Effects of Seed Size and a Fungal Pathogen, *Colletotrichum coccodes*, on Population Dynamics of Velvetleaf *(Abutilon theophrasti* Medic.)

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Short title:

Effects of Seed Size and *Colletotrichum coccodes* on Velvetleaf Competition

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Abstract

Experiments were conducted in controlled and field conditions to determine the effect of seed size, a fungal pathogen (*Colletotrichum coccodes*), and soybean interspecific competition on the population dynamics of *Abutilon theophrasti* (velvetleaf). Seed size differences among ten individual *A. theophrasti* plants significantly ($P<0.001$) affected seed germination and dormancy. Higher seed viability (98%) was observed among seeds having a weight above 6.0 mg. The response of *A. theophrasti* plants that originated from two extreme seed size groups (small < 7mg and large >12mg) to the pathogen, *C. coccodes*, did not change over generations, and the most vigorous plants produced heavier seeds regardless of the initial seed size or infection with *C. coccodes*. Under field conditions, the application of *C. coccodes* and the herbicide, bentazon, did not affect the vegetative and reproductive biomass of *A. theophrasti* plants when grown in monospecific stands. However, a split application of *C. coccodes* and bentazon significantly reduced the aboveground biomass and reproductive output of *A. theophrasti* plants when grown in competition with soybean. The frequency distributions of *A. theophrasti* plant height, aboveground biomass, and stem diameter were positively skewed (L-shaped) when competing with soybean. However, *A. theophrasti* plant height and stem diameters were negatively skewed (J-shaped) and the aboveground biomass was positively skewed (L-shaped) in monospecific stands. The allometric relationships of *A. theophrasti* aboveground biomass and stem diameter in comparison with plant height were curvilinear when grown alone and when in the presence of soybean. However, aboveground biomass and stem diameter showed a simple linear relationship on a log-log scale in both monospecific stands and in competition with soybean.

Résumé

L'effet de la taille de la graine, d'un pathogène fongique (*Colletotrichum coccodes*) et de la compétition interspécifique du soja sur la dynamique de la population d'*Abutilon theophrasti* (abutilon) ont été déterminé par des expériences en champ et en milieu contrôlé. Les différences de taille de graines de dix individus d'*A. theophrasti* ont eu un effet significatif ($P<0.001$) sur la germination et la dormance de la graine. Une plus grande viabilité de la graine (98%) a été observée parmi les graines ayant un poids supérieur à 6.0mg. Les individus d'*A. theophrasti* provenant de deux groupes de taille de graine extrêmes ont invariablement réagi au pathogène *C. coccodes* à travers les générations, et les plantes les plus vigoureuses ont produit des graines plus lourdes malgré le poids initial de la graine ou l'infection avec *C. coccodes*. En monoculture, l'application de *C. coccodes* et de l'herbicide bentazon a significativement réduit la biomasse aérienne et reproductive des plantes d'*A. theophrasti* lorsqu'en compétition avec le soja. Les fréquences de distribution de la taille, de la biomasse aérienne et du diamètre de la tige d'*A. theophrasti* étaient positivement asymétrique (de forme L) lorsqu'en compétition avec le soja. Cependant, la taille de la plante et le diamètre de la tige d'*A. theophrasti* étaient négativement asymétrique (de forme J) et la biomasse aérienne était positivement asymétrique (de forme L) en monoculture. Les relations allométriques de la biomasse aérienne et du diamètre de la tige d'*A. theophrasti* en comparaison avec la taille de la plante, présentaient une relation curvilinéaire lorsque cultivé seul et en présence du soja. Toutefois, la biomasse aérienne et le diamètre de la tige présentaient une simple corrélation linéaire sur une échelle logarithmique en monoculture et en compétition avec le soja.

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Description of Thesis Format

This thesis is comprised of original papers that have been submitted to appropriate scientific journals for publication. In accordance with Part B, section 2 of the "Guidelines for Thesis Preparation" from the Faculty of Graduate studies and Research, McGill University, I quote the entire text that applies to this format:

> *"**2/ Manuscript and authorship**: Candidate have the option of including, as part of the thesis, the text of one or more papers submitted, or to be submitted, for publication, or the clearly-duplicated text (not the reprints) of one or more published papers. These texts must conform to the Thesis Preparation Guidelines with respect to font size, line spacing and margin sizes and must be bound together as an integral part of the thesis. (Reprints of published paper can be included in the appendices at the end of the thesis). The thesis must be more than a collection of manuscripts. All components must be integrated into a cohesive unit with a logical progression from one chapter to the next. In order to ensure that the thesis has continuity, connecting texts that provide logical bridges between the different papers are mandatory. The thesis must conform to all other requirements of the "Guidelines for Thesis Preparation" in addition to the manuscripts. The thesis must include the following: A table of content; an abstract in English and French; an introduction which clearly states the rationale and objectives of the research; a comprehensive review of the literature (in addition to that covered in the introduction to each paper); a final conclusion and summary; and rather than individual reference lists after each chapter or paper, one comprehensive bibliography or reference list, at the end of the thesis, after the final conclusion and summary. As manuscripts for publication are frequently very concise documents, where appropriate, additional materials must be provided (e.g., in appendices) in sufficient detail to allow a clear and precise judgement to be made of the importance and originality of the research reported in the thesis. In general, when co-authored papers are included in a thesis the candidate must have made a substantial contribution to all papers included in the thesis. In addition, the candidate is required to make an explicit statement in the thesis as to who contributed to such work and to what extent. This statement should appear in a single section entitled "Contribution of Authors" as a preface to the thesis. The supervisor must attest to the accuracy of this statement at the doctoral oral defense. Since the task of the examiners is made more difficult in these cases, it is in the candidate's interest to make clearly specify the responsibilities of all the authors and of the co-authored papers."*

In order for this thesis to be consistent with the above statement, it is structured in the following manner:

The thesis begins with abstracts in English and French, followed by a table of contents. Chapter 1 comprises a general introduction in which background knowledge and the current state of the research of the thesis subject is presented. This section concludes with an outline of the specific thesis objectives. The next six chapters constitute the body of this thesis, each chapter being a one complete manuscript.

The various manuscript chapters are linked via connecting texts so as to establish logical bridges between the different papers.

A general discussion and synthesis of the major conclusions of the thesis are presented in Chapter 8. The main contributions to knowledge of this research are outlined in Chapter 9. An appendices section is also included.

Manuscript from Chapters 2, 3, 4, 5, and 7 are co-authored by Drs. A.K. Watson and A. DiTommaso. The candidate (A.H. Baloch) performed all the experimental research, statistical analyses, and is the primary author of the manuscripts. Drs. A.K. Watson and A. DiTommaso provided supervisory guidance and assisted in manuscript preparation.

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Chapter 1. General introduction

1.1 Weeds and biological control

A weed can be defined as any plant or vegetation interfering with the objective or requirements of people (Holzner and Numata 1982). For the control of major infestations of these unwanted plants, modern agriculture has been highly dependent on large inputs of chemical herbicides. Herbicides play a major role in maintaining world crop production. In 1995, global sales of herbicides amounted to approximately $14.28 billion U.S. (Powles *et al.* 1997), however our continued reliance on these products is threatened by the evolution of herbicide resistance in many weedy plant species. Since the first report of a formerly susceptible weed population of *Senecio vulgaris* (common groundsel) acquiring resistance to triazines (Ryan 1970), there has been a rapid increase in the incidence of herbicide resistance worldwide, especially over the past 15 years (Powles *et al.* 1997). To date, 233 herbicide resistant weed biotypes (129 dicots and 104 monocots) have been reported in 45 countries (Heap 2000). At least 61 or perhaps more weed species including 42 dicots and 19 monocots, have evolved resistance to triazine herbicides. Herbicide resistance has also been observed for many other chemical herbicide families and a wide range of weed species (Heap 2000). For example, *Lolium rigidum* in Australia (Christopher *et al.* 1991), *Lactuca serriola*, *Kochia scoparia* (Primiani *et al.* 1990), *Lolium perenne* and *Salsola iberica* in the USA (Saari *et al.* 1992) have all evolved resistance to acetolactate synthase (ALS) inhibiting herbicides including imazethapyr (2-[4,5-dihydro-4-methyl-4-(1-methylethyl)-5-oxo-1H-imidazol-2-yl]-5-ethyl-3-pyridinecarboxylic acid). According to a recent survey by Heap (2000), six of seven weeds that have evolved resistance to four or more herbicide modes of action were grasses; *L. rigidum*, *Avena fatua*, *Echinochloa crus-galli*, *Eleusine indica*, *Poa annua*, and *Alopecurus myosuroides*. Massive application of herbicides for weed control in the developing world has also contributed to the increased prevalence of new resistant weed species (Heap 2000). However, the failure of chemical herbicides to control a number of noxious weed species including *Abutilon theophrasti* (velvetleaf) and *Convolvulus arvensis* (field bindweed) has been instrumental in accelerating the search for alternative methods of controlling these troublesome weeds.

Cultural weed control includes decreasing crop row-spacing, selection of competitive cultivars, and crop rotation. Competitiveness between crops and weeds can be altered by row-spacing. When soybean (*Glycine max*) and maize (*Zea mays*) are planted in narrow row-spacing the inter-row between spaces are rapidly covered by the foliar canopy. Shading due to narrow rows not only prevented the further germination and emergence of weeds, but also suppressed the growth of established weeds (Shaw *et al.* 1989). For example soybean at 20 cm row spacing out yielded sicklepod (*Cassia obtusifolia*) as compared with plants grown at 40 and 80 cm row spacings (McWhorter and Sciumbato 1988). The competitive ability of weeds can also be affected by different crop cultivars. Anderson (1997) reported that the dwarf variety of leafy maize grown at 91 cm row spacing reduced weed growth and increased yield by 60% as compared with tall varieties planted at the same row spacing. Similarly, the establishment of high populations of certain weed species can be prevented by crop rotation (Anderson 1997). Mechanical methods of weed control include, tillage, hand weeding, hoeing, mowing, water management, burning, and smothering with non living materials such as straw, sawdust, wood chips, rice hulls, black paper, and plastic film (Anderson 1997).

Biological weed control is the deliberate use of natural enemies to suppress the growth or reduce the population of a weed species (Watson 1994). Mycoherbicides have been defined as fungal pathogens that are applied to control specific weed hosts in the same manner as chemical herbicides (TeBeest and Templeton 1985). Daniel *et al.* (1973) introduced this concept by demonstrating that an endemic fungus could be utilized to control its weed host by applying a massive dose of inoculum at a particular developmental stage of the weed. This strategy is now commonly referred to as the mycoherbicide or bioherbicide approach and aims to control troublesome naturalized species through the use of indigenous pathogens within a relatively specific area, such as in a single agricultural field.

To date, over 200 weed pathogens have been discovered and evaluated, but so far, few have been successfully utilized in agricultural, rangeland, forestry, or aquatic systems (TeBeest 1996a). The *classical* approach to biocontrol differs from the bioherbicide strategy. In the classical strategy, the biocontrol agent (typically an insect) is normally collected from the region of origin of the introduced weed and, once imported, is simply released (from one to many independent sites) into a new area where the target weed is a problem. The biocontrol agent is expected to increase and disperse naturally throughout the entire weed population without significant subsequent annual releases or augmentation of established populations. The natural increase of disease on susceptible plants is relied upon to control weeds either directly from plant death or indirectly through reduction of plant vigour and seed production over a broad geographical setting and within many ecological niches (Hasan and Ayres 1990, TeBeest 1996b). For example, the introduction of the rust pathogen, *Puccinia chondrillina* resulted in the control of one form of skeleton weed (*Chondrilla juncea*) in Australia and the United States of America (USA) (Hasan and Wapshere 1973, Adam and Lines 1984). Similarly, the white smut pathogen (*Entyloma ageratinae* sp. nov.) was introduced onto the Hawaiian islands for the control of mistflower (*Ageratina riparia*) (Trujillo *et al.* 1988). The disease established rapidly and the growth of mistflower was reduced up to 95% in less than one year after inoculation in areas with optimum temperatures of 18-20°C and with high rainfall.

According to Templeton *et al.* (1990), the application of mycoherbicides in the field must fulfill the following criteria to be successful: (a) the indigenous plant pathogen has potential as a biological control agent, but requires the inundative inoculation tactic (bioherbicide), (b) the fungal plant pathogen can be dried and used safely as a mycoherbicide in annual crops, (c) mycoherbicides can be successfully applied in mixture with chemicals in pest management systems, (d) environmental perturbation from use of mycoherbicides is essentially nil, merely that caused by the removal of the target weed, (e) growers and applicators understand and accept the few critical requirements for handling and storing a living product and can accurately identify weed species, (f) the high specificity of a mycoherbicide is particularly beneficial where pesticide sprays may drift onto non target crops grown in contiguous fields; and (g) mycoherbicides can be marketed profitably.

The first bioherbicide to be commercially developed was DeVINE® in the USA in 1981. This product was a liquid formulation of chlamydospores of *Phytophthora palmivora* used for the control of stranglervine (*Morrenia odorata*) in Florida citrus groves. COLLEGO®, which is a dried-spore powder formulation of *Colletotrichum gloeosporioides* f. sp. *aeschynomene*, was registered the following year (1982) in the USA for the control of northern jointvetch (*Aeschynomene virginica*) in rice and soybean (TeBeest and Templeton 1985, Hasan and Ayres 1990, Cross and Polonen 1996). A third mycoherbicide, BIOMAL®, is composed of spores of *C. gloesporioiodes* f.sp. *malvae* and was registered in 1992 in Canada for the control of round-leaved mallow (*Malva pusilla*) in wheat (*Triticum aestivum*) (Mortensen 1988, TeBeest 1996a). This product is still not commercially available (A. Watson, *personal communication*). In 1997, two additional biological control products became commercially available. The first, BIOCHON®, is a formulation of the fungus *Chondrostereum purpureum*, a wood decay promoter for the control of black cherry (*Prunus serotina*) and other forest woody weed species in conifer plantations (Dumas *et al.* 1997). The other bioherbicide product, CAMPERICO®, a bacterium-based (*Xanthomonas campestris* pv. *poae)* formulation, was registered in Japan and the USA in 1997 for the control of annual bluegrass (*Poa annua*) in golf course turf (Imaizumi *et al.* 1997).

Many other prospective candidates, although successful in research trials, have failed to gain registration and commercial use due to one or more of the following reasons: 1) lack of acceptable level of efficacy, 2) technical difficulties in production and marketing of a commercially acceptable formulation, 3) competition from chemical herbicides, and 4) unprofitable markets (Cross and Polonenko 1996).

To be effective, biological control must be viewed as a component of an integrated management system. Incorporating biological control within an integrated weed management system (IWMS) involves an understanding of the weed species, the role of crop rotation and interrow cultivation, the available herbicides, and the competitive ability of the crop. The IWM approach involves the combination (integration) of weed biological information with available control technologies (Ross and Lembi 1999). The present study examines the interaction of a chemical herbicide, a bioherbicide, and plant competition in a velvetleaf (*Abutilon theophrasti* Medic.) - soybean (*Glycine max* (L.) Merrill.) system.

1.2 The host plant - *Abutilon theophrasti* Medic.

Commonly referred to as velvetleaf, *Abutilon theophrasti* originated either in China or India (Mitich 1991). Its use as a fibre crop in China dates back to at least 2000 B.C. and it is presently still grown in these regions for making ropes, cloth, coarse nets, and paper (Spencer 1984). *A. theophrasti* first arrived in North America as a fibre crop probably before 1700, but it was widespread on the East Coast of the United States by the early 1700's. Attempts to process *A. theophrasti* fibre never succeeded economically, although it continued to be cultivated for more than 100 years in the USA (Spencer 1984). *A. theophrasti* is a member of the Malvaceae family and the genus *Abutilon* includes about 150 species, several of which are grown ornamentally. *A. theophrasti* is a major weed of maize, cotton (*Gossypium hirsutum*), soybean, and sorghum (*Sorghum bicolor*) in the eastern United States and parts of eastern Canada. The area where *A. theophrasti* occurs as a major agricultural weed lies between latitudes 32°N and 45°N (Spencer 1984). It is common in Europe particularly in southeastern and Mediterranean countries, and worldwide it is still spreading being first reported in the Netherlands in 1981 (Mitich 1991). *A. theophrasti* has become a troublesome weed in California only within the last decade (Holt and Boose 2000), its northern and southern ranges are expanding in the USA and was first reported 10 years ago in the Canadian Maritime provinces (Mitich 1991).

A. theophrasti produces vertical stems that support softly pubescent, heart-shaped leaves (Casper and Cahill 1998). Under favourable field conditions a plant may reach up to 1.5 to 2 m in height and produce leaves that are more than 20 cm in width. Under low population densities, *A. theophrasti* plants are heavily branched with branches arising from leaf axils (Casper and Cahill 1998). The yellow flowers, which also arise from leaf axils, are self-pollinated, but are capable of outcrossing (Garbutt and Bazzaz 1987).

Several important physiological characteristics of *A. theophrasti* have allowed it to be a particularly aggressive competitor in crop production systems. These adaptive features include:

1) *A. theophrasti* is self-fertile and can produce up to 17,000 seeds per plant that may be highly dormant. Seeds have tough seed coats that protect them against digestion by farm animals and soil microorganisms such that some seeds may remain viable in soil for up to 50 years (Warwick and Black 1988). In one study for example, a 43% germination level was obtained for *A. theophrasti* seeds that had been buried in soil for 39 years (Mitich 1991). *A. theophrasti* seeds and seed coats have also been found to contain anti-microbial compounds that inhibit the growth of soil bacteria and fungi (Kremer 1986). Seed dormancy is a major survival feature of *A. theophrasti*, often allowing seedlings to escape conventional control measures because of difficulties in predicting its variable germination both spatially and temporally (Burnside *et al.* 1996).

2. *A. theophrasti* biotypes have been found to be resistant to the widely used corn triazine herbicide, atrazine. Populations of *A. theophrasti* having a high degree of tolerance to

triazine herbicides are believed to have undergone chloroplast membrane alteration [(at a 32-kd protein (Qb=D, protein)] of Photosystem II which greatly reduces triazine binding at the site of action in resistant weed biotypes (Anderson and Gronwald 1986, Gronwald *et al.* 1989). A variety of physiological, biochemical, and anatomical conditions are associated with the evolution of triazine resistance. Much data support the possibility of reduced efficiency of the photosynthetic light reactions in triazine R-biotypes providing evidence for lower photosynthetic rate and enhanced detoxification and/or lower rate of Photosystem II electron transport (Ort *et al.* 1983, Hobbs 1987, McCloskey and Holt 1990).

3. *A. theophrasti* has the ability to inhibit competing plant growth by release of chemicals into the soil environment. Phytotoxins could be present in leachate from leaves of *A. theophrasti* or they could be released slowly during the decomposition of plant material following plant senescence (Colton and Enhillig 1980, Rose *et al.* 1983). Several phenolic groups were found by Colton and Enhillig (1980) to be present in *A. theophrasti* including: scopoletin, chlorogenic, isochlorogenic, ferulic, p-coumaric, caffeic, vanillic, and p-hydroxybenzoic acid. Colton and Enhillig (1980) reported that when radish seeds were soaked in aqueous extracts of *A. theophrasti* leaves for 24h, seed germination was reduced up to 80% as compared with the seeds that were soaked in distilled water alone. Similarly, soybean seedling growth was inhibited when grown in a medium containing the aqueous extracts from *A. theophrasti* leaves (Colton and Enhillig 1980).

4. *A. theophrasti* can overtop neighbouring crops due to its rapid growth rate. This is very common when both the crop and the weed emerge at the same time (Akey *et al.* 1990, DiTommaso and Watson 1997). *A. theophrasti* can effectively compete for light by

concentrating most of its branching at the top of the canopy so that it can intercept a greater percentage of light than crops such as soybean (Akey *et al.* 1990, Patterson, 1992, Sattin *et al.* 1992, Benvenuto *et al.* 1994, Scholes *et al.* 1995, Iliya *et al.* 1995, Tremmel and Bazzaz 1995). For instance, *A. theophrasti* interference reduced soybean leaf area and yield up to 50% at densities of 16 plants m^{-2} (Dekker and Meggitt 1993). Hagood *et al.* (1980) reported that the leaf area index, pod number, and seed yield of soybean were significantly reduced at densities of 2.5 to 40 *A. theophrasti* plants m^{-2}.

1.3 Seed size variation

For almost a century, researchers have examined the relationship between seed size and plant growth but a consistent pattern has not emerged (Stanton 1984b). Some studies report that larger seeds produce competitively superior seedlings (Thompson 1981, Stanton 1985, Wulff 1986, Choe *et al.* 1988), especially under unfavourable conditions such as shade and drought (Venable 1989, Kelly 1997). Meanwhile, other studies have shown that seedlings arising from plant species having heavier seeds have a slower relative growth rate during the first 10 days after germination than seedlings of species having lighter seeds (Stanton 1984a, Jurado and Westoby 1992). Moreover, seedlings from small seed have been shown to grow faster than seedlings produced from large seeds when supplied with sufficient nutrients (Fenner 1983). Zhang and Hamill (1997) found that the leaf chlorophyll content of young *A. theophrasti* seedlings as well as the total leaf area at harvest tend to increase with increasing seed weight. However, the aboveground biomass of plants produced was not affected by seed weight. Lindquist *et al.* (1995) demonstrated that seed size in *A. theophrasti* was dependent upon the intensity of competition for light with soybean. Moreover, seedlings emerging between eight and 33 days after planting (DAP) produced more and heavier seeds as compared with earlier or later emerging *A. theophrasti* in both monospecific stands and in mixture plots with soybean. However, net seed production was lower in *A. theophrasti* plants growing in a soybean crop than when growing alone (Lindquist *et al.* 1995).

The relative growth rate (RGR) of plants is the product of a morphological component, the leaf area ratio (LAR), and a physiological component, the net assimilation rate (NAR) (Siebert and Pearce 1993). Small-seeded species have typically been found to devote a greater percentage of biomass to leaf area thereby resulting in a greater RGR. Seed weight has also been negatively correlated with leaf weight and positively correlated with stem and root weight. As a result, it has been generally accepted that increases in percentage leaf biomass in small-seeded plants occurs at the expense of both root and stem biomass, but particularly the former. Individuals with large seed suffer a double disadvantage in that their seed dispersal is disproportionately reduced by the relatively large seed coat and its size advantage during establishment is disproportionately reduced by its low seedling/embryo ratio (Fenner 1983).

Such inconsistencies in the literature create the impression that seed size variation is ecologically irrelevant and of limited research value. However, most of these studies were carried out under glasshouse conditions or under field situations where seed size variation was minimal. Under such conditions, rapid early growth due to stored seed reserves may have little impact on ultimate plant size. In contrast, demographic studies of natural plant populations have consistently shown that attaining a large size early in life substantially reduces a seedlings' susceptibility to various biotic and abiotic stresses (e.g. shading by competitors, water, nutrients, space) (Harper 1977; Stanton 1984b).

1.4. Seed size and dormancy

Dormancy is recognized as an important factor in the persistence and survival of weed species by protecting the embryo (seed) during dissemination or during periods of unfavourable conditions for germination and successful establishment (Aldrich and Kremer 1997). Three broad types of dormancy are generally recognized: (1) innate, (2) induced, and (3) enforced. Innate dormancy, sometimes referred to as primary dormancy, is that which is present in the seed when released from the parent. This type of dormancy may be imposed and maintained by several mechanisms including: immaturity of the embryo, seed coats impermeable to water or inhibiting gaseous exchange, or simply as a result of a growth substance imbalance within the embryo. Induced dormancy (also referred to as secondary dormancy) is a result of conditions to which the seed is exposed after release from the parent plant. Once such dormancy is induced, germination or regrowth usually does not commence immediately when the condition is removed (e.g. light requirement after burial for an extended period of time). Enforced dormancy is that imposed by conditions unfavourable for growth, most commonly as a result of a shortage of a critical abiotic factor such as water or suitable temperature. Most weed species produce both dormant and non-dormant seed (Aldrich and Kremer 1997) and the percentage of seeds within each category varies with individual species. *A. theophrasti* seeds typically exhibit a high degree of dormancy mainly due to a thick, hard seed coat that is impermeable to water (physical seed dormancy) (Baskin and Baskin 1998). *A. theophrasti* seeds do not germinate until the seed coat is altered physically. Any process of breaking, scratching, or mechanically altering the seed coat to make it permeable to water and gases is known as scarification. In temperate regions, this often occurs over the winter as a result of freezing temperatures or microbial activities that modify the seed coat structure. Scarification also occurs when seeds are passed through the digestive tracts of various animals (Baskin and Baskin 1998).

There has been a substantial amount of research examining the effect of seed size on seed dormancy (e.g. Bello *et al.* 1995, Rees 1993, Anderson and Milberg 1998). Zhang and Hamill (1997) found that *A. theophrasti* seed weight differences within the range of 4.8 to 11.7 mg did not result in any significant differences in the germination ability of the seeds tested. Seeds from both extreme size fractions (i.e., < 4.8 mg and > 11.7 mg) either did not germinate or died. The enhanced germination associated with large seeds produced by plants under shaded conditions found in previous studies were more likely the result of inter-populational variation (Zhang and Hamill 1997) or differences in maternal environments (Bello *et al.* 1995). The work conducted by Bello *et al.* (1995) showed that *A. theophrasti* plants grown in full sunlight produced seeds that were approximately 20% less likely to germinate when subjected to optimal environmental conditions for germination compared with shaded plants. It was unclear from this study whether the decrease in seed dormancy when plants were shaded resulted in fewer seeds with a hard or thinner seed coat or if some other dormancy mechanism was responsible. To date, we still do not fully understand the manner in which seed dormancy in plant species, and *A. theophrasti* in particular, vary with seed size. Moreover, there is a paucity of information on the manner in which seed dormancy varies with seed size for different individuals within a population. The specific question to be addressed is whether the seed size-seed dormancy relationship within an *A. theophrasti* population holds constant regardless of individual examined. No research to date has addressed this key aspect of the population ecology of *A. theophrasti*. From a weed management perspective, such data are critical since they will provide information as to initial seedling vigour and relative ability to compete effectively with crop species. This may be a particularly important aspect for the biological control of *A. theophrasti* with the selective fungal pathogen *Colletotrichum coccodes* given that recent work has shown that a small number of individuals, within inoculated populations, are able to effectively escape disease and become established as dominants (DiTommaso *et al.* 1996). One reason that had been advanced for the observed results was that those individuals escaping control originated from relatively large-sized seed and were competitively superior to seedlings arising from small-sized seed. This hypothesis has never been tested explicitly in *A. theophrasti* and warrants further investigation. In one of the few studies examining the relationship between seed size and fungal pathogen susceptibility, Foster (1986) showed that Malaysian flora tree seedlings originating from small seed (< 3 mm in length) were more susceptible to fungal disease than seedlings from larger seeds.

1.5. The pathogen: *Colletotrichum coccodes*

Colletotrichum coccodes (Wallr.) Hughes belongs to the Fungi Imperfecti as it has no sexual stage. Cylindrical conidia are typically produced on conidiophores. Although this species is known to have a wide host range, both laboratory and field studies have shown that the host range of the *C. coccodes* isolate obtained from *A. theophrasti* is restricted to *A. theophrasti* and this fungus does not damage other plant species (Poirier 1984). The fungus causes gray-brown leaf lesions and black, sunken elongated stem lesions on *A. theophrasti*. Leaf lesions are generally observed within five days of inoculation and appear as small water-soaked spots that soon after enlarge into necrotic areas. Desiccated and diseased leaves are shed prematurely within five to 14 days after inoculation (Wymore *et al.* 1988). Disease effects of the pathogen are most evident after an 18-hour dew period at 24°C following inoculation. Disease development is most rapid at warmer incubation temperatures of 25/20°C and 35/30°C day/night than at 15/10°C. In general, *A. theophrasti* plants are killed only when inoculated at a relatively young age (i.e. cotyledon stage). When *C. coccodes* is applied at later growth stages, the pathogen causes extensive necrotic lesions on inoculated leaves, but although infected plants are stunted and development is delayed, *A. theophrasti* recovers (DiTommaso *et al.* 1996).

