>
</table>

Values are the means ± SE of the observations taken on 6\(^{th}\) fully expanded true leaf at different weeks after the start of light intensity treatments (1, 2, 3 and 4 weeks in experiment 1 and 1, 2 and 3 weeks in experiment 2) with five plants each time.

*Values followed by the same letter within experiment are not significantly (\( P \leq 0.05 \)) different.
Table 3.3. Time-course of effect of light intensity treatments during leaf development on transmission of FR light through lambsquarters leaf.

<table>
<thead>
<tr>
<th>Time (Weeks after treatment)</th>
<th>FR transmission (µmol m⁻² s⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Experiment 1</strong></td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>9.99 ± 0.10 a*</td>
</tr>
<tr>
<td>2</td>
<td>10.49 ± 0.10 b</td>
</tr>
<tr>
<td>3</td>
<td>10.91 ± 0.10 c</td>
</tr>
<tr>
<td>4</td>
<td>11.10 ± 0.11 c</td>
</tr>
<tr>
<td><strong>Experiment 2</strong></td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>9.80 ± 0.09 a*</td>
</tr>
<tr>
<td>2</td>
<td>10.10 ± 0.09 a</td>
</tr>
<tr>
<td>3</td>
<td>10.73 ± 0.10 b</td>
</tr>
</tbody>
</table>

Values are the means ± SE of the observations taken on 6th fully expanded true leaf at four different treatments (22, 33, 55 and 100% light intensity) with five plants per treatment.

*Values followed by the same letter within experiment are not significantly (P ≤ 0.05) different.
Transmission of FR light through LQ leaves increased with increase in weeks after the start of light intensity treatments (Table 3.3). Leaves transmitted significantly (P ≤ 0.05) more FR light at 3 and 4 weeks (wk) after the start of light intensity treatments compared to those at 1 wk after the start of light intensity treatments in experiment 1 (Table 3.3). LQ leaves transmitted 5, 9 and 11% more FR light at 2, 3 and 4 wk, respectively compared to those at 1 wk after the start of light intensity treatments in experiment 1 (Table 3.3). No significant (P ≤ 0.05) effect of leaf position was observed on the transmission of FR light through LQ leaves (Table 3.4).

3.4.3 Effect of light intensity and leaf age on SLW of lambsquarters
The light intensity treatments and the time after the start of light intensity treatments significantly (P ≤ 0.05) affected the SLW of LQ (Fig. 3.5). The interaction between light intensity treatments and time after the start of light intensity treatments was not significant (P ≤ 0.05). The SLW of LQ decreased with the decreasing light intensity (Fig. 3.5A). The leaf developed at 100% sunlight had significantly (P ≤ 0.05) higher SLW compared to those developed at 33 and 22% light intensities (Fig. 3.5A). SLW was 19, 34, and 46% lower for leaf developed at 55, 33 and 22% light intensity, respectively compared to those developed at 100% sunlight in experiment 2.

SLW increased significantly (P ≤ 0.05) with increase in time after the start of light intensity treatments in both experiments (Fig. 3.5B). The SLW at 3 and 4 wks after treatment was significantly (P ≤ 0.05) greater compared to the leaves at 1 week after the treatment in experiment 1; the difference in SLW of LQ at 2, 3 and 4 wks after treatment was not significant (P ≤ 0.05). In experiment 2, SLW at 3 wks after treatment was 19 and 37% higher compared to those at 1 and 2 wks after treatment, respectively.
Table 3.4. Effect on leaf position on transmission of FR light through leaves of lambsquarters.

<table>
<thead>
<tr>
<th>Leaf position</th>
<th>FR transmission</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Experiment 1</strong></td>
<td></td>
</tr>
<tr>
<td>7</td>
<td>10.49 ± 0.16 a*</td>
</tr>
<tr>
<td>8</td>
<td>10.19 ± 0.16 a</td>
</tr>
<tr>
<td>9</td>
<td>10.33 ± 0.15 a</td>
</tr>
<tr>
<td>10</td>
<td>10.48 ± 0.14 a</td>
</tr>
<tr>
<td>11</td>
<td>10.36 ± 0.14 a</td>
</tr>
<tr>
<td>12</td>
<td>10.44 ± 0.15 a</td>
</tr>
<tr>
<td>13</td>
<td>10.25 ± 0.15 a</td>
</tr>
<tr>
<td><strong>Experiment 2</strong></td>
<td></td>
</tr>
<tr>
<td>6</td>
<td>9.98 ± 0.21 a*</td>
</tr>
<tr>
<td>7</td>
<td>9.86 ± 0.21 a</td>
</tr>
</tbody>
</table>

Values are the means ± SE of the observations taken on 20 plants receiving four different treatments (22, 33, 55 and 100% light intensity) with five plants per treatment.