Recent research has demonstrated that the presence of *C. coccodes* can result in significant decreases in *A. theophrasti* yield when grown in mixtures with a soybean crop, although the effects in monospecific stands were minimal. In pure stand, intense intraspecific competition resulted in tall, spindly *A. theophrasti* individuals with a more or less uniform height hierarchy (DiTommaso *et al.* 1996). This general growth habit allowed most plants to obtain a share of available light. Consequently, the rapid increase in height exhibited by most *A. theophrasti* individuals in pure stand favoured the quick replacement of diseased leaves that had been prematurely shed. In mixture with the soybean crop, the stunting effect of *C. coccodes* on *A. theophrasti* provided enough of a delay to allow soybean with its large trifoliate leaves to effectively shade *A. theophrasti*.

1.6. Research goals and thesis objectives

The proposed research addresses a number of important, but not well understood, population ecology aspects of the *Abutilon theophrasti* - *Colletotrichum coccodes* weed-pathogen system. These include an examination of the relationship between seed size and dormancy in *A. theophrasti* as well as how dormancy varies within individual plants in the same population. The effect of seed size and disease incidence on plant growth and reproduction over several generations was also investigated and provided valuable data as to the long-term impact of this pathogen on *A. theophrasti* population dynamics. The effects of seed size, disease, and presence of a competing soybean crop on the biomass and height structure of the *A. theophrasti* population comprised another important facet of this research. Lastly, the suitability of implementing an integrated management approach for suppressing *A. theophrasti* was investigated in field trials that used reduced rates of the selective broadleaf herbicide, bentazon [3-(1-methylehtyl)-1*H*)-2,1,3-benzothiadiazin-4(3*H*)-one 2,2-dioxide] alone and in combination with a water-in-oil formulation of the biocontrol agent *Colletotrichum coccodes*.

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Connecting Text

The negative impact of *Abutilon theophrasti* on soybean growth and yield are well known. Much agronomic research has been conducted in this area however, information regarding the more specific interactions between *A. theophrasti* and soybean is lacking. *A. theophrasti* is a prolific seed producer, and its seeds maintain their viability in the seed bank for up to 50 years. The seeds of *A. theophrasti* also show a remarkable variation in dormancy, due in part to a highly impermeable seed coat. These characteristics make the germination of *A. theophrasti* highly unpredictable in cropping systems.

A. theophrasti seeds were collected from a natural population of plants at Macdonald campus of McGill University. Seeds were then subjected to different temperature regimes in a growth chamber under alternating light and dark conditions. In this chapter the effect of seed size and intra-population variability on *A. theophrasti* seed viability were investigated.

Chapter 2

Intra-population variation in *Abutilon theophrasti* Medic. (velvetleaf) seed mass and its effect on seed germination and dormancy

2.1 Abstract

Seed mass variation for ten randomly selected *Abutilon theophrasti* Medic. (velvetleaf) plants within a single agricultural population and its impact on seed germination and dormancy were examined under controlled environmental conditions. Seeds were collected in the fall of 1995 and stored in paper bags at 4°C until the start of trials in 1998. For each plant, between 549 and 1000 randomly selected seeds were separated into seven mass fractions based on individual seed weight, with classes ranging from < 6.0 mg to > 11.0 mg. Subjecting the seeds to a cold stratification (4°C) period for 7 days followed by a 21-day alternating day/night (25/14°C) temperature and 14-h photoperiod regime resulted in an overall germination of 75% and dormancy of 24%. The majority of the seeds (89%) germinated within seven days when exposed to the alternating temperature/light regimes. There was a significant ($P < 0.001$) difference in mean seed mass between the ten *Abutilon* plants, with mean mass ranging from 8.8 to 9.6 mg. For nine of the ten *Abutilon* plants, the greatest proportion of seeds occurred in the 9.0-9.9 mg mass fraction while the lowest proportion of seeds was generally found within the 6.0-6.9 mg mass fraction. Most seeds (96%) having a mass below 6.0 mg were non-viable. Seed mass had a highly significant impact ($P< 0.0001$) on the total germination and dormancy in *Abutilon*, but not on the rate of germination. Germination peaked for seed mass fractions comprising the highest proportion of total seeds (8.0 - 9.9 mg) and was lowest for seeds within extreme mass fractions. There was a trend of greater dormancy for the heavier seeds (>10.0 mg) compared with the lighter seeds. Maternal source had a significant effect ($P < 0.05$) on total germination, germination rate, and dormancy, over the 21-day experimental period. Findings from this study suggest that intra-population variation in *Abutilon* seed mass and its influence on germination and dormancy may play a significant role in maintaining a variable germination pattern and persistent seed bank in this troublesome annual agricultural weed.

2.2 Introduction

Seed size plays an important role in determining the successful establishment of individual plants within a population. Seed size variation may be due to trade-offs in resource allocation between seed size and number (Venable 1992), or as a response to environmental heterogeneity (Janzen 1977). Intraspecific seed size variation and its relation to survival have been demonstrated in a number of plant species (Meyer *et al.* 1995, Andersson and Milberg 1998).

The ability of a seed to germinate is controlled by several factors including genetic origin, parent growing environment during maturation, age of parent plant at the time of seed maturation, and the seed position on the plant (Bello *et al.* 1995, Dekker *et al.* 1996, Andersson and Milberg 1998, Wright *et al.* 1999). Germination and dormancy of seeds can also be influenced by seed size, shape, and surface orientation (Harper 1977, Moles *et al.* 2000). Seed dormancy has generally been viewed as an important physiological adaptation to variable, unpredictable environments (Fenner 1985, Allen and Meyer 1998).

Intra-population variation in seed mass and germination has been examined for a few species (e.g., Harper and Obeid 1967, Zammit and Zedler 1990, Stamp 1990, Evans and Cabin 1995, Milberg *et al.* 1996). In species exhibiting seed dimorphism such as *Bidens pilosa* and *Cakile edentula*, variability in seed mass resulted in differences in germination levels (Forsyth and Brown 1982, Zhang 1993). The relationship between seed mass and germination in plant species that do not produce dimorphic seeds are not as evident and often, in these studies, the confounding effect of environmental factors on seed size and germination has further complicated matters (Milberg *et al.* 1996). The relatively few studies that have attempted to relate individual seed size fractions to viability and germination rates have provided inconsistent results showing both that seed of greater mass exhibit higher (Zammit and Zedler 1990) and lower (Stamp 1990) germination and germination rate than seed of lower mass. Milberg *et al.* (1996) reported that there were large variations in germination rate between nine seed mass fractions in *Lithospermum arvense* and *Anchusa arvensis*. Moreover, the relationship between germination and seed mass differed in both species and between populations of the same species. Large seeds of *Lithospermum* always germinated well whereas; small seeds generally had poor germination levels. However, for one of the *Anchusa* populations, germination tended to decrease with increasing seed mass. Research by Harper and Obeid (1967) on fiber and oil seed flax cultivars demonstrated that seed of intermediate size germinated faster than seed from extreme size classes.

Abutilon theophrasti Medic. (velvetleaf) is a large, self-pollinated annual weed infesting maize and soybean crops in the Mid-western and Northeastern regions of the United States of America, Eastern Canada, and the Eastern Mediterranean regions. Each plant is capable of producing up to 17,000 seeds that exhibit a high degree of physical dormancy due to the presence of a thick, hard seed coat that is impermeable to water (Warwick and Black 1988, Baskin and Baskin, 1989). Under optimal conditions for germination, hard seeds cannot imbibe water and are unable to germinate. However, physical scarification resulting from regular cycles of freezing and thawing or from placement in boiling water for brief periods have been shown to disrupt the seed coat and increase germination in this species (Li *et al.* 1999).

In work by Zhang and Hamill (1997) *Abutilon* seeds from weight classes ranging from 4.8 to 11.7 mg did not exhibit significant differences in their germination and dormancy levels. Surprisingly, in that study, only 39% of *Abutilon* seeds germinated while a large portion of seeds (40%) were found to be non-viable. The remaining seeds (21%) were viable but dormant. Given the relatively high mortality rate of seeds in the Zhang & Hamill (1997) study, it was unclear whether the lack of a seed size effect on germination and/or dormancy in *Abutilon* is a general feature within this species or simply specific to the population tested. Moreover, no attempt was made to relate seed size variation and germinability for individual *Abutilon* plants. This may be especially important given the numerous instances where within-plant variation in seed size contributes most to the total seed mass variation within a population (Pitelka *et al.* 1983, Thompson 1984, Milberg *et al.* 1996). To date, the effect of *Abutilon* intra-population variation in seed size and its subsequent impact on seed germination, germination rate, and dormancy is not well understood and needs to be further studied.

Thus, the objectives of this study were: (1) to determine the variability in seed mass, total germination, and germination rate for the seeds of ten *Abutilon theophrasti* plants from a single agricultural population; and, (2) to determine the relationship between seed mass, total germination, and germination rate for these ten plants.

2.3 Materials and methods

Mature *Abutilon* capsules were randomly collected in fall 1995 from ten individually marked plants located within a 3 ha corn field at the Macdonald Campus Farm in Ste-Anne-de-Bellevue, Québec, Canada. Marked plants within the field were at least 30 m apart from each other. Capsules were stored at 4°C in paper bags until the start of the experiment in spring 1998. Seeds from the ten *Abutilon* plants were obtained by separating them from chaff by hand. Seeds from each plant were then weighed individually to the nearest 0.1 mg and grouped into one of twelve seed mass fractions (00-1.0, 1.1-2.0., ., ≥12 mg). The total number of seeds collected from each plant ranged from 549 to 1000. All seeds were placed on moistened filter paper (P 8, Fisher brand, Fisher Scientific, Nepean, Ontario) in 9-cm diameter plastic Petri dishes (Fisher Scientific, Nepean, Ontario) containing 8 ml of distilled water. No more than 50 seeds per mass fraction were placed within each Petri dish. Petri dishes were subsequently wrapped with Parafilm to prevent water evaporation during the experimental period. All seeds within Petri dishes were then subjected to a low-temperature (4°C) moist stratification treatment for 1 week in the dark. At the end of the stratification period, seeds were incubated in a controlled environment chamber programmed to provide a 25/14°C day/night temperatures, and a 14-h photoperiod at a light intensity of 400 $\mu Em^{-2}s^{-1}$ using fluorescent lamps. These environmental conditions are typical of Québec field conditions in late May when the first *Abutilon* germination flush generally occurs. The number of germinated seeds having a radicle at least 2 mm long was recorded daily for a period of 21 days and all germinated seeds were removed from the Petri dishes. At the end of the experiment, all non-germinated seeds were initially examined for viability by pressing them gently with a forcep. Seeds that were crushed under this moderate pressure were considered to be dead. The remaining seeds were then placed in boiling water for 10 seconds, removed and placed on moistened filter paper, and returned to the original controlled environment conditions for a period of 48 hours. All seeds that imbibed water or germinated following this additional germination period were characterized as being viable but dormant, while seeds that did not imbibe water during this 48-hr period were considered to be dead.

The rate of germination was determined for each *Abutilon* plant and for each of the seven seed mass fractions by first multiplying the total number of seeds germinating on the first day by 1, the total number of seeds germinating on the second day by 2, and so on. The average number of days that were required for seeds to germinate was then determined by dividing the sum of these terms by the total number of seeds that germinated.

Germination, dormancy, and viability data were square root transformed to homogenize variances prior to using the GLM analysis procedure in SAS (SAS, 1990). The analysis of variance (ANOVA) procedure was modified in order to take into account the potential heterogeneity of variances and lack of independence over time (from day 1 to day 21) of the temporal repeated measures of individual plants and seed mass (Dutilleul 1998). The model used for the modified univariate ANOVA was derived by adding the time effects plus all the interactions to the terms of the standard ANOVA model and using the REPEATED statement of the GLM procedure (SAS 1990). Most seeds below 6.0 mg were non-viable and thus were not included in the data analyses. Relationships between *Abutilon* seed mass, germinability, and dormancy were determined by both linear and non-linear regression analyses. The Kruskall-Wallis one-way ANOVA on ranks was used to determine differences in mean seed mass of *A. theophrasti* plants.

2.4 Results

2.4.1 Seed mass variation between *Abutilon* plants. For the ten *Abutilon* plants combined, 75% of the seeds had a mass within the 8.0-8.9mg and 9.0-9.9 mg ranges while only 1.5% of the seeds had a mass within the two extreme seed mass fractions of < 6.0 mg and > 11.0 mg (Fig. 2.1). The variation in seed mass for each of the ten plants was large with the greatest differences occurring for the 8.0-8.9 and 9.0-9.9 mg seed mass fractions (Fig. 2.1). There was a significant ($P < 0.000$) difference in median seed mass between the ten *Abutilon* plants, with seeds from individual 3 having the lowest median mass (8.8 mg) and seeds from individual 10 having the highest median mass (9.8 mg) (Fig. 2.2).

2.4.2 Germination and germination rate between *Abutilon* plants. Following the 21-day experimental period, seed germination levels were significantly different ($P < 0.05$) among the ten *Abutilon* plants, with germination for individuals 6 and 8 showing the greatest variation (Table 2.1, Fig. 2.3). For all plants and mass fractions combined, the overall seed germination level was 75%. In contrast, seed germination levels for individuals 6 and 8 were 57% and 92%, respectively. Overall, 24% of *Abutilon* seeds were dormant and 0.9% of seeds were non-viable.

Seventy-five percent of *Abutilon* seeds germinated within the first seven days of the experiment regardless of maternal source (Fig. 2.4). Germination declined sharply for all plants 10 days after the start of the experiment. The rate of germination differed significantly ($P < 0.05$) between *Abutilon* plants (Fig. 2.5). Across all seed mass fractions, the average number of days required for seeds to germinate ranged from 3.2 days in individual 1 to 5.6 days in individual 7, with an overall population mean of 4.6 days. Seeds from individuals 6 and 4 exhibited the greatest and lowest variation in germination rate, respectively.

2.4.3 Viability and germination rate as affected by seed mass. Seed size had a highly significant ($P< 0.0001$) impact on final germination levels (Table 2.1, Fig. 2.6). The highest germination levels were observed for the 7.0-7.9 and 8.0-8.9 mg seed mass fractions and the lowest levels for the lightest seed mass fraction (< 6.0 mg) in which no seeds germinated. Most non-viable seeds (96%) had seed masses below 7.0 mg (Fig. 2.6). A positive linear relationship was observed between mean seed mass and dormancy when data for all ten *Abutilon* plants were combined (Fig. 2.7).

The average number of days required for germination was not affected by seed mass (Fig. 2.8) although heavier seeds (> 11.0 mg) did require, on average, 1.5 additional days to germinate. Interestingly, germinating *Abutilon* seeds on the first day of the study had a substantially greater mass (9.7 mg) than seeds germinating during the following 14 days (Fig. 2.9). There was a trend of increasing time to germination for heavier seeds from day 4 to day 14 of the study (Fig. 2.9).

2.5 Discussion

The important differences in seed mass distribution found between the ten *Abutilon* plants were likely due to a number of environmental effects rather than genotypic variation (Zhang and Hamill 1997). It is plausible that the microenvironments in which the ten plants grew differed in their ability to supply essential resources such as nutrients and light. These differences would have resulted in *Abutilon* plants producing seeds that were particularly large or small. It is also possible that the variation in seed mass observed among the ten plants may have been due to differential seed filling in seeds harvested from different branch locations on parental plants (Gutterman 1992). Zhang and Hamill (1996) reported that mean seed weight in *Abutilon* plants varied depending on population, maternal environment, and their interaction. However, photosynthetic rate, number of leaves and flowers did not differ among the different populations. Baloch *et al.* (2001) reported that under favourable growing conditions, seed mass in *Abutilon* plants was negatively correlated with capsule position on parent plants. That is, seeds collected from early-maturing capsules (basipetal) had greater mean weights than seeds harvested from late-maturing (acropetal) capsules. Interestingly, capsule position did not affect seed mass in *Abutilon* plants that were infected by a selective fungal pathogen at high planting densities. Moreover, *Abutilon* plants grown under these stressful conditions produced fewer capsules having a larger seed mass than seeds collected from plants grown at lower densities and in the absence of disease. Vaughton and Ramsey (1998) also reported that mean seed mass in *Banksia marginata* was negatively correlated to the position of flowers on the main stem. Kane and Cavers (1992) noted that mean seed mass in *Panicum miliaceum* decreased over the growing season, both on individual panicles and all inflorescences of the plant. In contrast, Obeso (1993) observed no variation in mean seed mass at different fruit locations in *Asphodelus albus*.

Individual *A. theophrasti* plants within the agricultural population sampled exhibited a large degree of variation in the germinability of their seeds (from 57% to 92%). These differences in germination occurred despite a normal distribution of seed mass in the ten *Abutilon* plants sampled (data not shown). Thus, variation in seed mass cannot fully account for the variability in germination observed between the *Abutilon* plants. This finding suggests that differences in the maternal growing environment within this agricultural field (e.g. full sun versus shade) may have resulted in seeds from different *Abutilon* plants having divergent germination abilities (Fenner 1991, Bello *et al.* 1995). For instance, Bello *et al.* (1995) found that velvetleaf plants grown under full sunlight produced smaller-sized seeds that were 20% less likely to germinate under optimal environmental conditions than larger seeds produced from shaded plants. It was unclear from this study whether the decrease in seed dormancy when plants were shaded resulted in fewer seeds having hard seed coats or whether some other dormancy mechanism was responsible. It is also plausible that variation in germination ability for seeds from the ten plants may have been due, in part, to the harvesting of mature capsules on different positions of the plants. Research from several studies has shown large variability in germination levels of seeds collected from different branch positions on a single plant (Gutterman 1992, Dekker *et al.* 1996). No attempt was made in this study to harvest mature capsules from similar positions on each of the plants.

The rate of germination for seeds of the ten *Abutilon* plants also differed over the 21-day experimental period. There was no obvious trend observed between the average amount of time required for germination and median seed mass for each of the ten *Abutilon* plants. For instance, seeds of *Abutilon* individual 1 had a median mass of 9.7 mg and required an average 3.2 days to achieve germination whereas seeds of individual 7 had a similar median mass of 9.6 mg but required nearly 2.5 days more than individual 1 to achieve germination (5.6 days).

Zhang and Hamill (1997) revealed that there were no differences between the germination and dormancy patterns of *Abutilon* seed having weights ranging from 1 mg to > 12 mg. In the present study however, seed size had a significant impact on germination and dormancy with germination decreasing for extreme seed mass classes and dormancy increasing with greater seed sizes. The production of large *Abutilon* seeds (>11.0 mg) having high dormancy may be an adaptive feature in this species by providing a constant source of relatively dormant high nutrient-content seeds to the permanent soil seed bank. Although, the total number of large seeds (>11.0 mg) produced by *Abutilon* plants may be relatively small (19% of the nearly 9,000 seeds collected in this study), many of these dormant seeds may be responsible for the annual field fluctuations in *Abutilon* emergence levels observed in the field. Given that *Abutilon* plants may be able to produce as many as 17,000 seeds per plant (Mitich 1991), this would translate into approximately 3,200 large seeds (>11.0 mg) being produced per plant. Greipsson and Davy (1995) found that overall seed germination for the dune-building grass, *Leymus arenarius* was significantly greater for heavier seeds than lighter seeds. Moreover, median germination time was inversely related to weed weight.

Variations in the germinability and germination rate among different plant populations have been documented previously. For example, Kane and Cavers (1992) reported that *Panicum miliaceum* seeds from two populations separated only by a road differed from each other in survival, germination, and dormancy. Furthermore, genetic uniformity and heterogeneity in microenvironment were suggested as a possible causes of these variations (Kane and Cavers 1992). Similarly, Milberg *et al.* (1996) reported that germinability and germination rate varied significantly between seed mass fractions in *Lithospermum arvense* and *Anchusa arvensis* originating from different populations. Variability in parental growing environment was suggested to account for the differences in germination characteristics observed for the various seed mass classes.

Seeds of *Abutilon* having weights of less than 7 mg were largely non-viable (96%) although the proportion of non-viable seeds for each of the *Abutilon* plants was very low (1-2% of the total number of seeds collected). These findings contrast with those of Zhang and Hamill (1997) where overall velvetleaf seed non-viability was nearly 40% of the 1,536 seeds collected. Differences in *Abutilon* growing environment as well as duration and method of seed storage may account for the observed disparity in results. That most *Abutilon* seeds germinated within seven days of the start of the experiment is consistent with other research (Zhang and Hamill 1997). In the present study however, heavier seeds (mean weight of 10.9 mg) were first to germinate. It is generally agreed that seedlings originating from heavier (larger) seeds and that are the first to emerge have a competitive advantage over seedlings from lighter (smaller) seeds (Roach and Wulff 1987, Gutterman 1992, Lacey *et al.* 1997). Investigations of Zhang and Hamill (1997) demonstrated that under fluctuating environmental conditions seed mass plays an important role for the fitness of *Abutilon* plants. Recently, Zhang and Hamill (1996) reported that seed mass and germination rate varied among different populations of *Abutilon* plants when grown under different cropping systems. *Abutilon* plants produced significantly heavier seeds with higher germination rates when grown with a maize crop as compared with seeds produced from plants grown with a soybean crop (Zhang and Hamill 1996). It was suggested that the production of smaller-sized *Abutilon* seeds in a soybean versus maize crop was a result of a genetically based discriminative selection under these two crop management systems (Zhang and Hamill 1996).

Variations in mean seed mass for different *Abutilon* populations needs further investigation. Future research should be directed at understanding more fully the role that parental growing environment and seed position play in determining seed weight variation in *Abutilon* as well as other troublesome annual weed species. Moreover, the influence of these factors on seed germination and dormancy requires additional research.

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Table 2.1. Summary of repeated ANOVA for *Abutilon theophrasti* total germination as affected by plant source, seed mass fraction, and time of sampling (21 days)[1]. Seeds having a mass below 6.0 mg were omitted from this analysis as none of these seeds germinated.

Source	DF[2]	F-value	Prob	Adjusted Prob>F	
				G-G[3]	H-F
(a) Between subject effects					
Plant source	9	2.16	0.0433		
Seed mass	5	22.89	0.0001		
Error	45				
(b) Within subject effects					
Time	20	28.11	0.0001	0.0001	0.0001
Time x Plant source	180	2.41	0.0001	0.0001	0.0001
Time x Seed mass	100	1.61	0.0003	0.0213	0.0062
Time	900				

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[1] The Greenhouse and Geisser epsilon is a multiplicate factor by which the number of degrees of freedom of the F test for time-related effects are reduced in order to take the autocorrelation and heteroscedasticity over time into account (Dutilleul 1998).

[2] DF= degrees of freedom

[3] The G-G (Greenhouse-Geisser) and H-F (Huynh-Feldt) adjustment values are also shown G-G= Greenhouse-Geisser Epsilon = 0.3319

H-F= Huynh-Feldt Epsilon = 0.5165

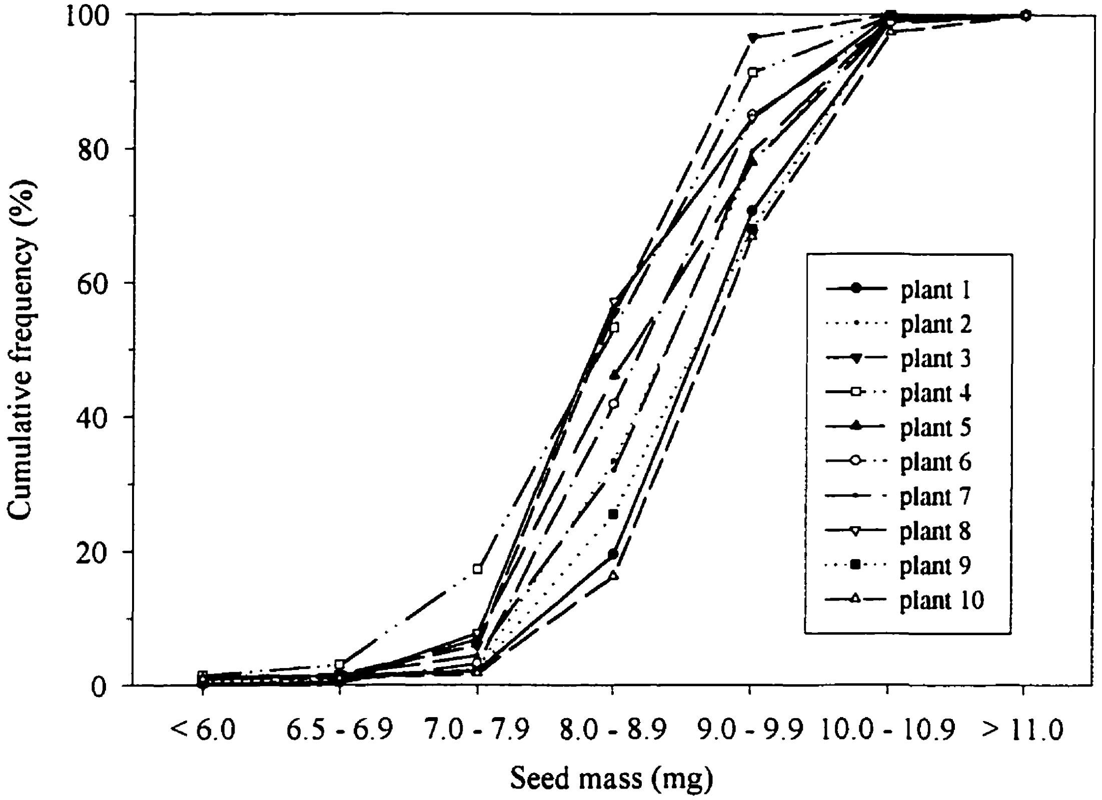

Figure 2.1. Cumulative frequency distributions of seed mass within seven seed fractions for ten *Abutilon theophrasti* plants collected from a single agricultural population. Curves are based on the individual masses of 1000 seeds except for plants 1 (898), 5 (900), 8 (549), 9 (713), and 10 (820).