*Values followed by the same letter within same experiment are not significantly (P ≤ 0.05) different.
Figure 3.5. (A) Effect of light intensity during leaf development on specific leaf weight of lambsquarters in experiment 1 (□) and experiment 2 (■). Values are means ± SE of four weeks (three in experiment 1) observations with five replicates of one plant per week. Different lowercase and the uppercase letters above the histograms represent significant (P ≤ 0.05) differences in means in experiment 1 and experiment 2, respectively.

(B) Effect of weeks after the start of light intensity treatments on specific leaf weight of lambsquarters in experiment 1 (□) and experiment 2 (■). Values are means ± SE of four light intensity treatments with five replicates of one plant per light intensity. Different lowercase and the uppercase letters above the histograms represent significant (P ≤ 0.05) differences in means in experiment 1 and experiment 2, respectively.
3.5 Discussion

Results of this study show that (i) the low light intensity during leaf development decreases the SLW and increases FR transmission through leaves, (ii) both the SLW and FR transmission increase with leaf age in LQ (iii) there is relatively low negative correlations between SLW and FR transmission in PW, compared to LQ and bean leaves, and (iv) SLW and FR transmission in PW was least affected by light intensity treatments during leaf development. Leaf position on plant stem did not influence FR transmission in this study.

In nature, leaves have to cope with reduced light intensities due to shading by neighbouring plants. The leaves developed at higher light intensity displayed significantly higher SLW (a measure of thickness) compared to those developed at lower light intensity in this study (Fig. 3.3B and 3.5A). Other studies have also reported thicker leaves of plants grown under higher light intensities (Lichtenthaler et al. 1981; Araus and Hogan 1994; Baltzer and Thomas 2005). It has been suggested that the change in sun light intensity signals the plant to adjust physiological processes for better adaptation and survival under new light environment (Kasperbauer 1987; Evans and Poorter 2001; Souza and Vailo 2003). Leaf thickness, leaf density, and mesophyll cell surface area and volume per leaf surface area increases with the increase in light intensity (Chabot and Chabot 1977). Under low light intensity, no palisade layer is developed and leaves are thin with only loose network of poorly differentiated cells in the mesophyll (Chabot and Chabot 1977). The mean absorption path of light within leaves increases with increased leaf thickness which in turn affects the light transmitted through leaves. Prasad (1997) reported that leaf absorbance increases while leaf transmittance decreases with the increase in the thickness of leaf. Thus light intensity by influencing the leaf thickness/anatomy alters the light quality under canopy by changing the leaf optical properties (Holmes and Smith...
The results presented in this chapter show an increase in FR transmission through leaves with decreasing light intensity and increase in weeks after the start of light intensity treatments. Leaf aging or environmental stresses are well known to reduce chlorophyll content and leaf thickness (Sims and Gamon 2002). Leaf thickness is considered to be the best indicator of leaf transmittance, reflectance and absorbance (Knapp and Carter 1998).

This study shows that light intensity during leaf development influences FR transmission through LQ leaves more than that from PW leaves. A small change in incident light can therefore alter the light environment under LQ canopy and affects plant-plant interaction by changing the R/FR ratio. FR transmission in PW on the other hand seems to be less sensitive to the changes in light intensity and could have less probability of altering the light environment in the crop canopy with a small change in incident light. Gorski et al. (2013) reported that germination is not induced under crop canopies with a reduced R/FR ratio. A high R/FR ratio is a positive regulator of plant defense against insects (Ballare et al. 2012). In a variety of herbaceous species an increase in insect herbivory and disease severity was observed when grown under lower R/FR ratio (Moreno et al. 2009). Result of this study shows higher transmission of FR light through PW leaves resulting in lower R/FR ratio below them compared to LQ and beans at all light intensities. This suggests that a plant growing under PW might be more susceptible to insects and diseases. PW might exert greater influence on seed germination and plant growth under its canopy at all light intensities. By contrast, crops grown under LQ canopy might be influenced more only under lower light intensities. The lack of a consistent effect of light intensity on FR transmission might be due to variability in anatomical properties of leaves (Prasad 1997). Bean leaves were thicker than PW leaves (Fig. 3.3A). LQ leaves contain epicuticular wax. It is reported that soft flexible, thin leaves have a higher transmittance than hard, coarse and thick
leaves. Surface reflectance is large when there is a wax covering, trichome or other specialized structure (Prasad 1997).