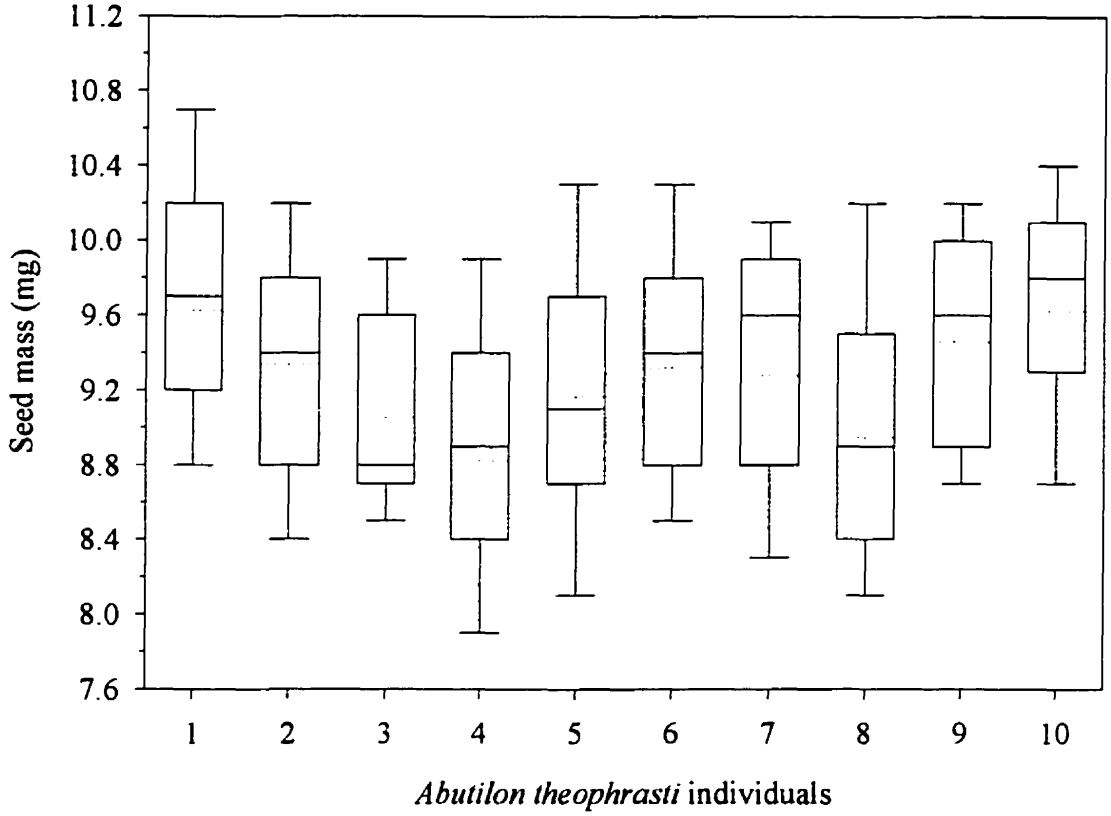

Figure 2.2. Box plots showing the median (solid line), mean (dotted line) and 25th and 75th percentiles of seed mass for each of ten *Abutilon theophrasti* plants from a single agricultural population. Error bars above and below each box indicate the 90th and 10th percentiles, respectively.

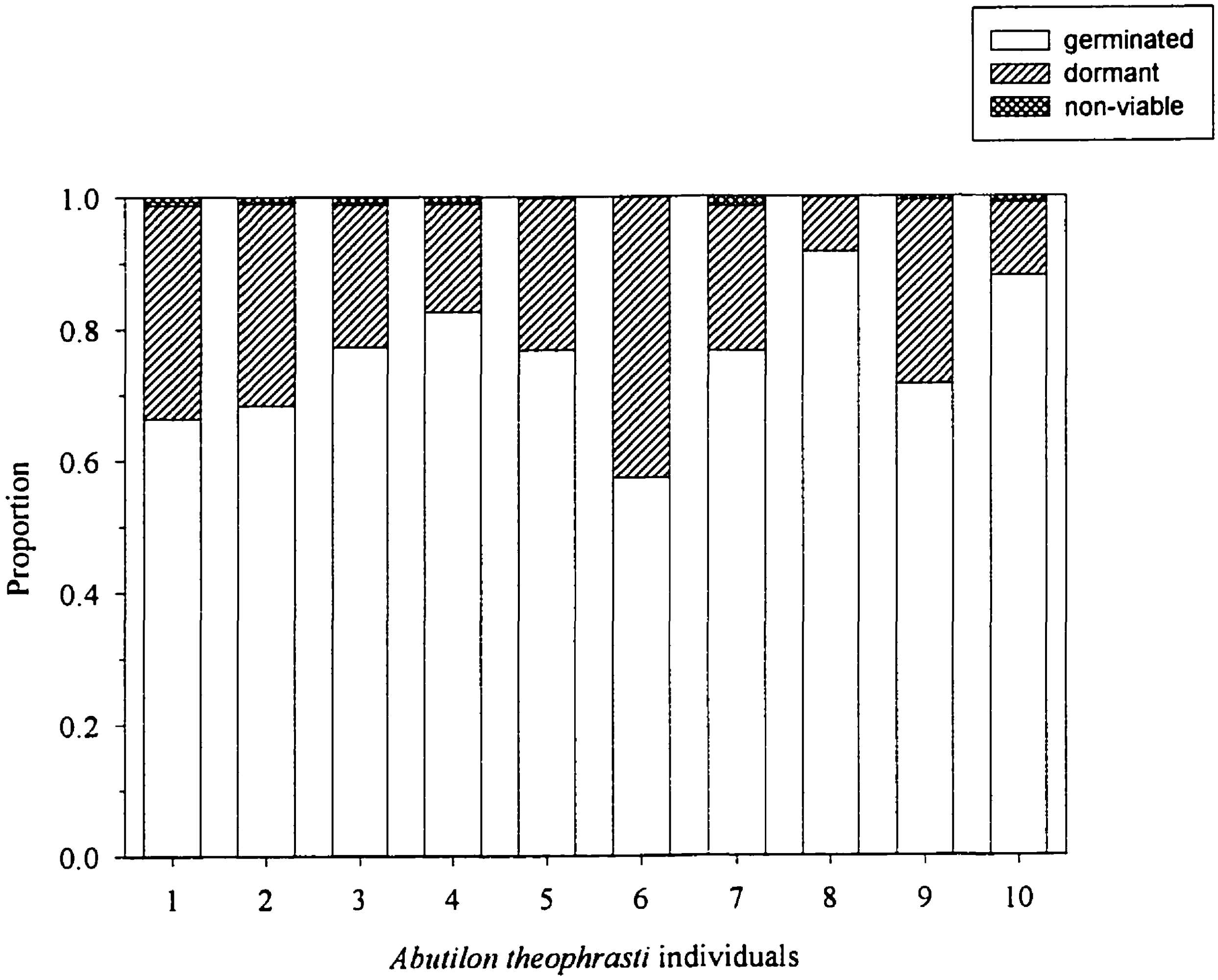

Figure 2.3. Proportion of germinated, dormant, and non-viable seeds for each of ten *Abutilon theophrasti* plants within a single agricultural population. Seeds were incubated under controlled environment conditions for a period of 21 days. The total number of seeds used for each plant was 1000, except for individual 1 (898), 5 (900), 8(549), 9 (713), and 10 (820).

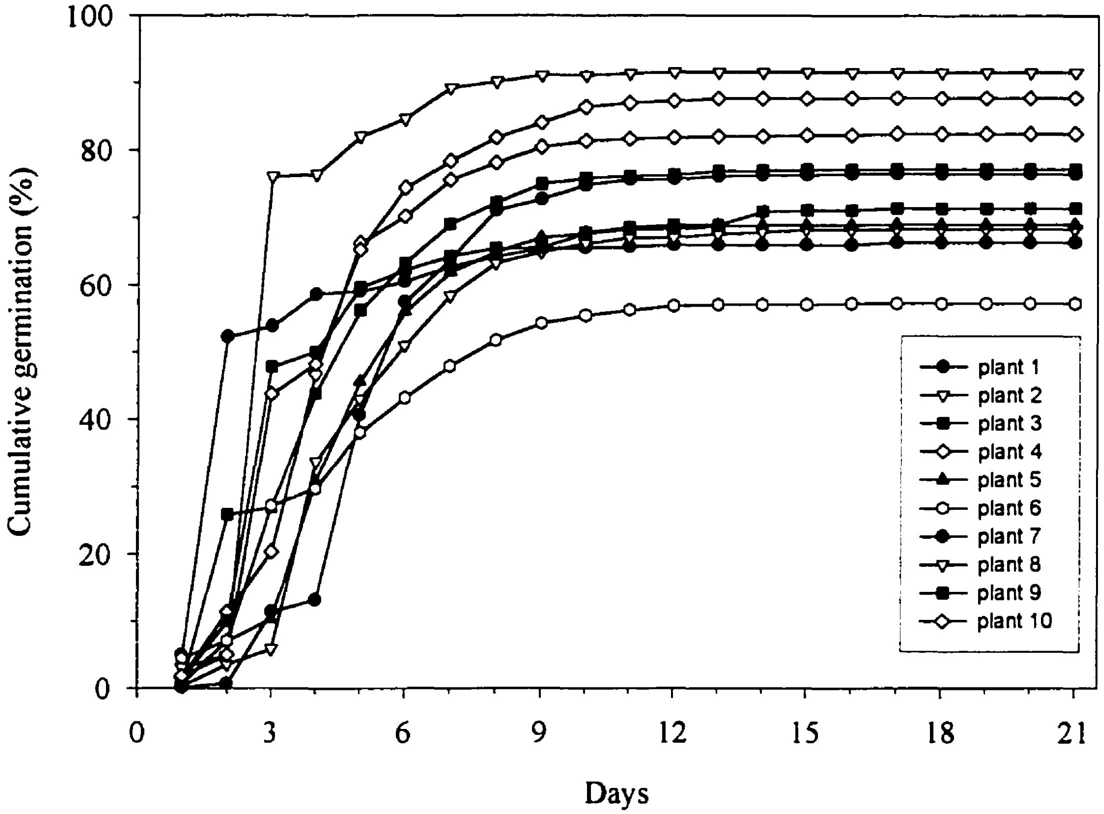

Figure 2.4. Cumulative germination (%) of *Abutilon theophrasti* seeds over a 21-day period for each of ten plants collected from a single agricultural population. A total of 549-1000 seeds were used for each plant.

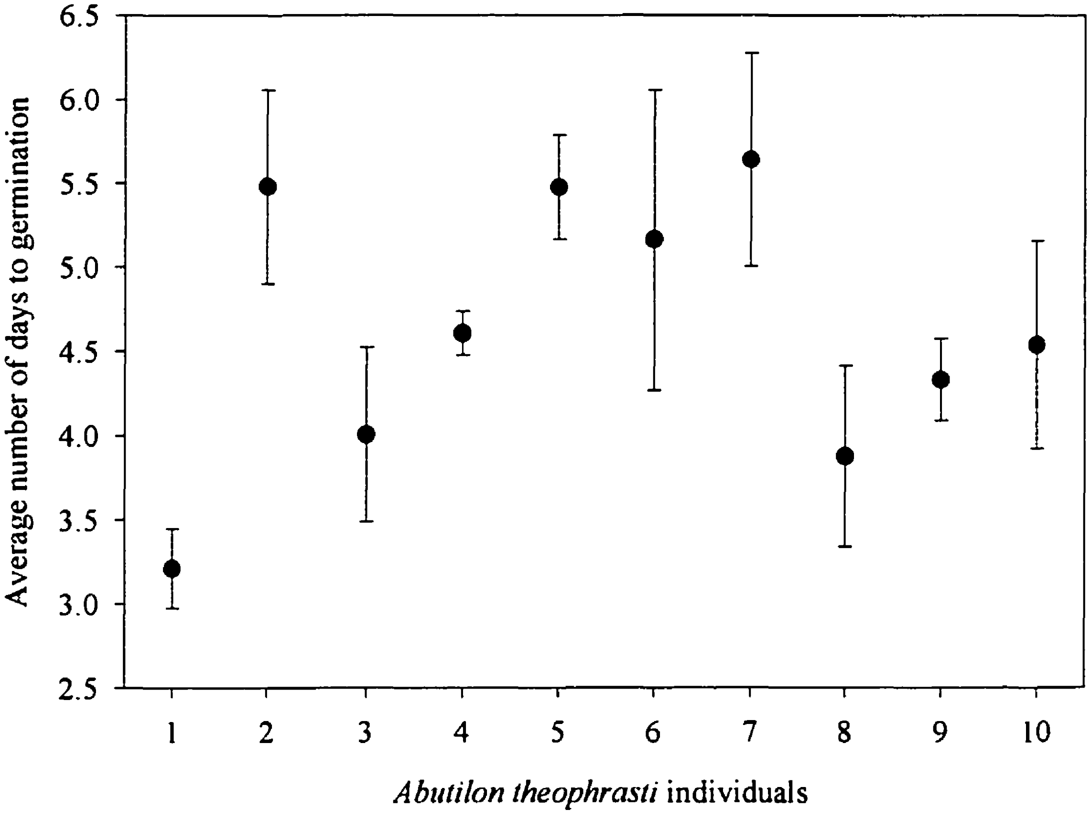

Figure 2.5. Average number of days to germination for seeds collected from ten *Abutilon theophrasti* plants from a single agricultural population. Bars indicate S.E. of the means.

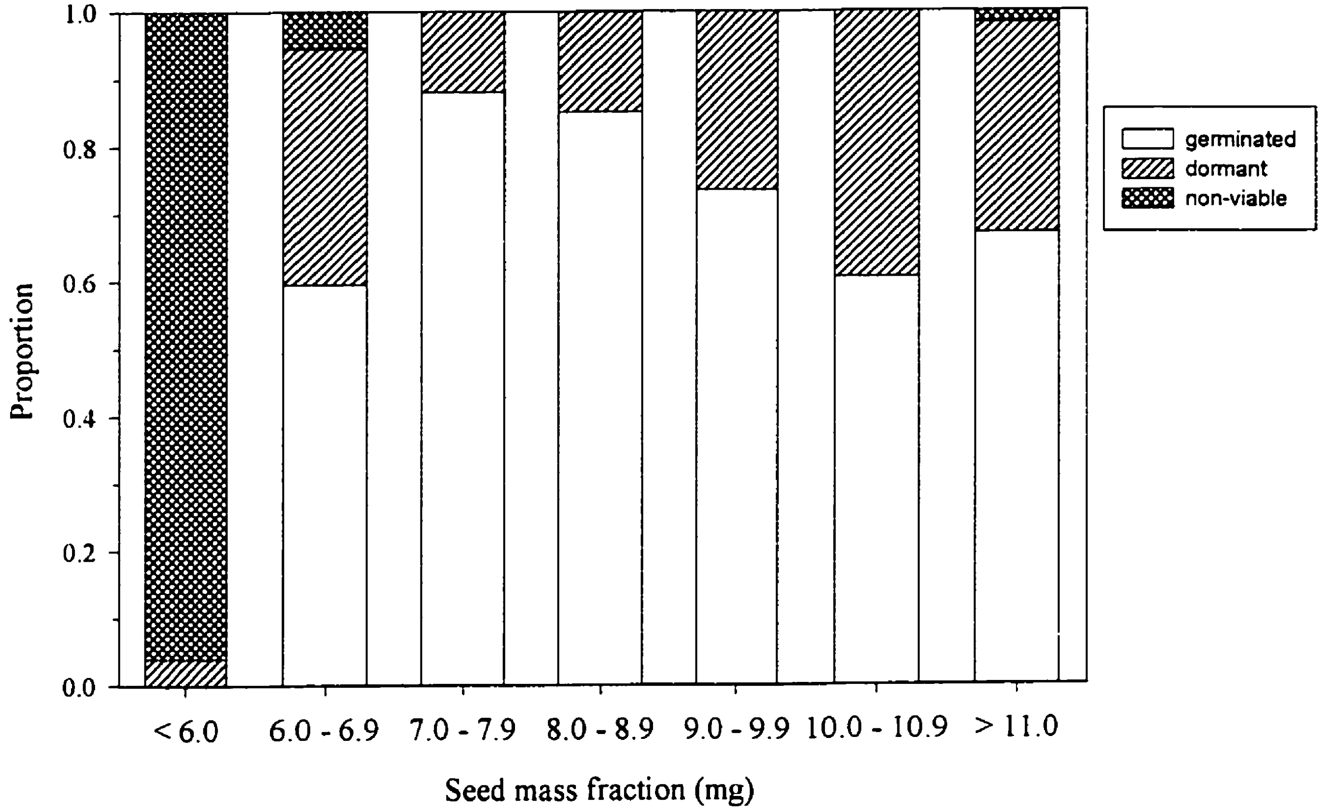

Figure 2.6. Proportion of germinated, dormant, and non-viable seeds within each of seven seed mass fractions collected from ten *Abutilon theophrasti* plants from a single agricultural population.

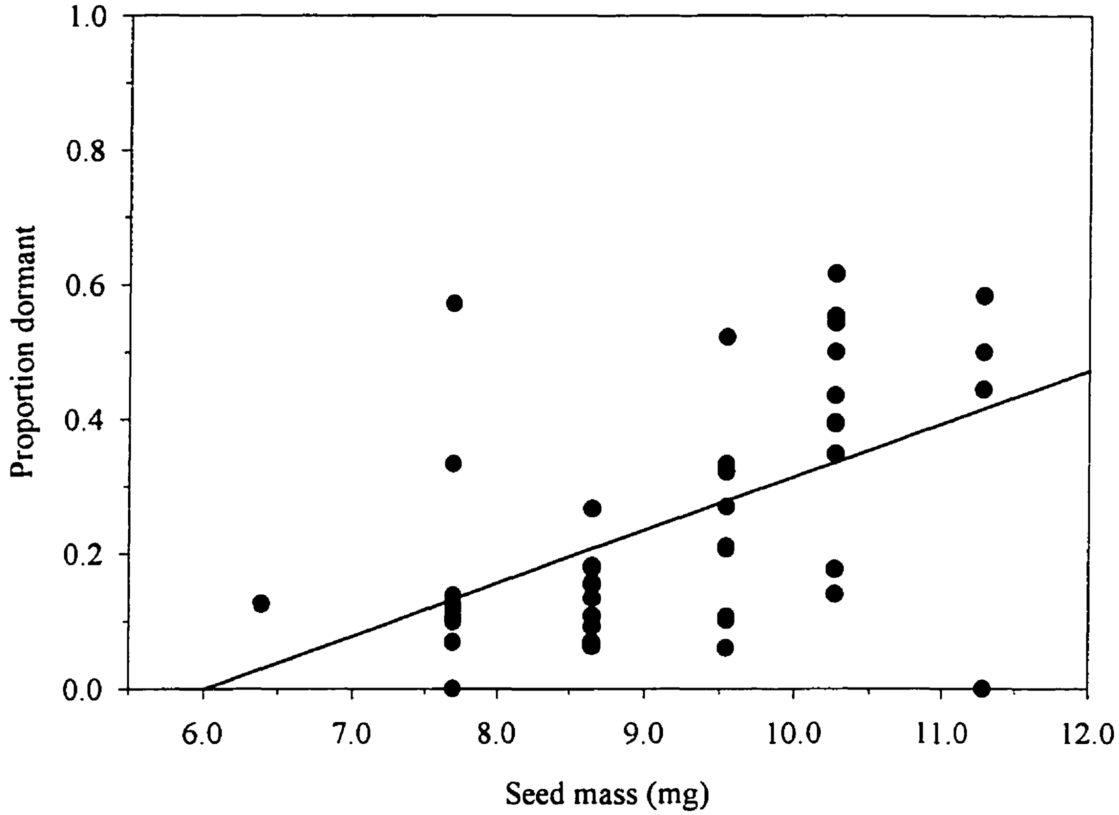

Figure 2.7. Relationship between the proportion of dormant seed and mean seed mass for seeds collected from ten *Abutilon theophrasti* plants from a single agricultural population. Data for seeds from only six seed mass fractions were used since for the lowest fraction (i.e., < 6.0 mg) most seeds were dead. Only mass fractions having more than 5 seeds were used in the analysis, $y = -47.3 + 7.9x$ $r^2 = 0.30^*$

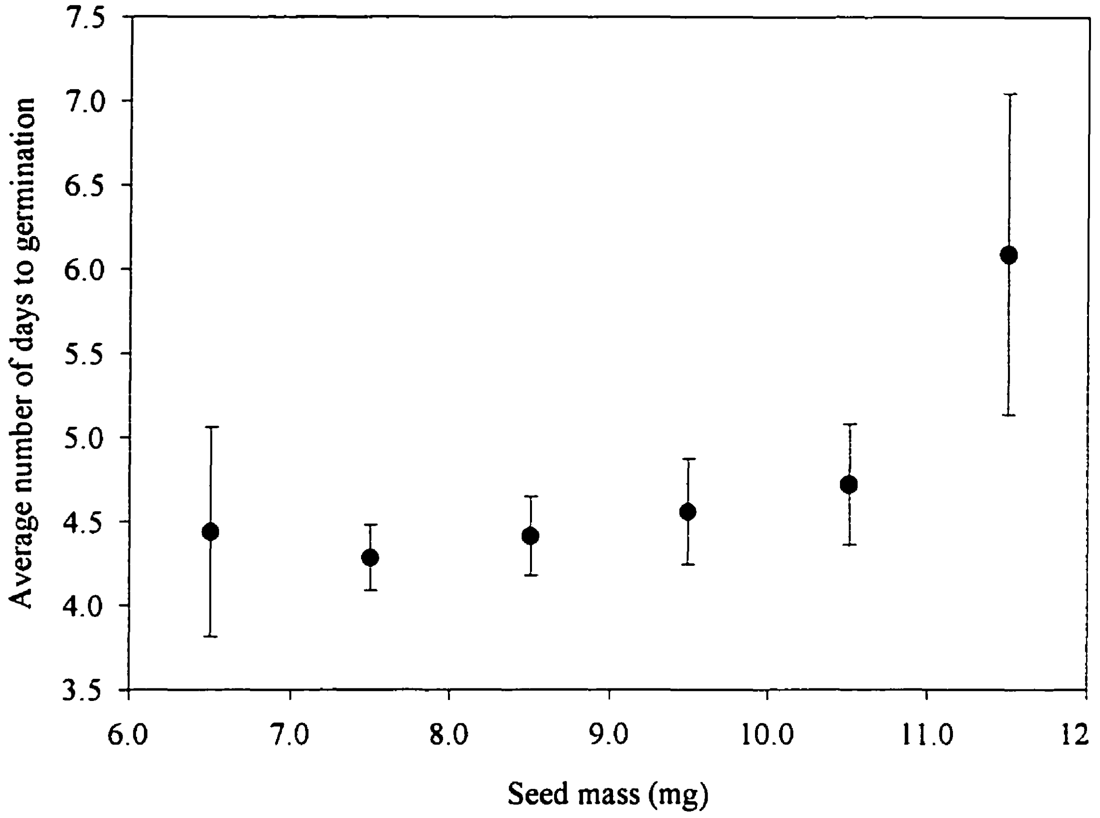

Figure 2.8. Average number of days to germination for seeds from six mass fractions collected from ten *Abutilon theophrasti* plants from a single agricultural population. Bars indicate S.E. of the mean. Seed mass is the mean value for each fraction. No seed germinated for < 6.0 mg mass fraction.

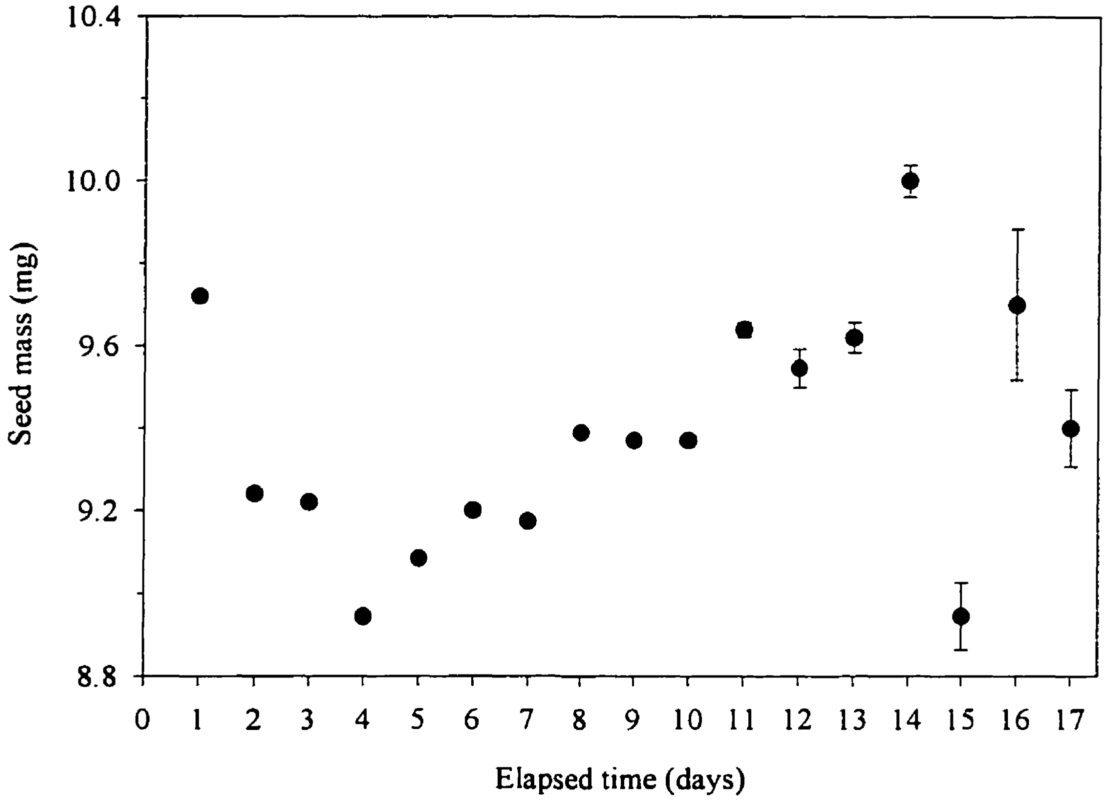

Figure 2.9. Mean mass and S.E. of *Abutilon theophrasti* seeds that germinated on each of the observed dates. No germination occurred after day 17. Data for the ten *Abutilon* plants were combined.

Connecting Text

Due in part to the rising concerns of herbicide resistance, methods to help reduce velvetleaf populations over the long term in an environmentally sustainable fashion are desirable. A fungal pathogen, *Colletotrichum coccodes*, has been identified as having some potential as a biological control agent of *A. theophrasti*. In this chapter, the effects of the fungal pathogen *C. coccodes* and seed size on *A. theophrasti* growth and reproduction were investigated over three successive generations

Chapter 3

Transgenerational effects of seed size and the fungal pathogen, *Colletotrichum coccodes*, on velvetleaf (*Abutilon theophrasti*) growth and reproduction

3.1 Abstract

Seed size plays an important role in determining the establishment success of individual plants within a population. Experiments were conducted in a controlled environment to determine the effects of initial seed weight and the subsequent foliar application of a fungal pathogen, *Colletotrichum coccodes*, on the growth and reproduction of *Abutilon theophrasti*. Seeds were collected from a local agricultural population and stored at room temperature for 30 months. Seeds were separated into two different size fractions (small ≤ 7 mg and large ≥12 mg). Two- to 3-leaf stage *A. theophrasti* plants from these two fractions were sprayed with *C. coccodes* at 1×10^9 conidia m^{-2}. Plants were harvested at 35 days after inoculation (DAI) and at 90 DAI. The experiment was performed at three sequential times wherein seeds generated from the first experiment were used for the second generation trial and seeds derived from the second experiment used in the third generation trial. Initial seed size did not significantly affect the growth (biomass, height, number of leaves, and stem diameter) and reproduction (capsule number, capsule weight, seed number, and seed weight) of *A. theophrasti*. In contrast, all these parameters were significantly ($P < 0.05$) affected by *C. coccodes* inoculation in all three generations. The deleterious effects of *C. coccodes* on *A. theophrasti* were more pronounced at 35 DAI than at 90 DAI. Inoculation of *C. coccodes* initially caused leaf defoliation in *A. theophrasti*, but further growth was not affected.

Seed size was not a good indicator of *A. theophrasti* vulnerability to the fungal pathogen *C. coccodes*. The most vigorous *A. theophrasti* plants produced heavier seeds regardless of their initial seed size and inoculation. Seeds collected from inoculated *A. theophrasti* plants showed significantly higher seed dormancy than seeds harvested from non-inoculated plants. The response of *A. theophrasti* plants to the pathogen did not change over the three generations suggesting that plants did not develop resistance to *C. coccodes* infection.

3.2 Introduction

The fitness of a plant may be influenced by the growing environment experienced by the parent plant in previous generations (Miao *et al.* 1991a). Environmentally induced maternal effects such as nutrients (Parrish and Bazzaz 1985), temperature (Alexander and Wulff 1985), day length (Cook 1975), herbivory (Willson and Price 1980), and predators and pathogens (Agrawal *et al.* 1999) can influence offspring phenotypes under unfavourable conditions. Maternal effects have generally been studied for only a single generation (e.g. Miao *et al.* 1991b), with only a few studies examining the impact over two or more generations (e.g. Agrawal *et al.* 1999, Miao *et al.* 1991b). Maternally induced transgenerational effects across multiple generations may provide more valuable insight into the longer-term impact of biotic factors such as disease incidence on plant growth and population dynamics (Agrawal *et al.* 1999). Maternal effects do not follow Mendelian inheritance principles but rather have a direct influence on offspring traits (Thiede 1998).

The role of non-Mendelian transgenerational effects on plant population growth and regulation has received little research attention (Thiede 1998). Transgenerational effects of predators, herbivores, and parasites have been observed both in plants (Roberts 1983) and animals (Shine and Downes 1999) with pathogens and predators typically affecting plant fecundity by reducing growth and reproduction (Agrawal *et al.* 1999). These biotic interactions often stimulate defense mechanisms in plants as well as compromising reproductive capacity (Agrawal *et al.* 1999). Agrawal (1998) found that leaf damage from *Pieris rapae* larvae stimulated a damage-induced response in wild radish, *Raphanus raphanistrum* that consequently increased plant fitness compared with undamaged plants.

The influence of seed size on the fitness of diseased plants has also drawn little attention (but see Augspurger 1984, Augspurger and Kelly 1984, Foster 1986) as most studies have focused only on the direct effects of seed size variation on plant fitness when plants are grown under stressful conditions (Fox 1990). Large seed size has been suggested to enhance plant resistance to fungal pathogens in three ways; 1) a thick seed coat can reduce the vulnerability of a seed to pathogen attack, 2) greater reserves of secondary compounds in the seed can increase seed and seedling defenses against the pathogen; and 3) higher nutrient reserves in the seed may be used to repair damage caused by the pathogen (Foster 1986). Ng (1978) carried out one of the few studies examining the relationship between seed size and susceptibility to fungal attack and found that Malaysian tree flora seedlings originating from small seed (< 3 mm in length) were more susceptible to fungal diseases than larger seeds. In contrast, Augspurger (1984) and Augspurger and Kelly (1984) reported that seed weight differences in

Platypodium elegans were not correlated with seedling vulnerability to damping off disease.

Previous studies on maternal effects have dealt with seed size (Zhang and Hamill 1997), seed size and a fungal pathogen (Augspurger 1984, Augspurger and Kelly 1984), and seed size and nutrient pulses over two successive generations (Miao *et al.* 1991a), but to date, the impact of fungal disease on host plants originating from seeds of different size has not been examined over multiple generations.

Velvetleaf (*Abutilon theophrasti* Medic; Malvaceae) is a troublesome annual weed of row crops in the Eastern and Mid-western United States, parts of Eastern Canada, and the Mediterranean regions of Europe. *A. theophrasti* produces up to 17,000 seeds in one growing season and seeds can survive in soil for up to 50 years (Warwick and Black 1988). Zhang and Hamill (1997) found that leaf chlorophyll content of young *A. theophrasti* seedlings and total leaf area of plants at harvest increased with increasing original seed weight. However, aboveground biomass of plants was not correlated with original seed weight. Lindquist *et al.* (1995) reported substantial decreases in individual weights of *A. theophrasti* seeds when plants experienced intense competition for light with a soybean crop.

Colletotrichum coccodes (Wallr.) Hughes (Fungi Imperfecti) is a selective foliar pathogen of *A. theophrasti* (Gotlieb *et al.* 1987). *C. coccodes* causes gray brown leaf lesions and black, sunken elongated stem lesions on *A. theophrasti*. Leaf lesions are generally observed within five days of inoculation (DAI) and appear as small water-soaked spots that enlarge into necrotic areas. Desiccated and diseased leaves are shed prematurely within five to 14 DAI (DiTommaso *et al.* 1996). In general, *A. theophrasti* plants are killed only when inoculated at the cotyledon to 1-leaf stage. When *C. coccodes* is applied at later growth stages of *A. theophrasti*, the pathogen causes extensive necrotic lesions on inoculated leaves with infected plants often stunted and development delayed. Nonetheless, affected plants often recover from these later applications of the pathogen (DiTommaso *et al.* 1996).

From a weed management perspective, transgenerational data describing the effects of both disease and seed size on *A. theophrasti* plant performance and reproduction are critical as they will provide information about initial seedling vigour, the ability of plants to overcome disease and/or herbivory, and subsequent ability to compete effectively and reproduce. This may be a particularly important aspect for the biological control of *A. theophrasti* with *C. coccodes* given the recent work showing that a small number of individuals within inoculated *A. theophrasti* populations may escape disease and produce large quantities of viable seeds (DiTommaso *et al.* 1996). One possibility advanced to explain these findings was that *A. theophrasti* individuals escaping control originated from relatively heavier seeds and thus produced competitively superior seedlings compared with plants originating from lighter seeds.

Hence, the objective of this research was to examine the effects of seed size and disease incidence on *A. theophrasti* plant growth and reproduction over three generations. It was hypothesized that the deleterious effects of *C. coccodes* would be more pronounced in plants originating from lighter seeds as compared with plants originating from heavier seeds and that these effects would be most evident in first generation as compared with later generations.

3.3 Materials and Methods

3.3.1.Seed Source. *A. theophrasti* seeds were collected in the fall of 1995 from a single plant growing in an agricultural field at the Emile A. Lods Agronomy Research Centre of McGill University, Ste-Anne-de-Bellevue, Québec, Canada. Individual seeds were weighed and ranked by weight into different size categories. From this single plant, 40 seeds from the two extreme seed size categories (heaviest and lightest seed weight classes) were selected. The two extreme size groupings chosen were ≤ 7 mg for the small-seeded treatment group and ≥12 mg for the large-seeded treatment group. The 40 seeds from each group were placed in boiling water for 10 seconds in order to break dormancy and subsequently placed on moistened filter paper (P 8, Fisher brand, Fisher Scientific, Nepean, Ontario) under room conditions for 24 hours. Germinated *A. theophrasti* seeds were seeded individually in 12.7-cm top-diameter plastic pots containing a commercial potting mixture (Promix Bx®, Premier Brands, Inc., NY, USA). Pots were then placed on a growth bench at 25/18°C day/night temperatures, 400 $\mu Em^{-2}s^{-1}$ fluorescent light and incandescent bulbs for 14 h d^{-1}, and watered as required with distilled water. Twice a week, 125 ml of 20-20-20 N-P-K (1.25 g L^{-1}) was added to each pot during the first generation, but this rate was reduced to once a week in later generations. The experiment was set up as a randomized complete block design with *A. theophrasti* seed size, *C. coccodes* inoculum application, and generation as main factors. There were five replications for each generation tested.

3.3.2. Inoculum Production and Application. A stock culture of *C. coccodes* was maintained on potato dextrose agar (PDA) slants under mineral oil at 3°C. Mycelium from the stock culture was transferred to PDA plates and incubated for ten days at 24°C.

Mycelial plugs were removed and transferred to 100 ml of a modified Richards' solution [10 g sucrose, 10 g KNO_3, 2.5 g $MgSO_4$, 5 g KH_2PO_4, 0.02 g $FeCl_3 \cdot 6H_2O$, 150 ml V-8 juice (Campbell Soup Co., Ltd., Toronto, Ontario, Canada) and distilled water to a final volume of 1L)] in 250 ml Erlenmeyer flasks (DiTommaso *et al.* 1996). Cultures were incubated for seven days on a rotary shaker (250 rpm) and conidia harvested and washed by filtering through four layers of cheesecloth and centrifuging (at 6500 *g* for 20 min). The spore pellet recovered was subsequently re-suspended in distilled water and the inoculum density adjusted using a haemocytometer (DiTommaso *et al.* 1996). *C. coccodes* inoculum was applied at the 2- to 3-leaf stage of *A. theophrasti* at a rate of 1×10^9 conidia m^{-2} using a spray chamber equipped with a Teejet® full cone nozzle (Teejet GTO.7 Spraying Systems Co., Wheaton, IL, USA) operating at 200 kPa air pressure, a nozzle speed of 0.85 km h^{-1}, and a spray volume of 500 L ha^{-1}. Control plants were sprayed with distilled water in the same manner. All sprayed plants were placed in a dark dew chamber (Percival model E-54U-DL, Boone, IA, USA) at 24°C and 100% relative humidity for 18h, and then returned to the growth chamber with the initial growing conditions as indicated earlier. Disease severity was visually assessed twice a week for 30 days after inoculation using a 10-point scale.

3.3.3. Harvest and Data Collection. At 35 DAI, half of the *A. theophrasti* plants from each treatment combination were harvested (five individual plants for each treatment). At this time, no plants had produced mature seed capsules. For each plant, the parameters measured were plant height, stem diameter, number of leaves, and aboveground dry biomass. Plant height was determined by measuring each plant from the soil surface to the shoot apex to the nearest 0.5 cm. Stem diameter was measured approximately 2 cm above soil level using a Marathon 150 mm electronic digital caliper (Marathon Management Co., Richmond Hill, Ontario, Canada). Aboveground dry biomass was determined by oven drying the plant material at 65°C for three days and weighing. Final harvest was carried out 90 DAI and additional data collected included the number of immature and mature capsules, capsule weight, number of seeds per capsule, and weight of seeds collected from different branching positions on plants. The effect of capsule position on seed size was examined by separating all harvested mature capsules into three groups representing early (basal), intermediate, and late (terminal) capsules. Aborted and immature capsules were not included. Harvested seeds were temporarily stored in paper bags at room temperature (21±1°C) before being placed in Petri plates lined with moistened filter paper containing 8 ml of distilled water. A maximum of 50 seeds per seed size fraction per plant was placed in Petri plates and the plates wrapped with Parafilm to prevent water loss. Petri dishes were then placed in the dark at 4°C for one week. At the end of this stratification period, seeds were incubated at 25/14°C day/night temperatures, with a 14-h photoperiod at 400 $\mu Em^{-2}s^{-1}$ fluorescent light. The number of germinated seeds having a radicle at least 2 mm long was recorded daily for 21 days and germinated seeds discarded. To determine the viability of non-germinated seeds, seeds were cut longitudinally through the embryo, soaked in 0.15% (w/v) tetrazolium solution (2,3,5-triphenyltetrazolium chloride, Sigma Chemical Co., St. Louis, MO, USA) for 20 to 24 h at 20°C in the dark, and scored according to intensity and location of staining using the method described by Kovach and Bradford (1992). Germination and viability tests were performed within 30 days of seed collection. Seeds harvested from this first trial (parental generation - P_1) within the two original seed size fractions (7 mg and ≥12 mg) were used for the second trial (F_1) and were subjected to the same treatments as in the first trial. These procedures were also followed for the third generation trial (F_2).

3.3.4. Statistical Analyses. Vegetative (aboveground biomass, height, number of leaves, and stem diameter) and reproductive (capsule number, weight, seed number, and seed weight) data for *A. theophrasti* were statistically analyzed using the PROC GLM procedure of SAS version 6.12 (SAS Institute Inc., 1990). All vegetative, reproductive, and disease rating (%) variables were square root transformed before analysis. Plant fitness was assessed using an index of lifetime that was determined by multiplying the seed number by the mean seed mass as described by Agrawal (1998).

3.4 Results

3.4.1. Disease severity of *C. coccodes* on *A. theophrasti* across generations. The application of *C. coccodes* on *A. theophrasti* seedlings at the 2- to 3-leaf stage produced gray brown foliar lesions that developed into necrotic spots and eventually resulted in the premature loss of infected leaves. The fungus only infected leaves present during the time of inoculation, and no disease symptoms were observed on leaves emerging after application. On average, *A. theophrasti* plants had 40-70% of leaves infected with *C. coccodes*, regardless of original seed size fraction or generation (Fig. 3.1). In all three generations, *A. theophrasti* mortality was below 5% for both the small and large seed size fractions. There were no significant differences in susceptibility to *C. coccodes* infection between *A. theophrasti* plants from the two seed size fractions, within a given generation (Table 3.1). However, transgenerational effects of *C. coccodes* were highly significant (*P*

< 0.001) (Table 3.1). Susceptibility of *A. theophrasti* plants to *C. coccodes* was greater in the second and third generations compared with the first generation.

3.4.2. Effects of seed size and *C. coccodes* infection on *A. theophrasti* mean seed weight. Despite differences in initial seed weight in the parental generation (P_1), the progenies of both inoculated and non-inoculated plants produced seeds with the same mean seed weight in subsequent generations. Transgenerational variation in seed size was more pronounced in the first generation than in later generations (Fig. 3.2). The mean weight of seeds produced by both inoculated (5.4 mg) and non-inoculated (5.8 mg) plants in the first generation was significantly different from the mean weight of seeds produced in the second and third generations (10.3 mg).

3.4.3 Effects of seed size and *C. coccodes* inoculation on *A. theophrasti* seed germination, dormancy, and viability. Seeds collected from inoculated *A. theophrasti* plants showed significantly higher seed dormancy than seeds from non-inoculated plants (Table 3.2). There was also a significant transgenerational effect on seed germination, dormancy, and viability ($P < 0.001$) (Table 3.2). For example, a lower proportion (34.3%) of seeds were dormant in the first generation compared with the second (78.0%) and third generations (86.2%). In the first generation, a substantial proportion (60.5%) of seeds produced died likely because of the high fertilization rate used. The interaction between seed size and *C. coccodes* inoculation on *A. theophrasti* seed viability was not significant over generations.

3.4.4. Effects of seed size and *C. coccodes* inoculation on *A. theophrasti* reproductive fitness. The cumulative effects of seed size and fungal infection by *C. coccodes* significantly decreased (40-50%) the index of lifetime of *A. theophrasti* plants originating from the small seed size fraction (Fig. 3.3). Although plants produced from larger seeds showed a 20-30% reduction in index of lifetime following inoculation with *C. coccodes*, this decrease in fitness was not significantly different from that of non-inoculated plants. The index of lifetime varied in *A. theophrasti* plants over generations with no significant differences in *A. theophrasti* fitness observed in the first generation (Fig. 3.3). The lower index of lifetime in the first generation was likely due to toxicity from over-fertilization and poor drainage of pots. These problems were rectified in the second and third generations, and resulted in substantially greater indices of lifetime (Fig. 3.3).

3.4.5. Effect of capsule maturation time on seed weight. In general, seeds that were produced from the earliest maturing capsules had the highest seed weights (Fig. 3.4). Seed weight per capsule gradually decreased for early- (10.8 mg) to late-maturing capsules (9.5 mg) in both inoculated and non-inoculated *A. theophrasti* plants. However, in the first generation, the weight of seeds from the late-maturing capsules was slightly greater than seeds produced from the early-maturing capsules (Fig. 3.4). Seed weight differences for the various capsule maturation periods were generally more pronounced in the latter two generations than in the first generation (Fig. 3.4).

3.4.6. Effects of seed size and *C. coccodes* inoculation on *A. theophrasti* growth over three generations. The application of *C. coccodes* at the 2- to 3-leaf stage of *A. theophrasti* enhanced defoliation and reduced overall plant growth compared with non-inoculated plants. The effects of *C. coccodes* inoculation had a highly significant ($P<0.01$) impact on *A. theophrasti* height, stem diameter, number of leaves at the first harvest (35 DAI) and across the three generations (Table 3.3.1). Seed size had no significant effects on any *A. theophrasti* growth parameters at first harvest (Table 3.3.2).

Seed size and *C. coccodes* inoculation had no significant effects on any *A. theophrasti* growth parameters, however, *C. coccodes* inoculation had a highly significant ($P<0.01$) impact on number of leaves at final harvest (Table 3.3.2).

3.4.7. Effects of seed size and *C. coccodes* inoculation on *A. theophrasti* reproduction over three generations. *C. coccodes* inoculation had a significant ($P<0.01$) influence on capsule production (Table 3.4). The number of mature capsules and the number of seeds per capsule were reduced when *A. theophrasti* plants were inoculated with *C. coccodes*. The weight of mature capsules and the weight of seeds per capsule remained constant for the non-inoculated plants. The number of mature capsules, number of immature capsules, number of seeds per capsule, and weight of seeds per capsule were relatively low in the first generation, however these reproductive parameters significantly increased in later generations.

3.5. Discussion

The deleterious effects of *C. coccodes* infection on *A. theophrasti* growth and reproduction over three generations were similar in plants originating from the small and large seed size fractions tested. The seed weight advantage of seedlings produced from heavier seeds was no longer apparent 15 days after germination (personal observation). The relationship between seed size and seedling success has been demonstrated to follow a sigmoidal rather than linear pattern such that increasing seed size does not improve seedling performance until a minimum threshold weight is attained (Marshall *et al.* 1985). Initial differences in parental seed size did not persist in the offspring in successive generations. These findings are consistent with those of Wulff (1986) showing that in the absence of competition, differences in parental seed size of *Desmodium paniculatum* were not observed in the form of seed weight and seed number variations of offspring. Similarly, Nobs and Hager (1974) observed uniform plant heights in *Atriplex hortensis* over time in plants originating from two seed size groups. Stanton (1984) reported that seedlings of wild radish (*Raphanus raphanistrum*) originating from relatively large seed (> 6 mg) were more likely to emerge and produce flowers than small seeds (< 4 mg). Schaal (1984) found that maternal effects in *Lupinus texensis* influenced plant size and persisted until reproduction. However, all these studies were conducted for single generations such that no data on the transgenerational persistence of seed size variability were collected. Regardless of initial parental seed size, *A. theophrasti* plants in this study produced heavier seeds in the last two generations. In the first generation, reductions in seed size and other reproductive parameters were likely caused by N-P-K over-fertilization.

It is generally accepted that severe herbivory has a negative impact on seed size (Lee and Bazzaz 1980). Most research investigating the effects of herbivory and/or disease on the weight of seeds produced have generally not considered the developmental stage of plants at the time of attack or infection (e.g. vegetative growth versus fruit maturation periods). For example, defoliation of *Catalpa speciosa* by *Ceratomia catalpae* (Sphingidae) during vegetative growth resulted in a lower mean seed weight compared with control plants (Stephenson 1980). In contrast, a 50% reduction in total leaf area during seed development of *Desmodium paniculatum* caused an increase in mean seed weight (Wulff 1986). Marshall *et al.* (1985) also found a positive correlation between herbivory and seed size.

The results of this study suggest that *A. theophrasti* capsule maturation timing has a significant effect on seed size, with this impact being more pronounced in later generations. Early-maturing capsules typically produced heavier seeds than late-maturing capsules regardless of *C. coccodes* inoculation. Despite observed differences in the seed weights of early- versus late-maturing capsules, defoliation caused by *C. coccodes* infection did not affect *A. theophrasti* mean seed weight compared with non-inoculated plants. Increased defoliation levels have been shown to reduce the seed weight of several annual crops (Walpole and Morgan 1974). Sugiyama and Bazzaz (1998) suggested that under nutrient stress conditions, *A. theophrasti* resource allocation to reproduction is negatively correlated with plant size thus resulting in a shift in the allocation of available resources to reproductive rather than vegetative structures. Resource stress due to defoliation in this study might have been responsible for the observed reduction in the weight of *A. theophrasti* seeds produced from later maturing capsules. Similarly, Marshall *et al.* (1985) suggested that a reduction in the ability of *Sesbania* species to acquire nutrients at later stages of growth were responsible for the observed decline in the number of seeds produced per fruit for early- versus late-maturing fruits.

The deleterious effect of *C. coccodes* infection was more pronounced in later generations as compared with the first generation indicating that this pathogen did not stimulate transgenerational induced resistance in *A. theophrasti*. The lower disease incidence in the first generation was due to toxicity from over-fertilization that effect *A. theophrasti* growth, however, these problems were rectified in the second and third generations, and resulted in substantially greater disease incidence. Using this same weed-pathogen system, DiTommaso and Watson (1995) reported that the reduced impact of this pathogen following multiple sequential applications within a single generation might have been due to an induced resistance reaction. Hong *et al.* (1999) also reported an induced resistance reaction in peppers (*Capsicum annuum*) following multiple sequential applications of *C. coccodes* inoculation. Since in this experiment *A. theophrasti* plants within a generation were inoculated only once, disease pressure might not have been severe enough to have stimulated an induced resistance reaction. Stommel and Haynes (1998) reported that anthracnose lesion number and size caused by *C. coccodes* in tomato fruits remained constant from year to year when the same tomato lines were inoculated. The reduction in height and stem diameter in *A. theophrasti* plants was significantly greater in the first harvest (35 DAI) compared with the final harvest (90 DAI) largely because of the loss of leaves following inoculation with *C. coccodes*. The indeterminate growth of *A. theophrasti* plants allowed them to recover from *C. coccodes* infection such that plant growth parameters did not differ significantly for inoculated and control plants at final harvest. Changes in root-to-shoot resource allocation patterns in *A. theophrasti* following leaf tissue losses might explain the recovery in growth of infected plants. These resource allocation changes have been documented in previous defoliation studies with *A. theophrasti* (Lee and Bazzaz 1980, Mabry and Wayne 1997).

The results from this study suggest that *C. coccodes* can have a negative impact on *A. theophrasti* growth and reproduction when applied at the 2- to 3-leaf stage. The results presented here support the previous findings of DiTommaso and Watson (1995) showing that *C. coccodes* application at 2- to 3-leaf stage enhances loss of infected leaves, but *A. theophrasti* plants can recover from these initial reductions in growth. Similarly, the application of fertilizer (20-20-20 N-P-K) on a weekly basis might also have enhanced the vigor of *A. theophrasti* plants. Despite initial differences in seed weights, the susceptibility of *A. theophrasti* plants originating from either large or small seed sizes to *C. coccodes* infection was similar.

3.6. References

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Table 3.1. Summary of ANOVA for the impact of *Colletotrichum coccodes* inoculation and initial *Abutilon theophrasti* seed size on disease ratings over three generations.

Source of variation	df	SS	MS	F Value	*Pr >F*
C. coccodes	1	0.4898	0.4898	0.76	0.3869
Seed size	1	0.1191	0.1191	0.19	0.6685
Block	4	4.8395	1.2098	1.89	0.1297
Generation	2	22.9903	11.4951	17.93	0.0001
Error	44	28.2165	0.6412		

Table 3.2. P-values from ANOVA for the effects of *Abutilon theophrasti* seed size, *Colletotrichum coccodes* inoculation and generation on seed germination, dormancy, and mortality.

Source	df	Germination	Dormancy	Mortality
Seed size (S)	1	0.9094	0.3247	0.3701
C. coccodes (C)	1	0.0837	0.020	0.4128
Generation (G)	2	0.0001	0.0001	0.0001
S x C	1	0.8013	0.2578	0.0747
S x G	2	0.4483	0.9692	0.4572
C x G	2	0.2914	0.5032	0.4101
S x C x G	2	0.8554	0.4966	0.0780
Error	30			

Table 3.3.1. Summary of the ANOVA for *Abutilon theophrasti* height, stem diameter, above-ground biomass, and number of leaves as affected by seed size and *Colletotrichum coccodes* inoculation over three generations (Generation) at first harvest (35 DAI).

Source	df	Height (cm)	Stem diameter (mm)	Biomass (g)	Number of leaves
		Pr > F	Pr > F	Pr > F	Pr > F
C. coccodes	1	0.0009	0.0001	0.0112	0.0001
Seed size	1	0.9550	0.9382	0.4319	0.6106
Block	4	0.7112	0.9064	0.5727	0.3209
Generation	2	0.0001	0.0001	0.2811	0.0072
Error	44				

Table 3.3.2. Summary of the ANOVA for *Abutilon theophrasti* height, stem diameter, above-ground biomass and number of leaves as affected by seed size and *Colletotrichum coccodes* inoculation over three generations (Generation) during the final harvest (90 DAI).

Source	df	Height (cm)	Stem diameter (mm)	Biomass (g)	Number of leaves
		Pr > F	Pr > F	Pr > F	Pr > F
C. coccodes	1	0.1800	0.0060	0.3873	0.0040
Seed size	1	0.2755	0.2428	0.4264	0.3133
Block	4	0.5294	0.8162	0.7970	0.4566
Generation	2	0.0001	0.0001	0.0001	0.0001
Error	44				

Table 3.4. Summary of the ANOVA for *Abutilon theophrasti* reproductive parameters at final harvest (90 DAI) as affected by initial seed size fraction and *Colletotrichum coccodes* inoculation over three generations.

Source	df	No. of mature capsules	No. of immature capsules	Weight of mature capsules	No. of seeds /capsules	Weight of seeds /capsules
		Pr > F	Pr > F	Pr > F	Pr > F	Pr > F
C. coccodes	1	0.0001	0.0090	0.0087	0.0001	0.0001
Seed size	1	0.5379	0.1188	0.6653	0.4085	0.4109
Block	4	0.7318	0.2862	0.3652	0.5101	0.4138
Generation	2	0.0010	0.0001	0.1576	0.0117	0.0004
Error	44					

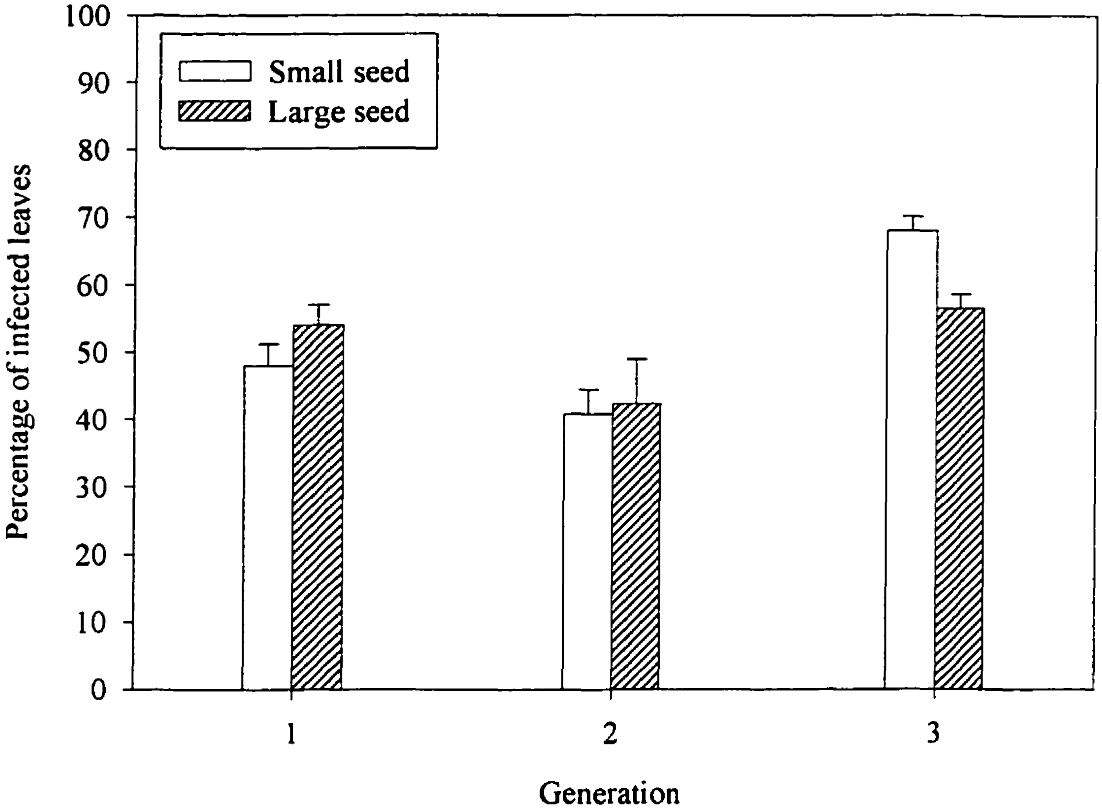

Figure 3.1. The effect of *Colletotrichum coccodes* on *Abutilon theophrasti* plants over generations on the proportion of infected leaves (± SE) for plants originating from two seedsize fractions.