LQ and PW are competitive weeds of agricultural ecosystem. PW might maintain its competitiveness by transmitting higher FR and decreasing the R/FR ratio below canopy while LQ might do it by adjusting its FR transmission with the change in light environment.
Chapter 4. General Discussion

Weeds growing under crops often deal with reduced quantity and altered quality of light due to shading. The light environment can affect the growth of neighbouring plants and/or of plants growing under a canopy, which influences the plant size and morphology. Competition for light, which commonly occurs in natural and agricultural ecosystems, is a major factor in the development of size hierarchy within plant populations. Individuals within a population may experience different R/FR ratios due to differences in optical properties of leaves due to age, position on the stem and species. Under low R/FR ratio, plants express a variety of shade-avoidance responses including stem elongation. Effects of leaf age or leaf position on the optical properties and of light intensity on size hierarchy have not been studied in weedy species. Field experiments were conducted to determine the effects of light intensity on development of size hierarchy in a weed population and transmission of FR light through leaves. Results from this study improve our understanding of underpinnings of plant-plant interaction and of the dynamics of size distribution within plant populations under different light intensities.

4.1 Light Intensity and Size Hierarchy

The growth and size inequality of pigweed population at different light intensities was assessed (Chapter 2). Results showed a strong influence of light intensity on size hierarchy.

1) The results showed a close correlation between size hierarchies and light intensity in PW populations. PW populations developed higher size hierarchy for plant height under lower light intensity. The results might suggest that size hierarchy may serve as an adaptive strategy for populations under stressful conditions.
2) The size hierarchy for plant height in PW decreased as plants grew. A decrease in size differences with time might occur because smaller plants had a higher growth rate compared to larger plants.

3) The magnitude of several growth/morphological characters of PW decreased with decreasing light intensity. The reduction in inflorescence length and weight with increase in size hierarchy suggested a negative correlation between levels of size hierarchy and reproductive allocation. The size of PW soil seed bank may therefore decrease over time when population size hierarchy is high.

In this study, the increase in size hierarchy and reduction in growth parameters along with the decrease in light intensity could indicate that intraspecific competition in PW populations might become more severe under greater light intensity stress.

### 4.2 Light Intensity and FR Transmission of Leaves

Light intensity influenced transmission of FR light through leaves (Chapter 3). It was found that:

1) Light intensity during leaf development affects the SLW and FR transmission through leaves. The FR transmission increased and SLW (leaf thickness) decreased at lower light intensity. Thinner leaves transmitted more FR light. The results might suggest that the change in FR transmission might be partly due to the change in leaf thickness.

2) The negative correlation between SLW and FR transmission was lower in PW leaves compared to LQ and bean leaves. This could be because factors other than leaf thickness might be contributing to observed changes in leaf FR transmission in PW. The variation might be due to pigment concentration, cuticular thickness, and/or palisade thickness. It
would be interesting to study species-specific changes in the chemical and anatomical characteristics of leaves under different light intensities and to understand which leaf property contributes more to the optical property of leaves.

3) FR transmission increases with leaf age in LQ - older leaves of LQ transmit more FR light. These results might suggest that plants growing under the canopy of older LQ leaves might perceive more FR light and are more likely to express shade avoidance syndrome (e.g. stem elongation) compared to those grown under a younger LQ canopy.

4) FR transmission varied with species. FR transmission through PW leaves was least affected by light intensity treatments during leaf development. PW leaves at all light intensities during leaf development tended to produce lower R/FR ratio (higher FR transmission) below its canopy compared to bean and LQ. Leaf area is generally considered a major determinant of competitiveness of a species. However, species-specific differences in FR transmission by leaves can influence perception of competition by plants growing under the same leaf area of different species. For example, if bean is growing under LQ and PW canopy with same leaf area, bean plants under PW canopy might be more likely to express shade avoidance syndrome at all light intensities compared to those grown under LQ canopy.

Light intensity influences FR transmission through bean, lambsquarters and pigweed leaves and the three species differ in this regard. This effect may in part be due to the influence of light intensity on leaf thickness. Leaf optical properties as well as leaf area should therefore be considered while assessing plant-plant interactions in mixed populations.
Bibliography