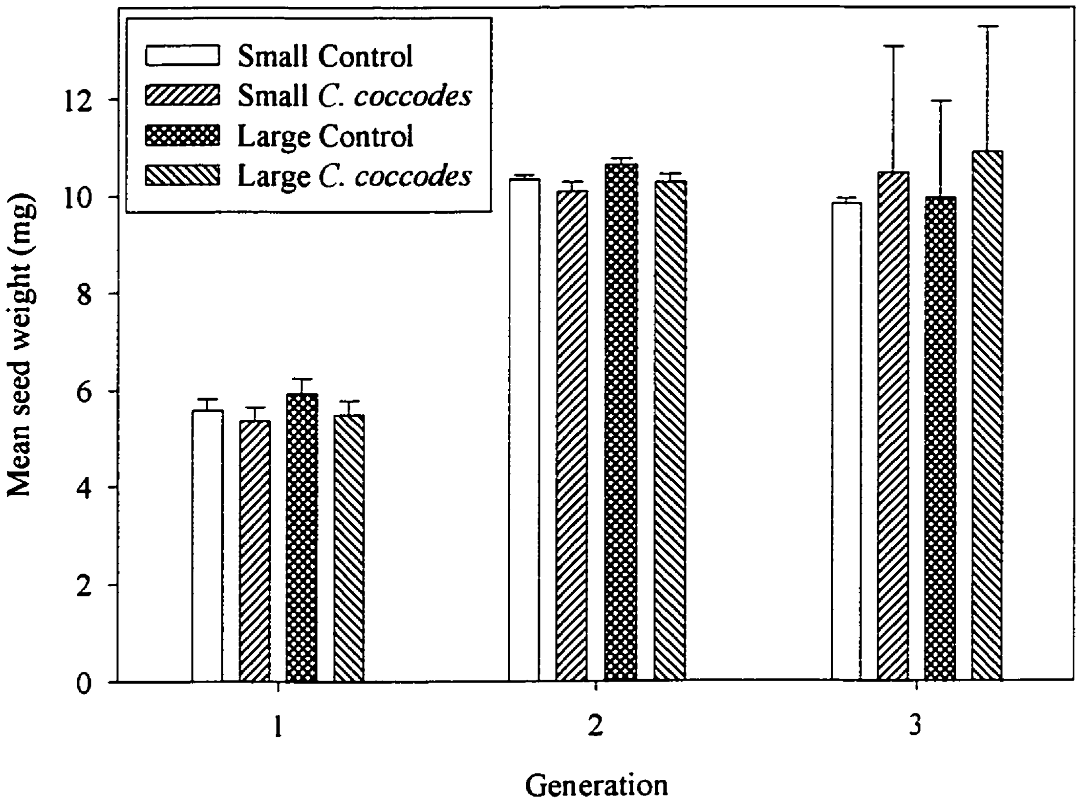

Figure 3.2. The effects of seed size and the application of the fungal pathogen *Colletotrichum coccodes* on *Abutilon theophrasti* mean seed weight (± SE) for three generations.

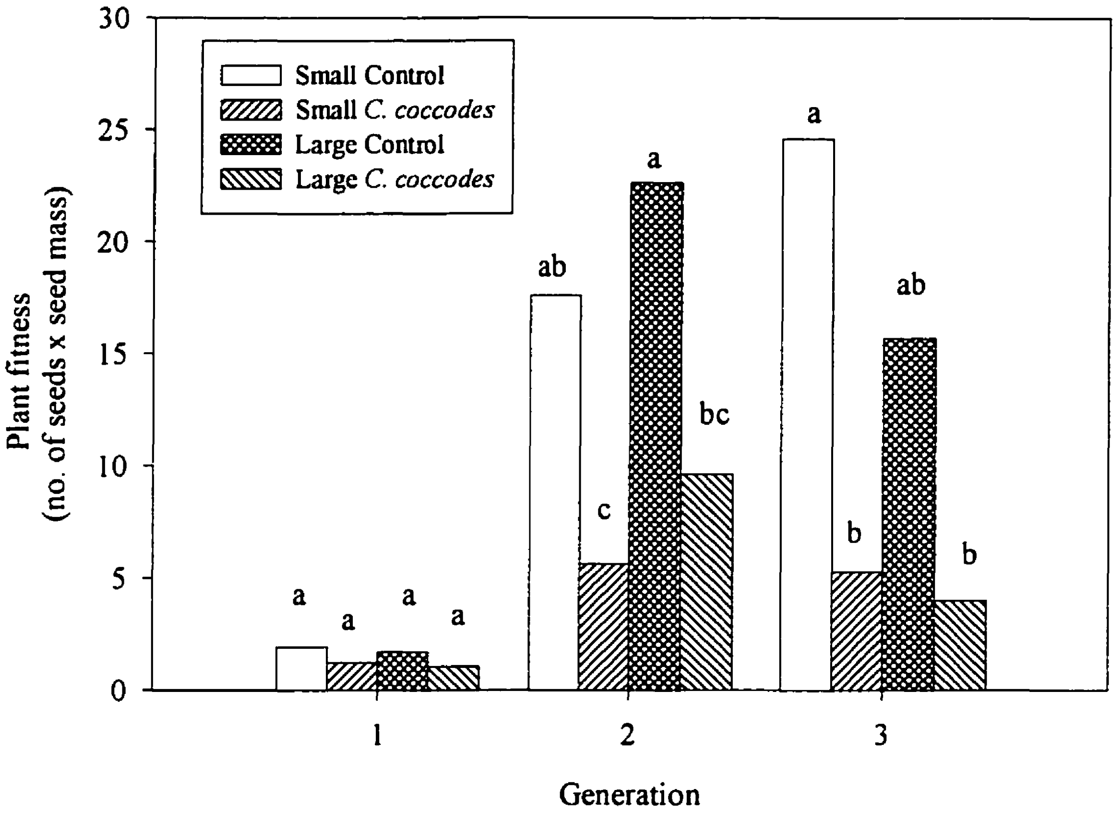

Figure 3.3. Reproductive fitness of *Colletotrichum coccodes* inoculated and non-inoculated (control) *Abutilon theophrasti* plants from two seed size fractions: small = 7 mg; large > 12 mg. Bars within a generation, having the same letters are not significantly different at $P < 0.05$ significant level according to Tukey's HSD test.

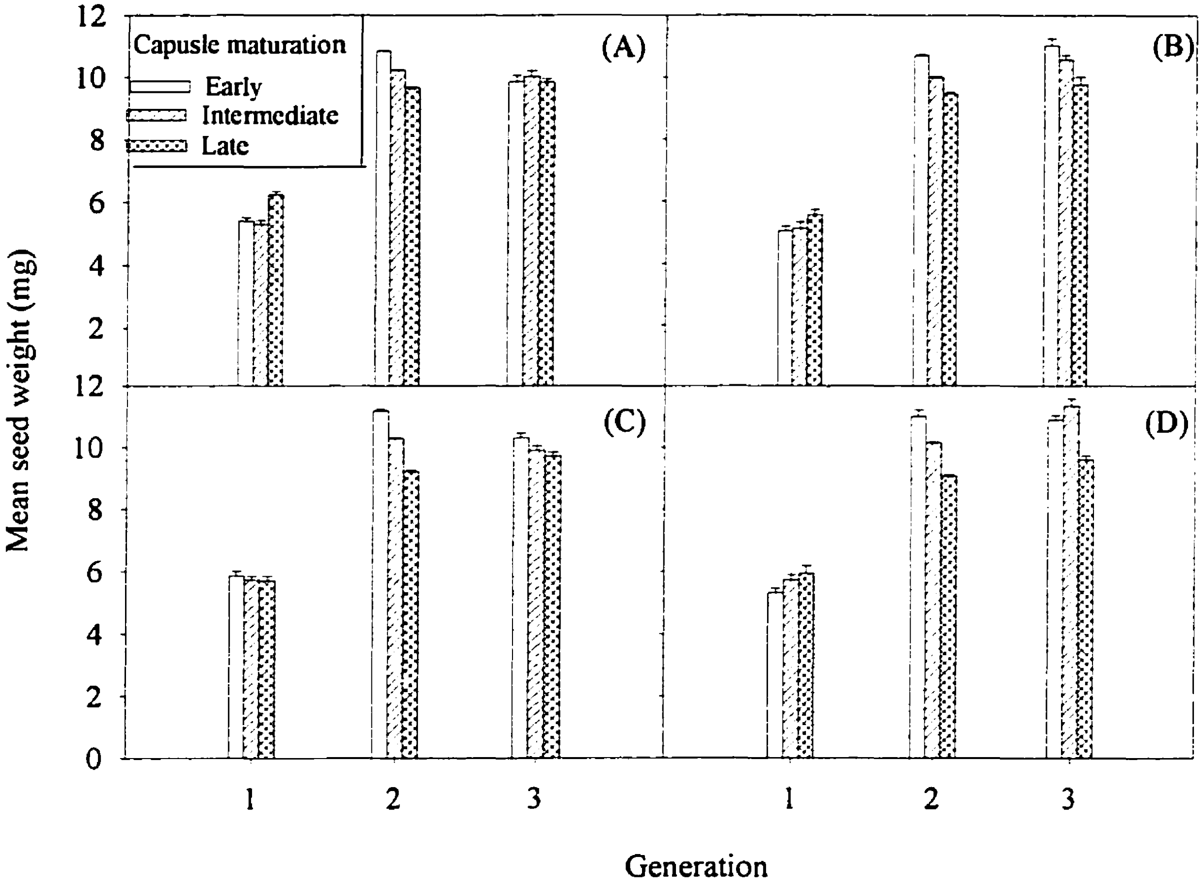

Figure 3.4. Relationship between seed weight (± SE) and capsule maturation period (i.e., early , intermediate, and late) for *Abutilon theophrasti* plants originating from two seed size fractions and inoculated with *Colletotrichum coccodes* or distilled water (control) over three successive generations; (A) small seed, non-inoculated, (B) small seed, inoculated, (C) large seed, non-inoculated, and (D) large seed, inoculated.

Connecting Text

In the previous chapter it was seen that the fungal pathogen, applied at the 2- to 3-leaf stage, had a deleterious effect on *A. theophrasti* growth and reproduction and successive generations of *A. theophrasti* did not develop acquired resistance.

This chapter focuses on the effects of biotic and chemical stresses on the growth of *A. theophrasti* under field conditions. *A. theophrasti* was established using either small or large seed sizes, and in either monospecific stands or in competition with soybean. The aim was to investigate the effects of *Colletotrichum coccodes* (a fungal pathogen) and bentazon (a herbicide) on *A. theophrasti* size hierarchies under field conditions.

Chapter 4

Effect of seed size and *Colletotrichum coccodes* infection on *Abutilon theophrasti* aboveground biomass, stem diameter, and height hierarchy development under stress conditions

4.1. Abstract

Velvetleaf (*Abutilon theophrasti*: Malvaceae) is a serious weed in the Corn Belt of North America and the Mediterranean regions of Europe. *A. theophrasti* is a strong competitor because of its rapid growth rate and architectural form, which provide an advantage by overtopping neighbouring plants and effectively competing for light. The effects of *A. theophrasti* seed size (small <10 mg and large ≥ 10 mg), the fungal pathogen *Colletotrichum coccodes* alone, and in combination with the herbicide, bentazon, and soybean interspecific competition on *A. theophrasti* size hierarchies were studied in the field during the summers of 1997, 1998, and 1999. *A. theophrasti* was harvested twice; a mid-season harvest [85 days after seeding (DAS)] and a final harvest (118 DAS). At each harvest, plant height, aboveground biomass, and stem diameter were measured. The split application of *C. coccodes* and bentazon drastically reduced (60-70%) *A. theophrasti* aboveground biomass when grown in competition with soybean. However, seed size differences did not affect *A. theophrasti* growth parameters measured. The distributions of *A. theophrasti* plant height, aboveground biomass, and stem diameter were positively skewed (L-shaped) when grown in competition with soybean. However, *A. theophrasti* plant height and stem diameters were negatively skewed (J-shaped) and aboveground biomass positively skewed in monospecific stands. Application of *C. coccodes* alone and in combination with bentazon did not affect *A. theophrasti* size distributions in

monospecific stands compared with unsprayed control plots. In contrast, size distributions were significantly altered by *C. coccodes* inoculation alone and in split applications with bentazon when *A. theophrasti* plants were grown with a soybean crop. Both sprayed and unsprayed control plots showed higher Gini coefficient values for height, aboveground biomass, and stem diameter when grown in competition with soybean than when grown in monospecific stands. These results illustrate the variable influence that intra- and interspecific competition has on *A. theophrasti* size hierarchies.

4.2. Introduction

Competition between individual plants for a limiting resource such as light is usually reflected in the development of size asymmetry in the population, where larger individuals often obtain a greater share of available resources and subsequently suppress the growth of their smaller neighbours (Weiner and Thomas 1986, Weiner 1988, Weiner 1990, Schwinning and Weiner 1998). The term asymmetry competition is synonymous with several other terms such as one-sided competition (Firbank and Watkinson 1987), dominance and suppression (Schwinning and Weiner 1998), resource preemption and snowball competition (Weiner and Thomas 1986). Competition for light differs from that for other resources such as nutrients in that competition for nutrients intensifies soon after germination whereas competition for light begins only when plants are large enough to shade one another (Weiner 1988).

Size inequality in plant populations can readily be calculated using various models and computer software (Sen 1973, Weiner and Solberg1984, Weiner 1986, Ellison 1987, Dixon 1993, Shumway and Koide 1995). Size asymmetry is a common feature in most plant populations, where taller and/or larger individuals have a competitive advantage over shorter and/or smaller individuals (DiTommaso and Watson 1997). Size asymmetry in plant populations may be determined by age differences, genetic differences, environmental heterogeneity, maternal effects such as seed size, effects of herbivores, parasites or pathogen, competition, and the interaction among these factors (Weiner 1985, Weiner and Thomas 1986, DiTommaso and Watson 1997).

Plant density plays an important role in determining size hierarchy in a species (Weiner and Thomas 1986, Miller and Weiner 1989). Weiner and Thomas (1986) listed 16 size-asymmetric competition cases, where 14 out of 16 became asymmetric with increasing density. It was observed that a population of a species grown at higher densities showed greater size asymmetry than a population grown at lower densities over the same period (Weiner and Thomas 1986). For example, *Salicornia europaea* grown at low monospecific densities were taller, heavier, had greater stem diameters and branched more profusely than for plants grown in pure stand at higher densities (Ellison 1987). The height inequality between low and high densities of *S. europaea* was, however, the same in monospecific stands, because *S. europaea* did not self thin (Ellison 1987). Ellison (1987) concluded that most annual plants exhibit lower height hierarchy variation in monospecific stands until density approaches 10,000 plants m^{-2}. Working on a *Trifolium incarnatum - Lolium multiflorum* competition system, Weiner (1985) reported that *L. multiflorum* in mixture with *T. incarnatum* showed a greater competitive ability resulting in lower inequality of dry biomass compared with *L. multiflorum* grown in monospecific stands. However, *T. incarnatum* in mixture exhibited a greater dry biomass inequality than in pure stand. Paul and Ayres (1986) found that rust infection by *Puccinia* *legenophorae* on *Senecio vulgaris* (groundsel) resulted in a positive skewing of plant size when grown in monospecific stands. Smaller *S. vulgaris* individuals in the population experienced substantially greater reductions in dry weight compared with non-inoculated plants thereby exaggerating size inequalities (Paul and Ayres 1986). In another experiment, Paul (1989) introduced a competing plant species, *Euphorbia peplus*, in the rust infected-*S. vulgaris* system. The presence of *E. peplus* had a limited effect on *S. vulgaris* dry weight with no significant differences in *S. vulgaris* biomass observed in monospecific stands and in mixture with *E. peplus* (Paul 1989).

The effect of *Colletotrichum coccodes* (Wallr.) Hughes, bentazon [3-(-1-methylethyl)-1*H*)-2,1,3-benzothiadiazin-4 (3*H*)-one 2,2-dioxide], on size hierarchies of the annual herbaceous weed, *Abutilon theophrasti* Medic. (velvetleaf) were studied in a soybean cropping system. *A. theophrasti* is a member of the Malvaceae family and is a troublesome weed in maize, soybean, and other crops in the eastern United States, parts of eastern Canada, and Mediterranean regions of Europe. An important feature of *A. theophrasti* that contributes to its competitive ability in soybean and maize fields is its architecture (Tremmel and Bazzaz 1995). *A. theophrasti* plants branch profusely especially at the top of the canopy such that they intercept a greater percentage of light than many competing plant species such as soybeans and maize (Akey *et al.* 1990, Sattin *et al.* 1992). Moreover, *A. theophrasti* has the ability to adjust its canopy architecture in response to available space (Sattin *et al.* 1992). At a lower planting density, *A. theophrasti* exhibits a two-dimensional (central main stem and lateral branches) architectural structure while at higher planting densities *A. theophrasti* displays a one-dimensional (central stem only) architectural form.

C. coccodes is a member of the Fungi Imperfecti as no sexual stage is known. This selective fungus causes gray brown leaf lesions and black, sunken elongated stem lesions on *A. theophrasti*. Leaf lesions are generally observed within five days of inoculation and appear as small water-soaked spots that enlarge into necrotic areas. Desiccated and diseased leaves are shed prematurely within 5-14 days of inoculum application (Wymore *et al.* 1988). Recently, DiTommaso and Watson (1997) reported that *A. theophrasti* height was positively skewed (L- shaped) at two weeks and negatively skewed (J-shaped) at three weeks after inoculation with the fungal pathogen *C. coccodes*. In contrast, non-inoculated control *A. theophrasti* plants showed a J-shaped frequency distribution two weeks after the start of the trial.

Bentazon is a contact herbicide that selectively controls broadleaf weeds in maize and soybean. When applied as a post-emergence herbicide on *A. theophrasti*, bentazon causes foliar injury by altering the D-1 quinone binding protein in photosystem II (Lycan and Hart 1999). Infected leaves become chlorotic, eventually turning brown and desiccating.

Lindquist *et al.* (1995) demonstrated that seed size variations increased in *A. theophrasti* when grown in a light limited environment. Similarly, Zhang and Hamill (1997) reported increases in leaf chlorophyll content of young *A. theophrasti* seedlings and total leaf area of plants at harvest with increasing original seed weight. The aboveground biomass of plants, however, was not affected by original seed weight.

Thus, the specific objectives of this research were to examine the effects of seed size and *C. coccodes* alone and in combination with bentazon on *A. theophrasti* size hierarchies when grown in monospecific stands and in competition with soybean. It is hypothesized that the deleterious effects of *C. coccodes* on *A. theophrasti* size hierarchy are more pronounced when grown in competition with soybean than when grown in monospecific stands. Similarly, *A. theophrasti* originating from the small seed size fraction will exhibit greater size inequality in monospecific stands compared with the large seed size fraction.

4.3. Materials and Methods

4.3.1. Study site. Field trials were conducted during the 1997, 1998, and 1999 growing seasons at the Emile A. Lods Agronomy Research Centre, Macdonald Campus of McGill University, Ste-Anne-de-Bellevue, Québec, Canada. Plots were located on a St. Bernard fine sandy loam (orthic melanic brunisol, pH= 6.8 and 3.0 % organic matter content).

4.3.2. Establishment of planting densities. In all years, the experimental site was moldboard plowed during the previous fall and disked and cultivated in the spring. Fertilizer [0-30-45 (N-P-K)] was applied each year at a rate of 250 kg ha^{-1}. Due to the presence of *Elytrigia repens* and *Cyperus esculentus* at the field site in 1999, the area was treated with 0.9 kg ha^{-1} of glyphosate [N-(phosphonomethyl)-glycine, isopropylamine salt] prior to seedbed preparation. Each year, between 22-29 May, soybeans cv. 'Bayfield' was seeded at a population density of 350,000 plants/ha and a row spacing of 40 cm using a Bolens 5-row plot seeder.

4.3.3. Experimental design. During each of the three years, monospecific stands of *A. theophrasti* and mixture plots with soybean were established in 1m by 2m plots arranged in a 2 x 2 x 3 randomized complete block design with four replicates. The three factors were seed size, competition, and weed control treatment. Previously collected *A.*

theophrasti seeds were separated into two size fractions (small <10 mg and large seed size ≥ 10 mg). In each of the pure stand and mixture plots, 200 pre-germinated *A. theophrasti* seeds were planted in the 1 by 2m area on June 3rd in 1997 and May 27and 29 in 1999 and 1998. Within each plot, two subplots of 0.25 m^2 (50 cm by 50 cm) were established. *A. theophrasti* plants in each of the subplots were harvested at two different times. Soybeans were manually removed from *A. theophrasti*-designated monospecific stands as soon as they emerged. Similarly, all weeds were removed by hand from soybean pure stand-designated plots.

4.3.4. Inoculum Production. A stock culture of *C. coccodes* was maintained on potato dextrose agar (PDA) slants under mineral oil at 3°C. Mycelium from the stock culture was then transferred to PDA plates and incubated for ten days at 24°C. Mycelial plugs were removed and transferred to 100 ml of a modified Richards' solution [10g sucrose, 10 g KNO_3, 2.5 g $MgSO_4$, 5 g KH_2PO_4, 0.02 g $FeCl_3 \cdot 6H_2O$, 150 ml V-8 juice (Campbell Soup Co., Ltd., Toronto, Ontario, Canada) and distilled water to a final volume of 1L] in 250 ml Erlenmeyer flasks (DiTommaso and Watson 1997). Cultures were incubated for seven days on a rotary shaker (250 rpm) and conidia harvested and washed by filtering through four layers of cheesecloth and centrifuging (at 6500 *g* for 20 min.). The spore pellet recovered was subsequently re-suspended in distilled water and the inoculum density adjusted using a haemocytometer (DiTommaso and Watson 1997).

4.3.5. Inoculum and herbicide application. *C. coccodes* conidia were applied to *A. theophrasti* monospecific plots and mixture plots with soybean, either alone or in a split application with bentazon at a rate of 240g a.i. (active ingredient) ha^{-1} (25% of the recommended rate). In the split application treatment, bentazon was applied 17 DAS (days after seeding) when *A. theophrasti* plants were at the 2- to 3-leaf stage and soybean plants were at the first trifoliate leaf stage. *C. coccodes* was sprayed five days later (22 DAS) at the 2- to 3-leaf stage of *A. theophrasti* plants, at a rate of 1×10^8 conidia m^{-2} in an oil-in-water formulation (5% corn oil plus 4% oil surfactant (15% of Tween® 80 (polyoxyethylenesorbitan monooleate)), and 85% v/v of Span® 80 (Sorbitan monooleate), ICI, Brantford, Ontario) using a pressurized hand-held sprayer operating at 200 kPa and delivering 450 L ha^{-1}. The herbicide was also sprayed using this equipment, but at a total volume of 300 L ha^{-1}.

4.3.6. Harvest procedure. In each main plot, one subplot was harvested at 85 DAS and the other subplot was harvested at 118 DAS. At harvest, main stem diameter (between cotyledons and first pair of true leaves), height (from the cotyledonary node to the apical meristem), and aboveground biomass of *A. theophrasti* plants were recorded.

4.3.7. Disease rating. A disease rating based on a visual estimate of the percentage leaf area infected was carried out at 29, 36, 41, and 48 DAS.

4.3.8. Environmental data. Daily precipitation and maximum/minimum temperatures between April and October in 1997, 1998, and 1999 were obtained from Environment Canada for the Ste-Anne-de-Bellevue Station located approximately 1 km away from the field site. For each year, leaf wetness within the plant canopy was determined visually (observing the presence or absence of dew in early morning 5-7 AM) for 3 days after inoculation with *C. coccodes*.

4.3.8. Statistical analyses. Due to large variations in weather conditions in each of the years, results for each year were analyzed separately. The normality of data was determined using the PROC UNIVAR procedure of SAS (SAS 1990). The effects of seed size, *C. coccodes* alone and in combination with bentazon on size hierarchies of *A. theophrasti* grown in monospecific stands and in competition with soybean were determined by using a factorial GLM procedure of SAS (SAS, 1990). To meet the assumptions of ANOVA, the data of aboveground biomass, height, and stem diameter were square root transformed in order to homogenize variances. The skewedness and kurtosis of the data were determined with SAS (SAS 1990). Skewedness provides a measure of the degree of asymmetry in the frequency distribution (DiTommaso and Watson 1997). Positive and negative values of skewedness are expressed as L-shaped and J-shaped distributions, respectively. Zero skewedness suggests a symmetrical distribution (DiTommaso and Watson 1997). Kurtosis indicates the peakedness of the distribution (Nagashima *et al.* 1995) and positive or negative values of kurtosis suggest that the distribution is more peaked (leptokurtic) or bimodal (platykurtic) (Nagashima *et al.* 1995).

The inequality among *A. theophrasti* plants in height, dry weight, and stem diameter was assessed using the Lorenz curve and the Gini coefficient (Weiner and Solberg 1984). The Lorenz curve provides the detailed structure of size inequality and allows one to identify the regions where significant size differences occur between distributions. Using the Lorenz curve, individual *A. theophrasti* plants were ranked from the smallest to the largest with respect to the parameter measured. The cumulative fractions of individual plants (p) were plotted against the cumulative fraction of the dependent variables L (p) such as plant height, aboveground biomass, and stem diameter (Mehran 1975, Weiner 1985, Shumway and Koide 1995). The Lorenz curve for p and L (p) range from $[p_0, L(p_0)]$, $[p_1, L(p_1)]$, ..., $[p_k, L(p_k)]$, $[p_{k+1} = L(p_{k+1})]$, with $p_0 = L(p_0)$

$= 0$ and $p_{k+1} = L(p_{k+1}) = 1$. Specifically, the value of the Gini coefficient is equal to twice the area between L (p) and the 45° line of equality (Mehran 1975).

The Gini coefficient has a minimum value of 0, when all of the individual *A. theophrasti* plants have the same height for example, while the maximum value 1.0 represents an infinite population in which all individuals, but one, have a value of 0 (Weiner and Solberg 1984). For n plants having a mean height, dry weight, and stem diameter of x, the Gini coefficient (G) is given by,

$$G = \frac{1}{2\bar{x}n(n-1)} \sum_{i=1}^{n} (2i - n - 1)X_i$$

where, X_i are the sizes sorted from smallest to largest, $X_1 \leq X_2 \leq \ldots\ldots X_n$. (Dixon *et al.* 1987). The precision and confidence intervals for the Gini coefficient were calculated by using the bootstrapping method defined by Dixon *et al.* (1987) and Dixon (1993). The bootstrapping procedure provides error estimates and 95% confidence intervals (CI) for the Gini coefficients of plant height, aboveground biomass, and stem diameter (Weiner and Solberg 1984). The bootstrapping sequence was carried out using the BASIC program language (Teshler, M. *personal communication*).

4.4. Results

4.4.1. Effects of *C. coccodes* and bentazon on *A. theophrasti*

In 1997, the temperature was relatively high and the humidity was low at the time of spraying and there was no precipitation till one week after spraying of *C. coccodes* and bentazon (Figs. 4.1 to 4.2). The higher temperature and lower relative humidity persisted for a week. These limiting factors not only affect the viability of *C. coccodes*, but also retarded the growth of the pathogen resulting in delayed infection and provided enough time for *A. theophrasti* to over come any effect of the pathogen (Table 4.1). In 1997 all sprayed plants showed 10-15% infection regardless of seed size (Table 4.1). The effect of *C. coccodes* was more pronounced in 1998 and 1999 as compared with 1997. In general, there was no difference in disease severity between the two size groups, regardless of growing seasons. *C. coccodes* caused gray brown foliar lesions, the infected leaves turned necrotic and were shed prematurely. The disease did not persist for a long period of time and only three to four leaves per plant were symptomatic (personal observations). Symptoms were also noticed on older branches and the main stem. *C. coccodes* did not cause any *A. theophrasti* mortality in any year. The effect of bentazon varied over seasons with poor efficacy in 1997 due to prolonged dryness while bentazon performed better in 1998 and 1999 and reduced the aboveground biomass of *A. theophrasti* (data not shown). The effect of benatzon was more pronounced on *A. theophrasti* populations competing with soybean. The split application of benatzon and *C. coccodes* enhanced stresses on *A. theophrasti* resulting in higher reduction in the aboveground biomass (chapter 6).

4.4.2. Effects of seed size and *C. coccodes*/bentazon on *A. theophrasti* growth parameters. The seed size differences in *A. theophrasti* did not have significant effects on height, aboveground biomass, or stem diameter at two harvests (Tables 4.2 to 4.4). Soybean interspecific competition significantly ($P<0.05$) reduced *A. theophrasti* height, aboveground biomass, and stems diameter at the two successive harvests in 1998 and 1999 and aboveground biomass in 1997 (Tables 4.2 and 4.3). The effects of the split application of *C. coccodes* with bentazon persisted only for a short period resulting in a significant effect on *A. theophrasti* plants only at the first harvest as compared with the final harvest (Tables 4.2 to 4.4). The higher disease incidence and the effect of the herbicide in 1998 significantly ($P<0.0001$) decreased *A. theophrasti* plant height. However, in 1997 the sprayed plants recovered from the mild damage caused by the fungal pathogen and the herbicide, and as a result, there was no significant effect on plant height (Tables 4.2 and 4.3). In contrast, the aboveground biomass of sprayed plants in soybean interspecific competition, was significantly ($P<0.01$) reduced at two successive harvests in three growing seasons (Tables 4.2 to 4.4.). However, there was no significant effects of the split application of *C. coccodes* and bentazon on the aboveground biomass of *A. theophrasti* plants as compared with not sprayed plants when grown in monospecific stands at two successive harvests (Tables 4.4.1 and 4.4.2). A significant difference in stem diameter between non-sprayed and sprayed *A. theophrasti* was only observed at the first harvest ($P<0.01$) in 1998 (Table 4.2). The split application of *C. coccodes* and bentazon significantly affected ($P<0.05$) *A. theophrasti* plant height at the two successive harvests in 1999 (Tables 4.2 and 4.3). However, there was no significant effect of *C. coccodes* and bentazon on stem diameter of *A. theophrasti* plants at two harvests in 1999 (Tables 4.2 and 4.3).

4.4.3. Effects of *C. coccodes* alone and with bentazon on *A. theophrasti* height hierarchy grown in soybean. The height hierarchy among *A. theophrasti* plants was negatively skewed (J-shaped) in monospecific stands and positively skewed (L-shaped) in competing populations with soybean at the two successive harvests in 1998 and 1999 (Figs. 4.3 and 4.4). However, the frequency distributions for height was negatively skewed in both monospecific stands and competing populations with soybean in the field trials of 1997 (Figs. 4.3 and 4.4). The values of skewedness, kurtosis, and unbiased Gini coefficient for height, aboveground biomass, and stem diameter are shown in Tables 4.5 to 4.10. Non-sprayed *A. theophrasti* and those sprayed with *C. coccodes*, displayed negative frequency distributions of plant heights (-0.93 and -0.93) in monospecific stands and (–0.94 and –1.41) in competition with soybeans at 85 DAS in 1997 (Table 4.5). The skewedness of frequency distributions of *A. theophrasti* plant height remain unchanged (0.19 and -0.31 in monospecific stands and –1.4 and -0.92 for competing populations with soybean) at 118 DAS in 1997 (Table 4.6). The kurtosis for *A. theophrasti* biomass sprayed with *C. coccodes* alone and in a split application with bentazon were higher in competing populations with soybean (1.56 and 2.58) as compared with monospecific stands (-0.27 and 0.95) at 85 DAS in 1997 (Table 4.5). The unbiased Gini coefficient values for *A. theophrasti* plant height indicated that size inequality was relatively lower in monospecific stands (less than 0.2) at the two successive harvests in 1997 (Tables 4.5 and 4.6). However, the unbiased Gini values were relatively higher in populations competing with soybean (Tables 4.5 and 4.6).

The skewedness of the frequency distribution of *A. theophrasti* plant heights in 1998 showed a positive skewedness (0.9 and 0.6 at 85 and 118 DAS, respectively) when grown in competition with soybean and negative skewedness when grown in monospecific stands (Tables 4.7 and 4.8). Application of *C. coccodes* alone and in combination with bentazon did not change the skewedness frequency distribution in *A. theophrasti* plant heights in 1998 (Tables 4.7 and 4.8). The value of unbiased Gini coefficient were relatively higher for *A. theophrasti* plant heights when grown in competition with soybean as compared with monospecific stands (Table 4.7 and 4.8).

The height hierarchy among *A. theophrasti* plants in the field trials of 1999 was similar to those of 1997 and 1998 (Tables 4.9 and 4.10). Despite the higher disease incidences (48 %) and deleterious effect of bentazon alone in 1999, the height frequency distribution in *A. theophrasti* was negatively skewed in both monospecific stands and in competition with soybean (Tables 4.9 and 4.10). Similarly, the unbiased Gini values for the *A. theophrasti* height hierarchy in 1999 was similar with the results of preceeding years (Tables 4.5 to 4.10). In general, the height hierarchy in *A. theophrasti* varied among treatments and years, however, the soybean interspecific competition greatly influenced the inequality in height.

4.4.4. Effects of *C. coccodes* alone and with bentazon on *A. theophrasti* biomass hierarchy in soybean. The aboveground biomass showed higher inequality among *A. theophrasti* plants as compared with plant height. The aboveground biomass was positively skewed in all three years. Most of the plants were distributed to lower frequency classes as compared with the height distributions (Figs. 4.5 and 4.6 and Tables 4.5 to 4.10). Large positive values were obtained for skewedness (>3.5) when *A. theophrasti* plants were sprayed with *C. coccodes* and grown in competition with soybean in 1997 at 118 DAS and in 1998 at 85 DAS (Tables 4.6 and 4.7). However, negatively skewed frequency distribution was observed for *A. theophrasti* aboveground biomass grown in monospecific stands at 85 DAS in 1997 (Fig. 4.5). The changes in the values of the unbiased Gini coefficients as compared with values for plant height indicated the higher inequality in the aboveground biomass in *A. theophrasti* plants (Tables 4.5 to

4.10). The Gini coefficient values were higher when *A. theophrasti* was grown in competition with soybean as compared with monospecific stands in 1998 and 1999. The highest inequality based on unbiased Gini coefficient values occurred among *A. theophrasti* grown in the 1998 field trials (Tables 4.7 and 4.8).

4.4.5. Effects of *C. coccodes* and bentazon on stem diameter hierarchy of *A. theophrasti* plants grown in soybean. The inequality in *A. theophrasti* stem diameter was correlated with the aboveground biomass. The frequency distribution of stem diameter of sprayed and non-sprayed *A. theophrasti* plants were positively skewed when grown in monospecific stands and in competition with soybean (Figs. 4.7 and 4.8, Tables 4.5 to 4.10). The unbiased Gini values of stem diameter were relatively higher in sprayed and non- sprayed *A. theophrasti* plants in monospecific stands and competition with soybean as compared with plant height.

4.4.6. Lorenz curve and size hierarchies

The lower Gini value for *A. theophrasti* plant height resulted in a less concave area below the diagonal in the Lorenz curve (Figs. 4.9 and 4.10). However, for the aboveground biomass and stem diameter, the area below the diagonal was more concave (Figs 4.11 to 4.14). The combination of the Lorenz curve data, the size frequency distributions, and the unbiased Gini coefficient values clearly show that soybean interspecific competition increased the inequality in *A. theophrasti* growth parameters.

4.5. Discussion

The results of present study demonstrate that seed size differences did not affect the *A. theophrasti* growth parameters measured. The initial advantage of seeds from the large size fraction that conceivably had greater carbohydrate reserves did not persist at later growth stages. Wulff (1986) reported similar effects of seed size in *Desmodium paniculatum* where emergence and early seedling growth were affected by seed size but initial differences in growth were not observed at later growth stages. However, at higher planting densities, *Desmodium paniculatum* plants originating from lighter seed exhibited delayed flowering due to a slower growth rate compared with plants grown at lower planting densities (Wulff 1986). Similarly, Cideciyan and Malloch (1982) found that *Rumex crispus* and *R. obtusifolius* plants in pure stands and originating from small seed size fractions had lower growth rates and were unable to reproduce compared with plants originating from larger seeds. Zhang and Hamill (1997) reported that differences in aboveground biomass and total leaf area between *A. theophrasti* plants separated into different seed size classes was the result of intraspecific competition rather than seed size differences. In contrast, Bello *et al.* (1995) reported that *A. theophrasti* plants under shade and originating from larger seed size fractions had greater leaf chlorophyll content than leaves of plants under full sunlight.

The frequency distribution of *A. theophrasti* plant height was J-shaped as compared with aboveground biomass and stem diameter, which were L-shaped in three successive years of field trials. In monospecific stands, the J-shaped frequency distribution of plant height may be the result of differences in time of emergence among *A. theophrasti* plants. For example, the majority of early emerging *A. theophrasti* plants not only occupied more space, but also grew taller and attained their final heights earlier as compared with later emerging *A. theophrasti* plants. The L-shaped frequency distributions observed for most *A. theophrasti* growth parameters in mixture plots was the result of the presence of large numbers of smaller *A. theophrasti* plants compared with the presence of relatively few larger plants. Nagashima *et al.* (1995) suggested that at early stages of growth, aboveground biomass frequency distribution in *Chenopodium album* was nearly bimodal as compared with later growth stages where frequency distributions became more positively skewed. Findings in the present study showed that despite two successive harvests, positive skewness in aboveground biomass was observed and may be due to the fact that these harvests were taken relatively late in the growth of *A. theophrasti* (85 and 118 DAS).

Important differences in unbiased Gini values (G') were observed among *A. theophrasti* plants grown in monospecific stands and in competition with soybean in all three years. The higher G' values for plants grown in competition with soybean as opposed to plants grown in pure stand possibly reflected increased competition for light in mixture plots such that the differential competitive ability of crop and weed plants resulted in the greater size inequalities observed for *A. theophrasti* plants. The application of *C. coccodes* alone and in combination with bentazon on did not increase size inequalities for the various growth parameters in *A. theophrasti* monospecific stands.

The large size inequalities observed in *A. theophrasti* populations within mixture plots compared with monospecific plots were likely due to the variability in the total plant density of plots for the two treatment plots (i.e., 100 plants m^{-2} in pure stand versus 135 plants m^{-2} in mixtures) and on plant architectural differences between *A. theophrasti* and soybeans. Weiner (1985) reported that G' values of aboveground biomass in *Lolium multiflorum* were positively correlated with planting density. At higher densities, *L. multiflorum* aboveground biomass frequency distributions were positively skewed and had greater G' values as compared with plants grown at lower densities (Weiner 1985). DiTommaso and Watson (1997) reported that G' values at three *A. theophrasti* seeding densities (125, 250, and 350 seeds m^{-2}) were relatively low when plants were grown in monospecific stands. However, size inequalities were significantly greater (i.e. higher G' values) when *A. theophrasti* plants were inoculated with *C. coccodes* and harvested at 2, 5 and 8 weeks after application of the fungal pathogen.

The results of this study indicate that soybean interspecific competition had a substantial effect on *A. theophrasti* size hierarchy development possibly because of direct interference in light interception. Early in the growing season, *A. theophrasti* plants grew relatively faster than soybeans due largely to the availability of space and resources in mixture stands. However, this favourable growing environment in mixture plots gradually changed as soybean canopy closure progressed and was complete by 50 days after emergence (personal observation). Those *A. theophrasti* individuals that were able to outpace soybean canopy closure grew to relatively large sizes, but many of these plants were not able to break through the canopy, thus increasing the size inequality in these plots. Walker *et al.* (1981) reported that soybean seeded at a narrow row spacing of 25.4cm significantly reduced sicklepod (*Cassia obtusifolia*) growth compared with weed plants grown in monospecific stands.

Architectural differences between *A. theophrasti* and soybean may have also been responsible for the increased size inequalities observed in mixture plots as opposed to *A. theophrasti* pure stands. Architectural complexity in soybean depends largely upon the branching pattern around the main stem including true branches and petioles with trifoliate leaves (Foroutan-Pour 1999). The branching pattern in soybean provides an optimal arrangement of leaves in space such that plants are more efficient at intercepting sunlight and at developing sufficient leaf tissue to cover inter-row spaces rapidly. In contrast, *A. theophrasti* plants grown in the presence of soybean produced only a main stem with alternate simple leaves, while in monospecific stands *A. theophrasti* plants also produced lateral branches in addition to the main stem. These structural differences exaggerated *A. theophrasti* size inequalities in mixture plots. Umeki (1997) also found that architectural complexities in soybean plant structure were asymmetric thereby providing a structural advantage over relatively symmetric *A. theophrasti* plants. Plant populations that developed asymmetric crowns had lower coefficients of variation and skewness and a more regular spatial pattern than plant populations that developed symmetric crowns (Umeki 1997).

Differences in spatial pattern between *A. theophrasti* and soybean might also have affected the development of size hierarchies. Weiner (1985) reported that typically sown crop plants had significantly lower size inequalities compared with randomly emerging weeds. In the present study, the soybean crop was sown in a regular pattern while *A. theophrasti* were randomly seeded between the soybean rows. This spatially and temporally variable seeding pattern in *A. theophrasti* and, weeds in general, is likely to result in some individual plants being in very close proximity to neighbours thereby experiencing intense competitive interactions, while other individual plants might be located at far enough distances from neighbours that they have little influence of their growth.

The findings of this work demonstrated that soybean interspecific competition was largely responsible for the size hierarchy differences observed in *A. theophrasti* populations. Application of *C. coccodes* alone, and in combination with bentazon did not increase size inequality in *A. theophrasti* plants grown in monospecific stands. Disease caused by *C. coccodes*, however reduced seed production in inoculated *A. theophrasti* plants due to premature loss of infected leaves. The greater asymmetric size inequalities obtained for *A. theophrasti* plants grown under stressful conditions such as high planting densities, interspecific competition, and presence of disease are important because they impact the fitness of individual plants and the population as a whole. It is likely that under the stress conditions examined in this study, few large individuals will contribute relatively more biomass and reproductive output to the population than suppressed individuals. These differences will be less apparent in monospecific stands where plant architecture and competitive abilities will be relatively equivalent. The findings in this research also suggest that soybean can effectively suppress *A. theophrasti* growth and reproduction under Quebec growing conditions.

4.6. References

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Table 4.1. The relative susceptibility of *Abutilon theophrasti* plants originating from two seed size classes to *Colletotrichum coccodes* in 1997, 1998, and 1999[1].

Year	Seed size	Percentage of infected leaves
1997	Small	10.9 (±2.6)c[2]
	Large	9.1 (±1.9[3])c
1998	Small	46.7 (±2.1)ab
	Large	42.7 (±2.1)b
1999	Small	47.7 (±2.3)a
	Large	48.7 (±2.4)a

[1] Data were combined for all assessment dates.

[2] means in each column, followed by different letters differ significantly ($P < 0.05$) according to Tukey's HSD test.

[3] number in parenthesis indicates standard error.

Table 4.2. Probability values from the ANOVA for the effects of seed size (S), competition (C), and weed control treatments (T) on *Abutilon theophrasti* plant height, aboveground biomass, and stem diameter when harvested at 85 days after seeding in 1997, 1998, and 1999.

	1997[1]		1998			1999		
Source	Height	Biomass	Height	Biomass	Diameter	Height	Biomass	Diameter
Block	0.088	0.938	0.262	0.012	0.171	0.0001	0.003	0.0001
Seed size (S)	0.209	0.838	0.372	0.704	0.921	0.499	0.306	0.346
Competition (C)	0.367	0.001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001
Weed control treatments (T)	0.007	0.055	0.0006	0.002	0.001	0.0008	0.214	0.380

[1] Stem diameter was not measured at 85 days after seeding in 1997

Data were square root transformed before analysis.

Table 4.3. Probability values from the ANOVA for the effects of seed size (S), competition (C), and weed control treatments (T) on *Abutilon theophrasti* plant height, aboveground biomass, and stem diameter when harvested at 118 days after seeding in 1997, 1998, and 1999.

Source	1997			1998			1999		
	Height	Biomass	Diameter	Height	Biomass	Diameter	Height	Biomass	Diameter
Block	0.399	0.7808	0.3954	0.01	0.0092	0.0127	0.005	0.001	0.008
Seed size (S)	0.137	0.2309	0.0613	0.8612	0.7861	0.766	0.066	0.221	0.230
Competition (C)	0.806	0.002	0.051	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001
Weed control treatments (T)	0.751	0.9748	0.1332	0.0253	0.209	0.0628	0.037	0.850	0.891

Data were square root transformed before analysis.

Table 4.4.1. Effects of *Colletotrichum coccodes* alone, and bentazon split application followed by *C. coccodes* on aboveground biomass of *Abutilon theophrasti* plants grown in monospecific stands and in competition with soybean at 85 days after seeding in 1997, 1998, and 1999.

Seed size	Treatment	1997	1998	1999
			$g\ m^{-2}$	
Small	Cont. Mon[1].	1021.7 (±53.6[2])a[3]	729.5 (±12.9)a	518.9 (±32.4)abc
	Cont. Mix.	620.2 (±10.0)abc	239.5 (±15.4)bcd	386.2 (±14.3)abc
	Cc. Mon.	1141.1 (±48.8)a	496 (±11.7)abc	682.6 (±54.3)ab
	Cc. Mix.	601.1 (±15.7)abc	76.6 (±4.9)d	328.6 (±29.6)abc
	Cc. b. Mon.	1142.5 (±56.0)a	602.8 (±23.6)ab	519.3 (±28.2)abc
	Cc. b. Mix.	364.4 (±23.6)bc	75.6 (±8.8)d	144.7 (±9.8)c
Large	Cont. Mon.	781.1 (±15.5)abc	719.3 (±19.8)a	787.5 (±28.2)a
	Cont. Mix.	723.4 (±22.9)abc	270.5 (±15.3)bcd	386.7 (±17.9)abc
	Cc. Mon.	883.4 (±16.5)ab	829.9 (±25.5)a	538.3 (±40.4)abc
	Cc. Mix.	554.5 (±20.9)abc	255.9 (±8.1)bcd	221.9 (±5.5)bc
	Cc. b. Mon.	702.2 (±29.3)abc	503.5 (±31.7)abc	602.7 (±42.6)abc
	Cc. b. Mix.	173.5 (±8.5)c	177.4 (±36.2)cd	112.7 (±8.6)c

[1] Cont. = not sprayed, Cc = sprayed with *C. coccodes*, b = sprayed with bentazon, Mon. = *A. theophrasti* in monospecific stands, Mix = *A. theophrasti* grown in competition with soybean.

[2] number in parenthesis indicates standard errors.

[3] means in the same column followed by different letters differ significantly ($P < 0.05$) according to Tukey's HSD test.

Table 4.4.2. Effects of *Colletotrichum coccodes* alone, and bentazon split application followed by *C. coccodes* on aboveground biomass of *Abutilon theophrasti* plants grown in monospecific stands and in competition with soybean at 118 days after seeding in 1997, 1998, and 1999.

Seed size	Treatment	1997	1998	1999
			g m^{-2}	
Small	Cont. Mon[1].	607.1 (±13.9[2])ab[3]	359.7 (±10.1)ab	477.3 (±15.2)a
	Cont. Mix.	372.5 (±16.2)ab	118.8 (±8.4)de	256.2 (±14.4)abc
	Cc. Mon.	822.3 (±39.7)a	249.3 (±9.3)a-e	322.3 (±7.9)abc
	Cc. Mix.	395.1 (±12.2)ab	140.8 (±12.2)c-e	311.6 (±8.4)abc
	Cc. b. Mon.	580.4 (±42.2)ab	323.9 (±11.9)a-d	257.4 (±13.1)abc
	Cc. b. Mix.	353.5 (±28.8)ab	90.9 (±10.4)e	146.7 (±8.9)c
Large	Cont. Mon.	605.6 (±31.4)ab	342.9 (±7.1)a	514.9 (±33.9)ab
	Cont. Mix.	461.5 (±20.9)ab	156.7 (±8.1)b-e	355.3 (±14.5)abc
	Cc. Mon.	639.1 (±30.4)ab	350.4 (±15.9)a-c	338.1 (±15.3)abc
	Cc. Mix.	383.4 (±29.4)ab	200.6 (±14.4)a-e	213.6 (±15.5)bc
	Cc. b. Mon.	592.5 (±22.5)ab	296.1 (±14.8)a-e	254.8 (±11.4)abc
	Cc. b. Mix.	234.7 (±9.2)b	92.4 (±2.3)e	86.9 (±13.2)c

[1] Cont. = not sprayed, Cc = sprayed with *C. coccodes*, b = sprayed with bentazon, Mon. = *A. theophrasti* in monospecific stands, Mix = *A. theophrasti* grown in competition with soybean.

[2] number in parenthesis indicates standard errors.

[3] means in the same column followed by different letters differ significantly ($P< 0.05$) according to Tukey's HSD test.

Table 4.5. Effects of *Colletotrichum coccodes* alone, and bentazon split application followed by *C. coccodes* on size hierarchies in *Abutilon theophrasti* plants grown in monospecific stands and in competition with soybean at 85 days after seeding in 1997.

Growth parameter	Treatment	n[1]	SK	KR	G’	SE	G’ CI	
							lower	upper
Height	Cont. Mon.	43	-0.930	0.005	0.132	0.02	0.110	0.150
	Cont. Mix.	40	-0.940	0.664	0.062	0.04	0.027	0.101
	Cc. Mon.	47	0.113	-0.933	0.106	0.01	0.099	0.114
	Cc. Mix.	43	-1.410	3.810	0.122	0.02	0.102	0.137
	Cc. b. Mon.	49	-0.149	-1.370	0.143	0.05	0.086	0.187
	Cc. b. Mix.	41	-0.121	-0.440	0.149	0.06	0.097	0.206
Biomass	Cont. Mon.	43	0.993	0.473	0.360	0.02	0.351	0.383
	Cont. Mix.	40	0.292	-0.724	0.185	0.11	0.09	0.306
	Cc. Mon.	47	0.964	-0.272	0.354	0.03	0.316	0.383
	Cc. Mix.	43	1.268	1.565	0.293	0.09	0.207	0.371
	Cc. b. Mon.	49	1.419	0.951	0.402	0.15	0.251	0.559
	Cc. b. Mix.	41	1.495	2.581	0.432	0.10	0.338	0.523

[2] n = number of *A. theophrasti* plants, SE = standard error of Gini values, SK = skewedness, KR = kurtosis, G’ = unbiased Gini coefficient, G’ CI = 95% confidence interval of G’’were obtained from the “ bootstrapping” procedure. Cont. = not sprayed, Cc = sprayed with *C. coccodes*, b = sprayed with bentazon, Mon. = *A. theophrasti* in monospecific stands, Mix = *A. theophrasti* grown in competition with soybean.

Stem diameter was not measured at 85 DAS in 1997.

Due to similarity of variances, the data of the two seed weight classes were pooled for size hierarchy distributions of *A. theophrasti* plants.

Table 4.6. Effects of *Colletotrichum coccodes* alone, and bentazon split application followed by *C. coccodes* on size hierarchies in *Abutilon theophrasti* plants grown in monospecific stands and in competition with soybean at 118 days after seeding in 1997.

Growth parameter	Treatment	n	SK	KR	G'	SE	G' CI lower	upper
Height	Cont. Mon.	87	0.193	-1.001	0.194	0.03	0.149	0.216
	Cont. Mix.	45	-1.381	2.275	0.107	0.04	0.065	0.148
	Cc. Mon.	79	-0.312	0.892	0.134	0.02	0.112	0.153
	Cc. Mix.	59	-0.915	1.460	0.119	0.03	0.081	0.151
	Cc. b. Mon.	60	-0.348	-0.458	0.169	0.05	0.113	0.215
	Cc. b. Mix.	39	0.185	-0.895	0.081	0.02	0.067	0.093
Diameter	Cont. Mon.	87	1.193	1.796	0.275	0.03	0.228	0.293
	Cont. Mix.	45	0.217	-0.361	0.183	0.04	0.162	0.249
	Cc. Mon.	79	1.045	2.788	0.170	0.05	0.151	0.256
	Cc. Mix.	59	0.497	0.152	0.201	0.02	0.186	0.225
	Cc. b. Mon.	60	0.443	-0.144	0.278	0.03	0.226	0.292
	Cc. b. Mix.	39	0.360	-0.416	0.126	0.04	0.104	0.207
Biomass	Cont. Mon.	87	1.706	3.225	0.454	0.06	0.423	0.529
	Cont. Mix.	45	0.828	-0.343	0.333	0.03	0.299	0.375
	Cc. Mon.	79	2.991	11.42	0.330	0.10	0.271	0.454
	Cc. Mix.	59	3.633	18.76	0.378	0.08	0.306	0.472
	Cc. b. Mon.	60	2.189	6.125	0.414	0.12	0.308	0.526
	Cc. b. Mix.	39	1.481	2.903	0.385	0.05	0.261	0.481

Cont.

n = number of *A. theophrasti* plants, SE = standard error of Gini values, SK = skewedness, KR = kurtosis, G' = unbiased Gini coefficient, G' CI = 95% confidence interval of G' were obtained from the " bootstrapping" procedure. Cont. = not sprayed, Cc = sprayed with *C. coccodes*, b = sprayed with bentazon, Mon. = *A. theophrasti* in monospecific stands, Mix = *A. theophrasti* grown in competition with soybean.

Table 4.7. Effects of *Colletotrichum coccodes* alone, and bentazon split application followed by *C. coccodes* on size hierarchies in *Abutilon theophrasti* plants grown in monospecific stands and in competition with soybean at 85 days after seeding in 1998.

Growth parameter	Treatment	n	SK	KR	G’	SE	G’ CI	
							lower	upper
Height	Cont. Mon.	50	-0.885	1.537	0.085	0.04	0.054	0.131
	Cont. Mix.	57	0.110	-1.537	0.254	0.07	0.184	0.310
	Cc. Mon.	39	-0.842	1.116	0.086	0.02	0.065	0.108
	Cc. Mix.	57	1.875	2.778	0.310	0.09	0.186	0.352
	Cc. b. Mon.	56	-1.209	0.626	0.148	0.07	0.094	0.208
	Cc. b. Mix.	37	0.891	-0.625	0.282	0.03	0.250	0.306
Diameter	Cont. Mon.	50	0.726	0.818	0.131	0.02	0.107	0.149
	Cont. Mix.	57	0.280	-1.075	0.288	0.08	0.237	0.395
	Cc. Mon.	39	0.019	0.628	0.146	0.04	0.108	0.197
	Cc. Mix.	57	2.201	4.866	0.325	0.11	0.207	0.414
	Cc. b. Mon.	56	-0.373	-0.114	0.197	0.09	0.121	0.333
	Cc. b. Mix.	37	1.075	0.138	0.282	0.09	0.184	0.364
Biomass								
	Cont. Mon.	50	2.033	0.192	0.296	0.07	0.201	0.361
	Cont. Mix.	57	0.892	0.209	0.554	0.14	0.437	0.731
	Cc. Mon.	39	1.453	0.128	0.332	0.10	0.246	0.446
	Cc. Mix.	57	3.773	0.389	0.638	0.22	0.436	0.851
	Cc. b. Mon.	56	0.795	0.087	0.327	0.14	0.258	0.520
	Cc. b. Mix.	37	1.996	0.347	0.607	0.19	0.328	0.788

Cont.

n = number of *A. theophrasti* plants, SE = standard error of Gini values, SK = skewedness, KR = kurtosis, G' = unbiased Gini coefficient, G' CI = 95% confidence interval of G' were obtained from the " bootstrapping" procedure. Cont. = not sprayed, Cc = sprayed with *C. coccodes*, b = sprayed with bentazon, Mon. = *A. theophrasti* in monospecific stands, Mix = *A. theophrasti* grown in competition with soybean.

Table 4.8. Effects of *Colletotrichum coccodes* alone, and bentazon split application followed by *C. coccodes* on size hierarchies in *Abutilon theophrasti* plants grown in monospecific stands and in competition with soybean at 118 days after seeding in 1998.

Growth parameter	Treatment	n	SK	KR	G'	SE	G' CI lower	upper
Height	Cont. Mon.	50	-0.014	0.184	0.126	0.03	0.089	0.157
	Cont. Mix.	42	0.073	-1.715	0.270	0.08	0.188	0.346
	Cc. Mon.	43	-0.916	1.913	0.126	0.03	0.102	0.161
	Cc. Mix.	50	0.613	-1.386	0.373	0.11	0.230	0.464
	Cc. b. Mon.	54	-0.201	-0.108	0.205	0.08	0.129	0.281
	Cc. b. Mix.	37	0.641	-0.957	0.285	0.04	0.253	0319
Diameter	Cont. Mon.	50	-0.198	-0.236	0.161	0.05	0.096	0.200
	Cont. Mix.	42	0.213	-1.378	0.285	0.08	0.188	0.361
	Cc. Mon.	43	0.153	0.101	0.209	0.03	0.181	0.241
	Cc. Mix.	50	0.651	-1.197	0.399	0.12	0.250	0.496
	Cc. b. Mon.	54	0.605	0.557	0.272	0.07	0.182	0.319
	Cc. b. Mix.	37	0.632	-0.727	0.252	0.05	0.203	0.295
Biomass	Cont. Mon.	50	1.506	3.474	0.270	0.07	0.202	0.314
	Cont. Mix.	42	0.877	-0.100	0.487	0.13	0.352	0.620
	Cc. Mon.	43	1.463	2.015	0.287	0.10	0.190	0.374
	Cc. Mix.	50	1.153	-0.030	0.595	0.10	0.485	0.692
	Cc. b. Mon.	54	2.315	6.400	0.436	0.13	0.203	0.566
	Cc. b. Mix.	37	1.178	0.339	0.499	0.06	0.437	0.565

Cont.

n = number of *A. theophrasti* plants, SE = standard error of Gini values, SK = skewedness, KR = kurtosis, G' = unbiased Gini coefficient, G' CI = 95% confidence interval of G' were obtained from the " bootstrapping" procedure. Cont. = not sprayed, Cc = sprayed with *C. coccodes*, b = sprayed with bentazon, Mon. = *A. theophrasti* in monospecific stands, Mix = *A. theophrasti* grown in competition with soybean.

Table 4.9. Effects of *Colletotrichum coccodes* alone, and bentazon split application followed by *C. coccodes* on size hierarchies in *Abutilon theophrasti* plants grown in monospecific stands and in competition with soybean at 85 days after seeding in 1999.

Growth parameter	Treatment	n	SK	KR	G'	SE	G' CI lower	upper
Height	Cont. Mon.	41	-0.311	-0.422	0.151	0.04	0.109	0.197
	Cont. Mix.	45	0.200	1.032	0.078	0.14	0.069	0.098
	Cc. Mon.	71	0.177	-0.172	0.167	0.01	0.153	0.176
	Cc. Mix.	61	-0.350	-1.221	0.152	0.07	0.085	0.205
	Cc. b. Mon.	43	-1.402	1.868	0.118	0.04	0.082	0.166
	Cc. b. Mix.	28	-0.059	-0.375	0.128	0.04	0.066	0.088
Diameter	Cont. Mon.	41	0.338	0.296	0.216	0.06	0.154	0.267
	Cont. Mix.	45	0.811	0.825	0.144	0.01	0.133	0.150
	Cc. Mon.	71	0.973	1.387	0.221	0.02	0.203	0.236
	Cc. Mix.	61	0.139	-0.682	0.178	0.04	0.146	0.217
	Cc. b. Mon.	43	-0.444	-0.258	0.203	0.05	0.153	0.242
	Cc. b. Mix.	28	0.407	-0.103	0.168	0.05	0.110	0.222
Biomass	Cont. Mon.	41	1.796	3.749	0.489	0.11	0.365	0.577
	Cont. Mix.	45	2.115	5.498	0.285	0.03	0.245	0.329
	Cc. Mon.	71	2.850	9.406	0.419	0.10	0.346	0.532
	Cc. Mix.	61	0.913	0.602	0.393	0.08	0.268	0.452
	Cc. b. Mon.	43	0.321	-0.545	0.361	0.04	0.314	0.402
	Cc. b. Mix.	28	2.530	8.872	0.407	0.05	0.344	0.440

Cont.

n = number of *A. theophrasti* plants, SE = standard error of Gini values, SK = skewedness, KR = kurtosis, G' = unbiased Gini coefficient, G' CI = 95% confidence interval of G' were obtained from the " bootstrapping" procedure. Cont. = not sprayed, Cc = sprayed with *C. coccodes*, b = sprayed with bentazon, Mon. = *A. theophrasti* in monospecific stands, Mix = *A. theophrasti* grown in competition with soybean.

Table 4.10. Effects of *Colletotrichum coccodes* alone, and bentazon split application followed by *C. coccodes* on size hierarchies in *Abutilon theophrasti* plants grown in monospecific stands and in competition with soybean at 118 days after seeding in 1999.

Growth parameter	Treatment	n	SK	KR	G'	SE	G' CI lower	upper
Height	Cont. Mon.	59	-0.280	0.125	0.115	0.05	0.051	0.162
	Cont. Mix.	57	-0.202	-0.560	0.173	0.02	0.157	0.193
	Cc. Mon.	38	-0.179	-0.539	0.149	0.06	0.102	0.209
	Cc. Mix.	51	-1.419	1.550	0.126	0.07	0.057	0.185
	Cc. b. Mon.	22	-0.863	1.151	0.151	0.06	0.097	0.211
	Cc. b. Mix.	27	0.075	-1.391	0.165	0.09	0.055	0.251
Diameter	Cont. Mon.	59	1.079	2.429	0.174	0.04	0.139	0.207
	Cont. Mix.	57	0.606	-0.391	0.210	0.01	0.200	0.228
	Cc. Mon.	38	-0.169	-0.36	0.201	0.09	0.127	0.288
	Cc. Mix.	51	-0.336	0.937	0.161	0.05	0.109	0.224
	Cc. b. Mon.	22	1.100	3.005	0.257	0.04	0.205	0.292
	Cc. b. Mix.	27	0.489	-1.108	0.151	0.05	0.077	0.190
Biomass	Cont. Mon.	59	1.110	1.140	0.315	0.08	0.242	0.402
	Cont. Mix.	57	0.938	0.493	0.429	0.04	0.368	0.458
	Cc. Mon.	38	2.185	5.553	0.281	0.13	0.158	0.415
	Cc. Mix.	51	2.116	6.485	0.306	0.09	0.270	0.450
	Cc. b. Mon.	22	1.456	1.275	0.432	0.10	0.348	0.526
	Cc. b. Mix.	27	0.539	-0.761	0.342	0.19	0.162	0.553

Cont.

n = number of *A. theophrasti* plants, SE = standard error of Gini values, SK = skewedness, KR = kurtosis, G' = unbiased Gini coefficient, G' CI = 95% confidence interval of G' were obtained from the " bootstrapping" procedure. Cont. = not sprayed, Cc = sprayed with *C. coccodes*, b = sprayed with bentazon, Mon. = *A. theophrasti* in monospecific stands, Mix = *A. theophrasti* grown in competition with soybean.

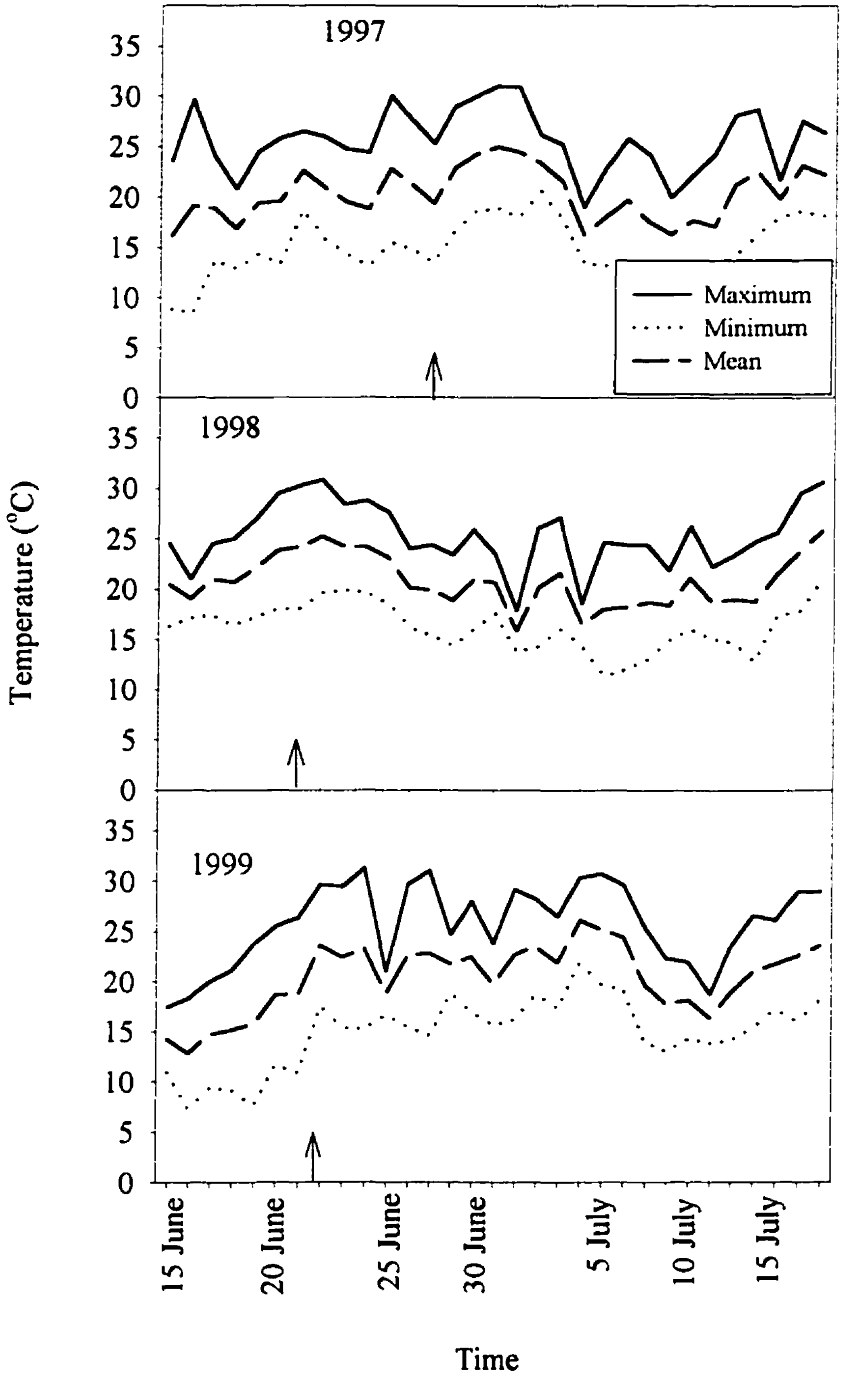


Figure 4.1. Air temperature (solid line: maximum, dotted lines, minimum: dashed, mean) during field trials of 1997, 1998, and 1999. Arrows indicate the application of *Colletotrichum coccodes*.

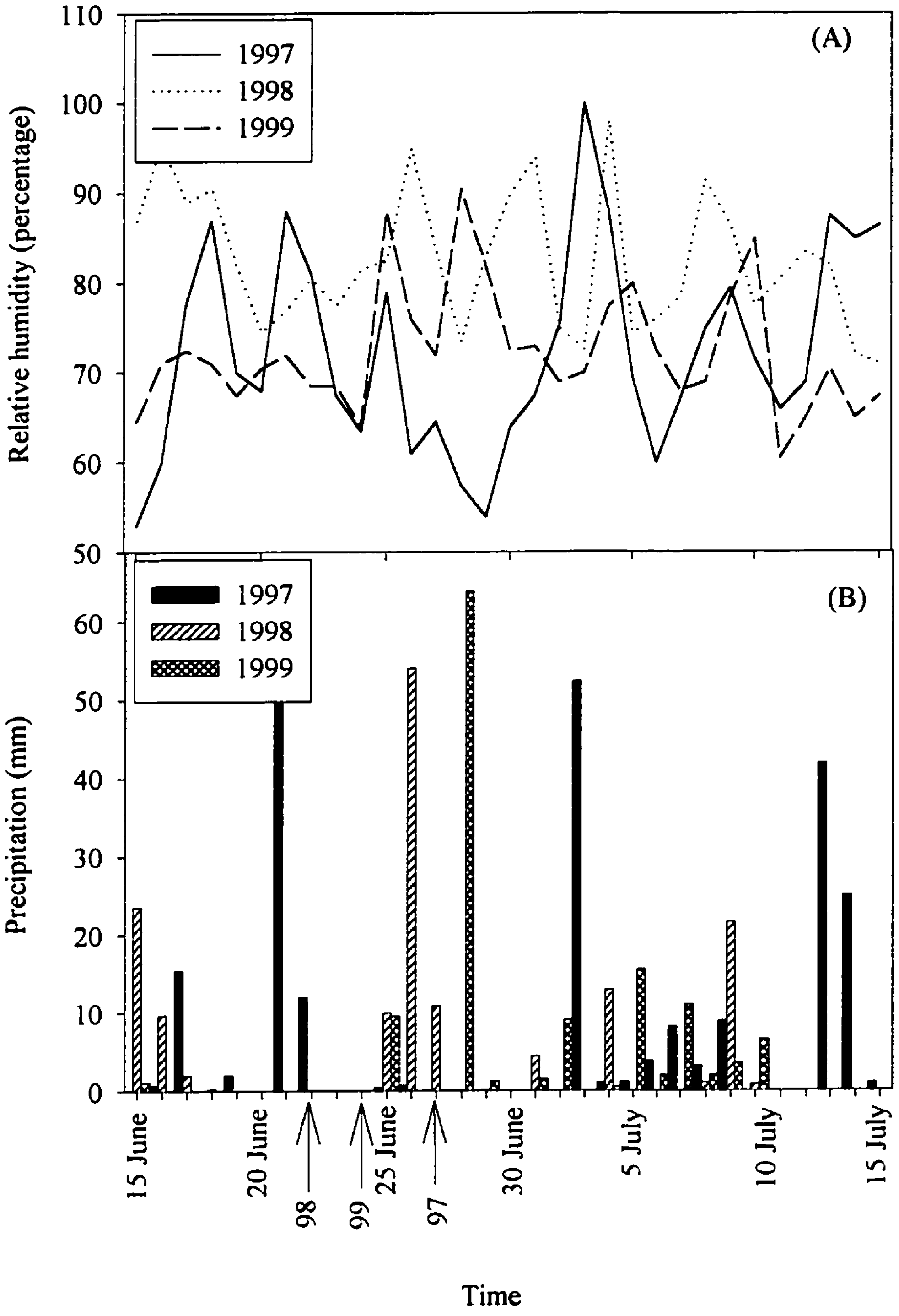


Figure 4.2. Relative humidity (A) and precipitation (B) at the time of *Colletotrichum coocodes* application during 1997, 1998, and 1999 field trials. Arrows indicate the application of *C. coccodes*.

Figure 4.3. Frequency distributions of *Abutilon theophrasti* height hierarchy development for not sprayed (A, B), sprayed with *Colletotrichum coccodes* (C, D) alone, and in combination with bentazon (E, F) when grown in monospecific stands and in competition with soybean at 85 days after seeding in 1997, 1998, and 1999.

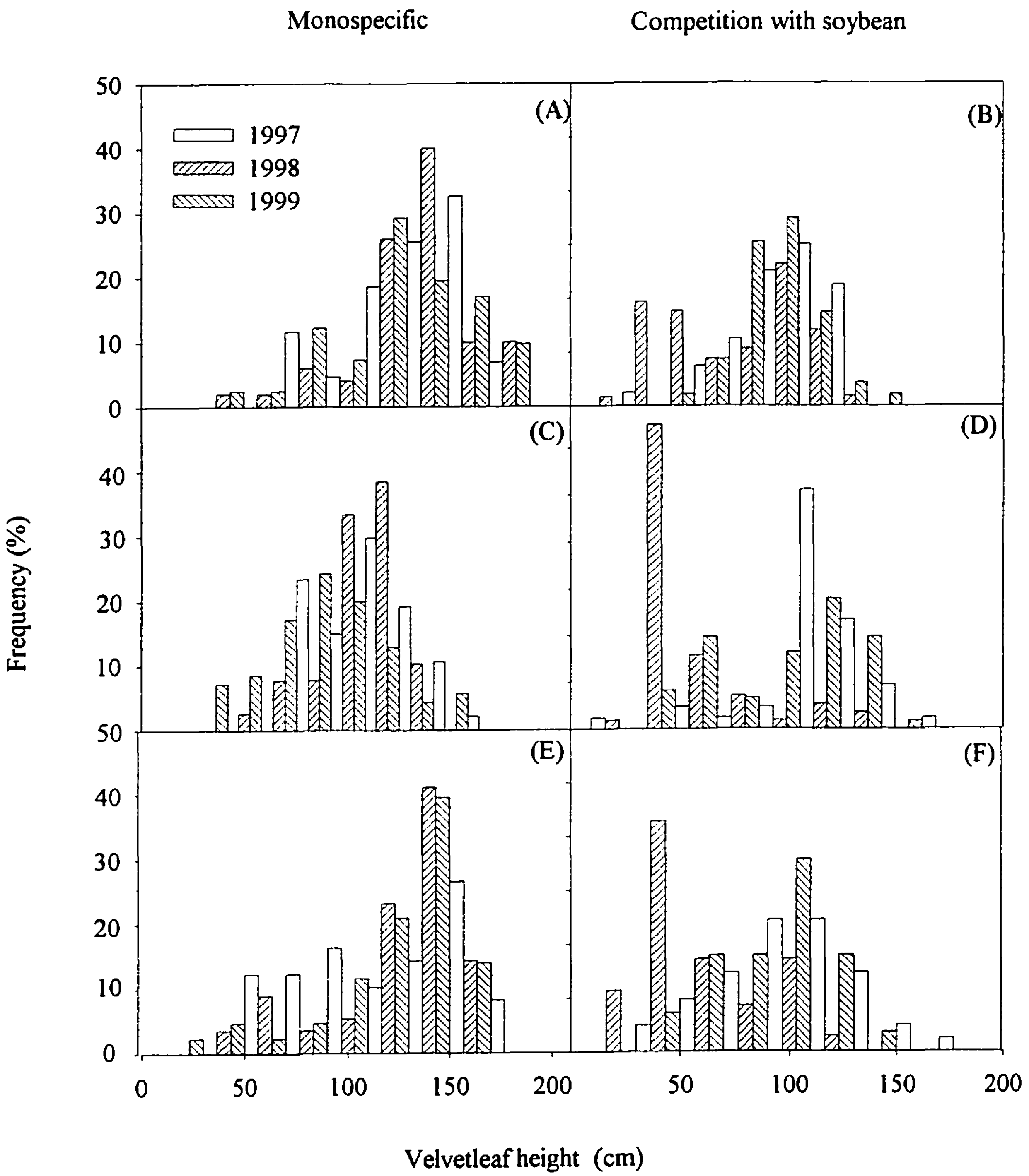

Monospecific
Competition with soybean
(A)
(B)
(C)
(D)
(E)
(F)
1997
1998
1999
Frequency (%)
0
10
20
30
40
50
0
50
100
150
200
Velvetleaf height (cm)

Figure 4.4. Frequency distributions of *Abutilon theophrasti* height hierarchy development for not sprayed (A, B), sprayed with *Colletotrichum coccodes* (C, D) alone, and in combination with bentazon (E, F) when grown in monospecific stands and in competition with soybean at 118 days after seeding in 1997, 1998, and 1999.

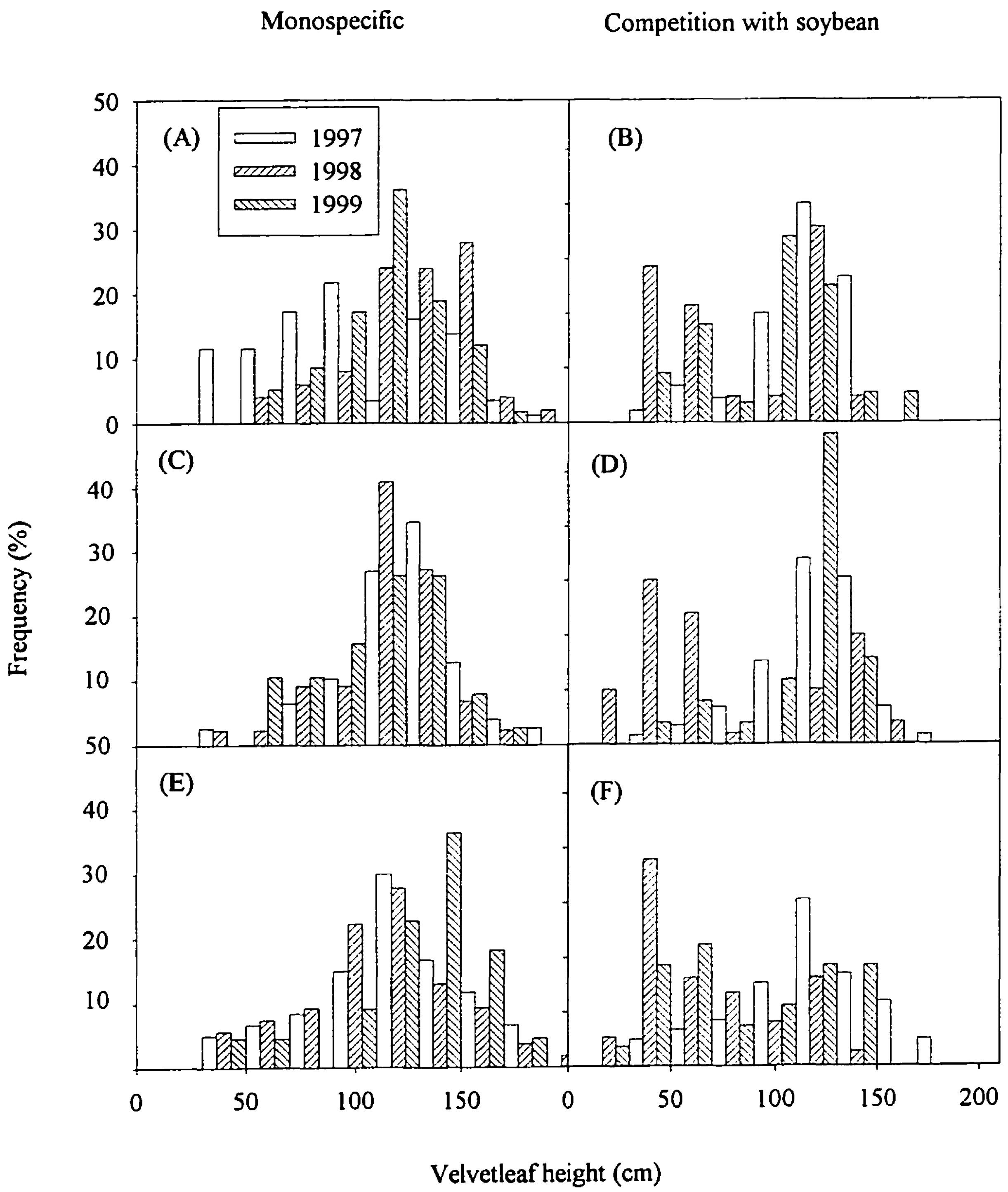
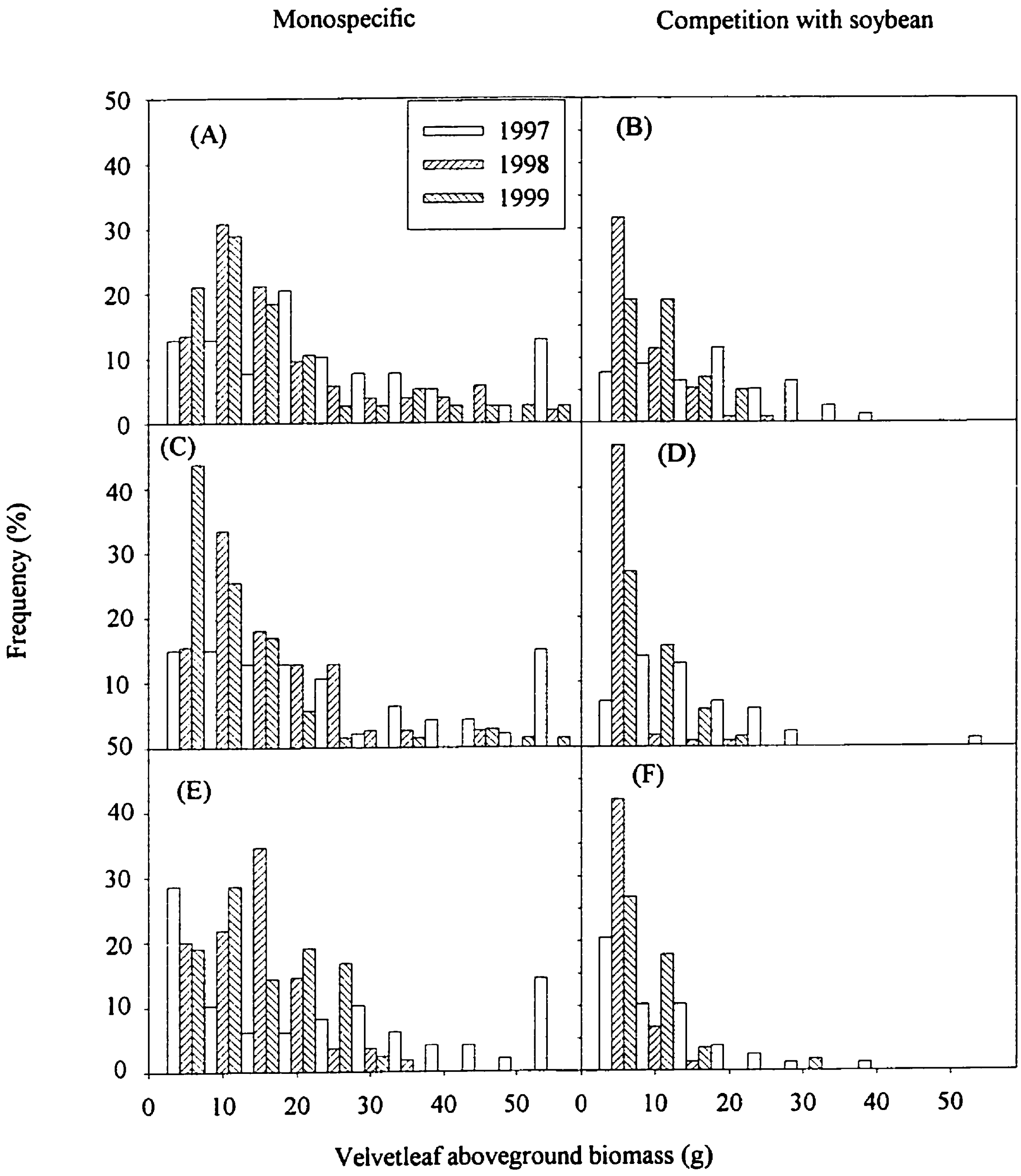

Monospecific
Competition with soybean
(A)
(B)
(C)
(D)
(E)
(F)
1997
1998
1999
Frequency (%)
0
10
20
30
40
50
0
50
100
150
200
Velvetleaf height (cm)

Figure 4.5. Frequency distributions of *Abutilon theophrasti* aboveground biomass hierarchy development for not sprayed (A, B), sprayed with *Colletotrichum coccodes* (C, D) alone, and in combination with bentazon (E, F) when grown in monospecific stands and in competition with soybean at 85 days after seeding in 1997, 1998, and 1999.



Monospecific
Competition with soybean
(A)
(B)
(C)
(D)
(E)
(F)
1997
1998
1999
Frequency (%)
0
10
20
30
40
50
Velvetleaf aboveground biomass (g)

Figure 4.6. Frequency distributions of *Abutilon theophrasti* aboveground biomass hierarchy development for not sprayed (A, B), sprayed with *Colletotrichum coccodes* (C, D) alone, and in combination with bentazon (E, F) when grown in monospecific stands and in competition with soybean at 118 days after seeding in 1997, 1998, and 1999.

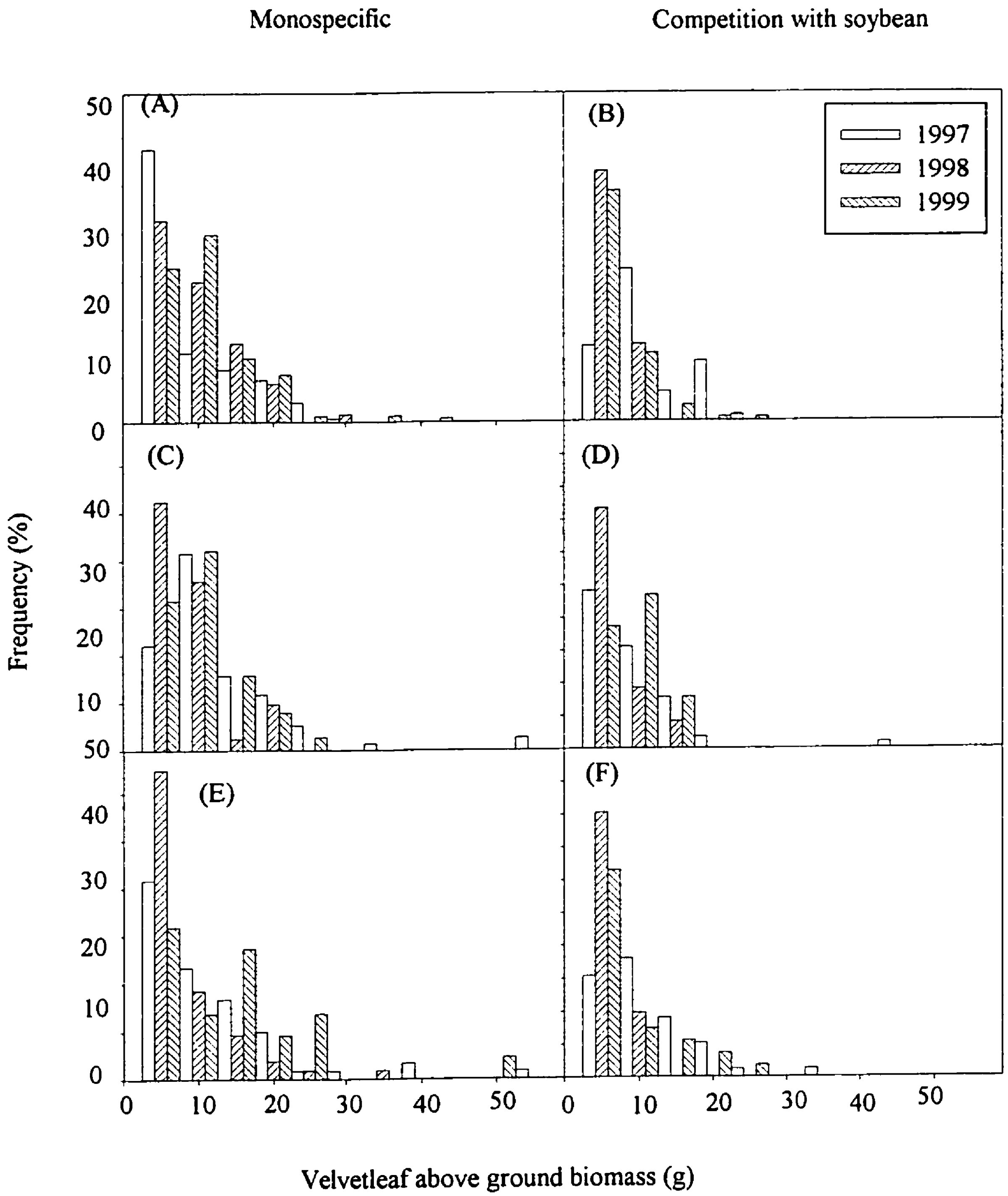

Monospecific
Competition with soybean
(A)
(B)
(C)
(D)
(E)
(F)
1997
1998
1999
Frequency (%)
50
40
30
20
10
0
40
30
20
10
50
40
30
20
10
0
0
10
20
30
40
50
0
10
20
30
40
50
Velvetleaf above ground biomass (g)

Figure 4.7. Frequency distributions of *Abutilon theophrasti* stem diameter hierarchy development for not sprayed (A, B), sprayed with *Colletotrichum coccodes* (C, D) alone, and in combination with bentazon (E, F) when grown in monospecific stands and in competition with soybean at 85 days after seeding in 1998 and 1999. Stem diameter was not measured at 85 days after seeding in 1997.

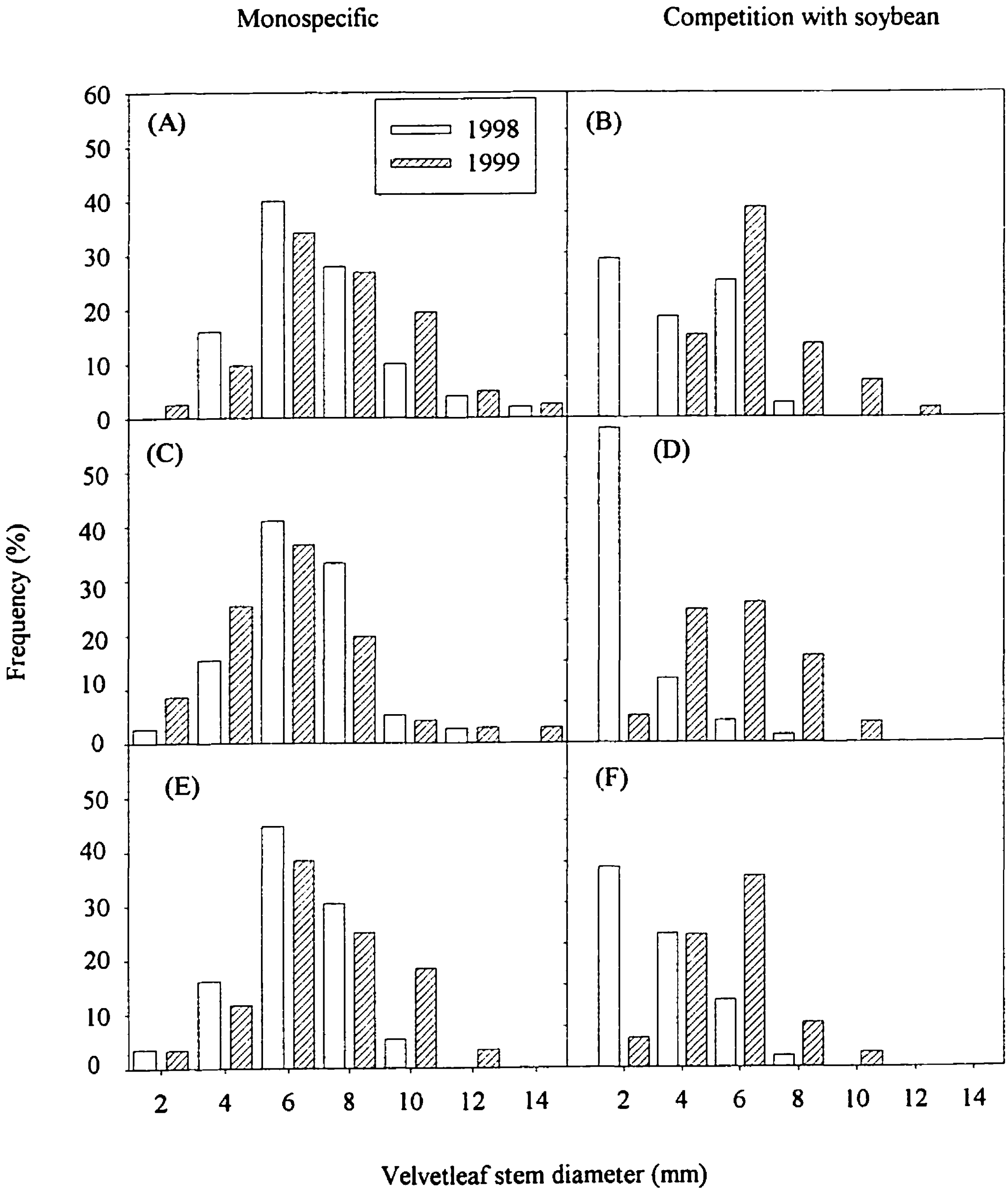

Monospecific
Competition with soybean
(A)
(B)
(C)
(D)
(E)
(F)
1998
1999
Frequency (%)
0
10
20
30
40
50
60
2
4
6
8
10
12
14
Velvetleaf stem diameter (mm)

Figure 4.8. Frequency distributions of *Abutilon theophrasti* stem diameter hierarchy development for not sprayed (A, B), sprayed with *Colletotrichum coccodes* (C, D) alone, and in combination with bentazon (E, F) when grown in monospecific stands and in competition with soybean at 118 days after seeding in 1997, 1998, and 1999.

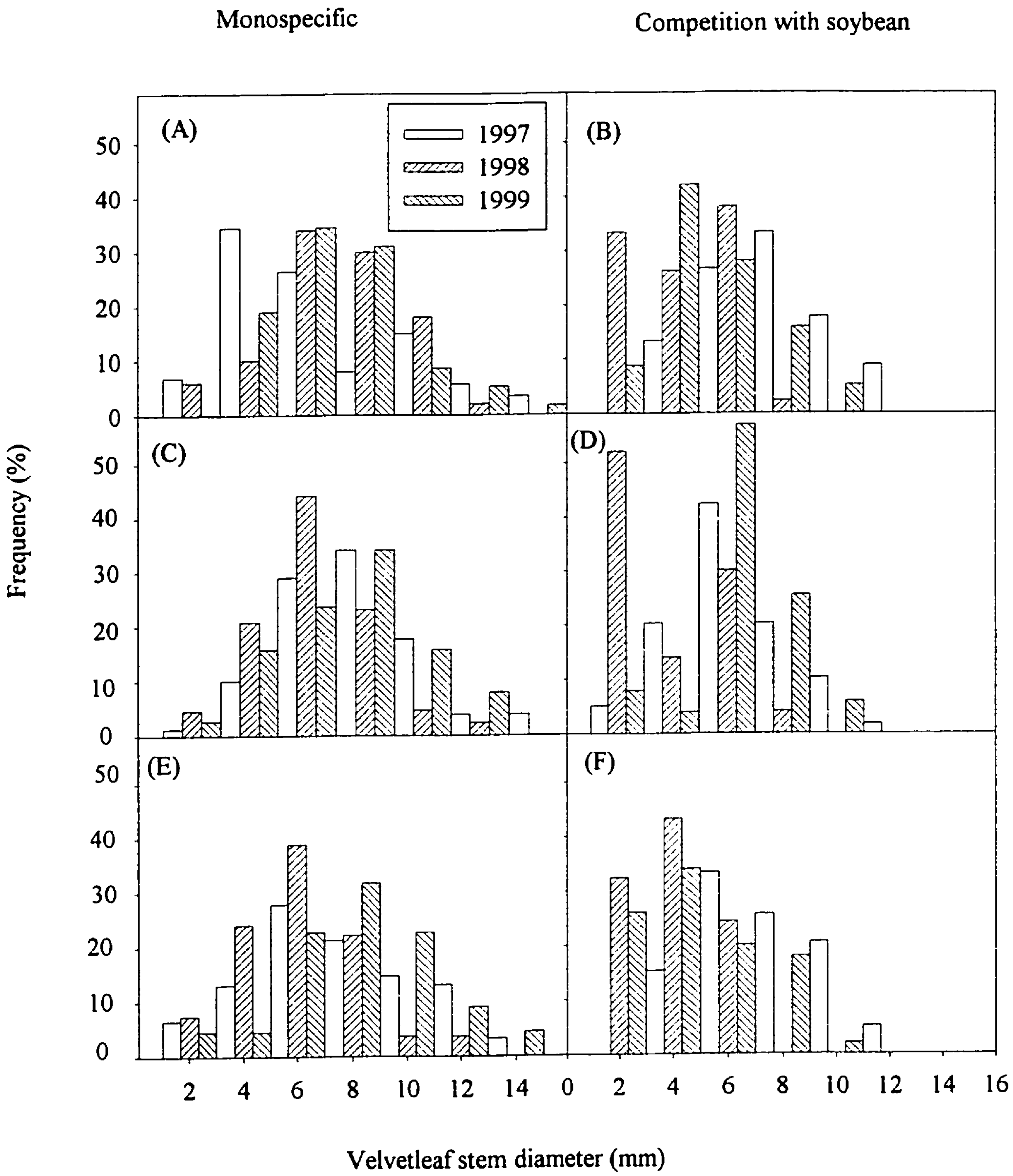

Monospecific
Competition with soybean
(A)
(B)
(C)
(D)
(E)
(F)
1997
1998
1999
Frequency (%)
0
10
20
30
40
50
2
4
6
8
10
12
14
16
Velvetleaf stem diameter (mm)

Figure 4.9. The Lorenz curve as applied to height hierarchies in *Abutilon theophrasti* of not sprayed (A, B), sprayed with *Colletotrichum coccodes* alone (C, D), and in combination with bentazon (E, F) when grown in monospecific stands and in competition with soybean and harvested 85 days after seeding in 1997, 1998, and 1999. The area under the diagonal is equal to one-half the value of the Gini coefficients.

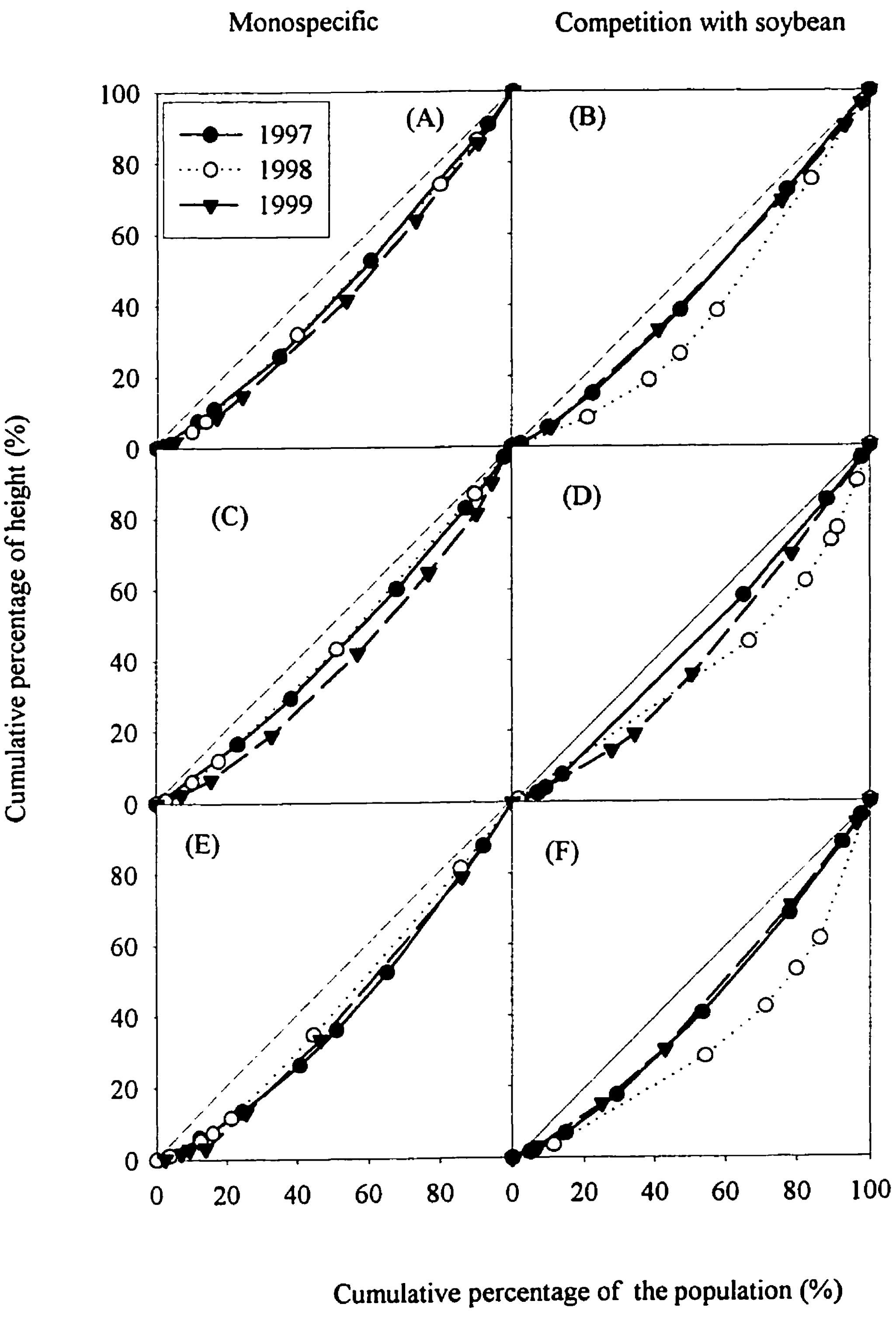

Monospecific
Competition with soybean
(A)
(B)
(C)
(D)
(E)
(F)
1997
1998
1999
Cumulative percentage of height (%)
Cumulative percentage of the population (%)
0
20
40
60
80
100
0
20
40
60
80
0
20
40
60
80
100

Figure 4.10. The Lorenz curve as applied to height hierarchies in *Abutilon theophrasti* of not sprayed (A, B), sprayed with *Colletotrichum coccodes* alone (C, D), and in combination with bentazon (E, F) when grown in monospecific stands and in competition with soybean and harvested 118 days after seeding in 1997, 1998, and 1999. The area under the diagonal is equal to one-half the value of the Gini coefficients.

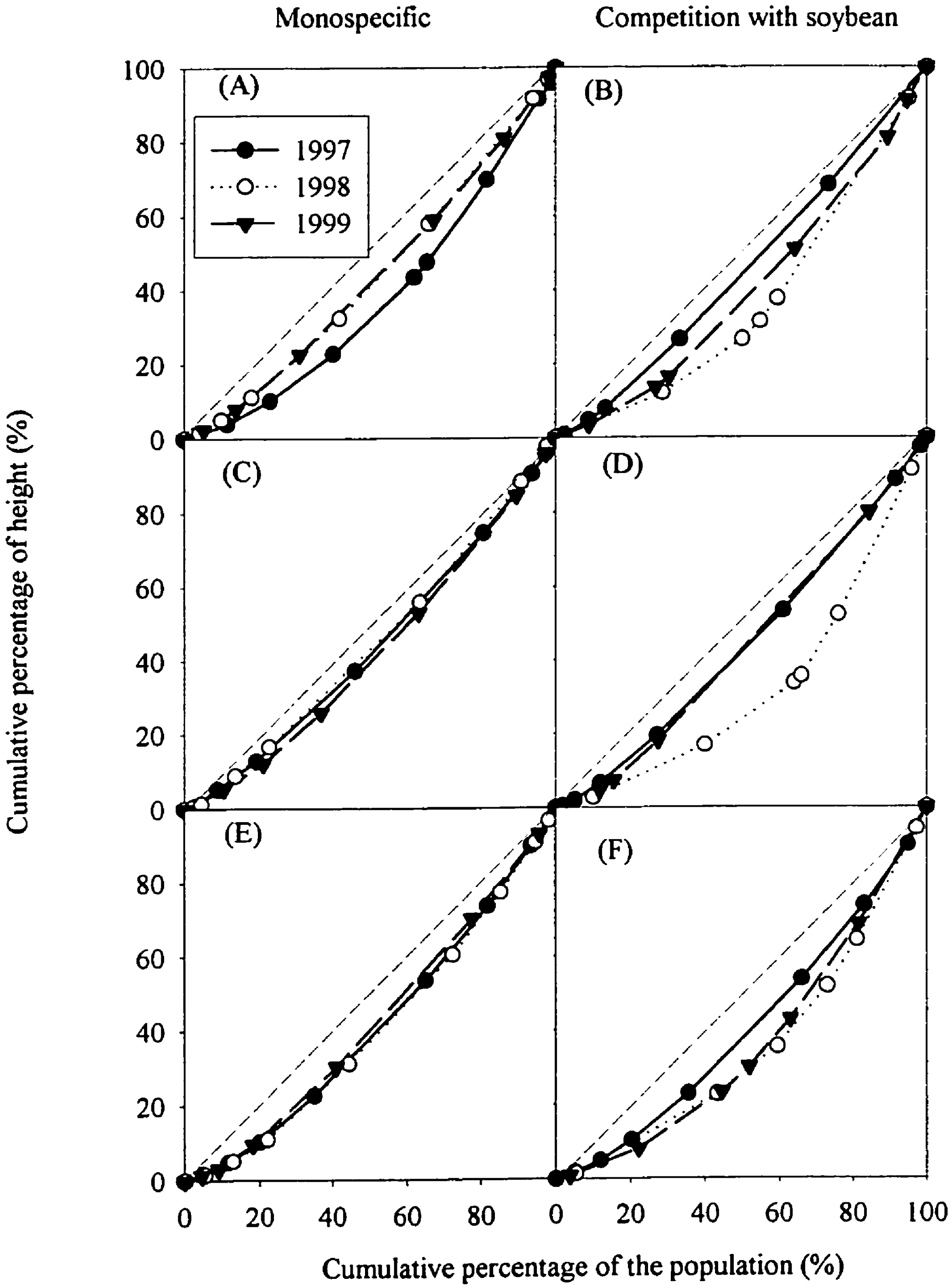
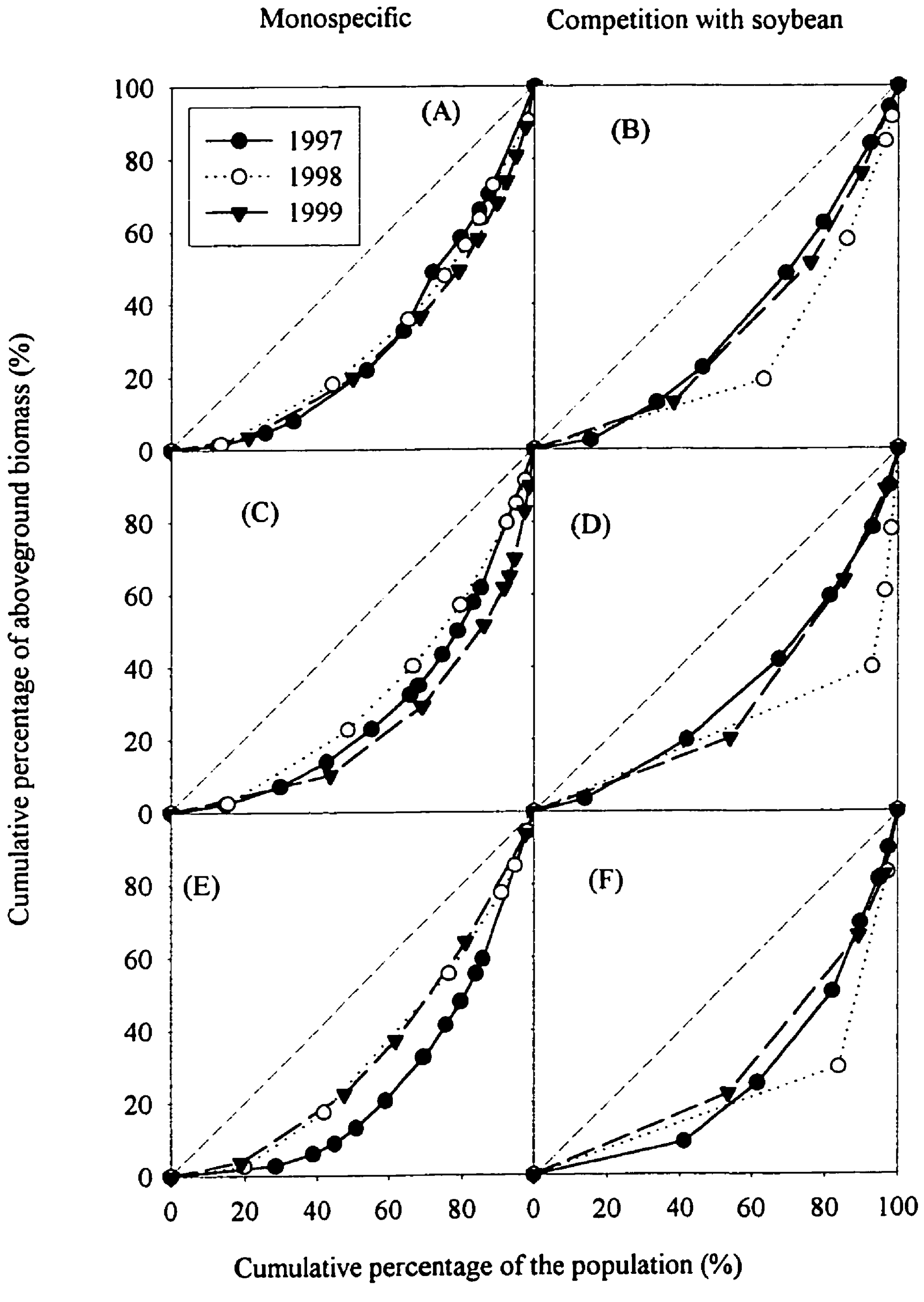

Monospecific
Competition with soybean
(A)
(B)
(C)
(D)
(E)
(F)
1997
1998
1999
Cumulative percentage of height (%)
Cumulative percentage of the population (%)
0
20
40
60
80
100

Figure 4.11. The Lorenz curve as applied to aboveground biomass hierarchies in *Abutilon theophrasti* of not sprayed (A, B), sprayed with *Colletotrichum coccodes* alone (C, D), and in combination with bentazon (E, F) when grown in monospecific stands and in competition with soybean and harvested 85 days after seeding in 1997, 1998, and 1999. The area under the diagonal is equal to one-half the value of the Gini coefficients.



Monospecific
Competition with soybean
(A)
(B)
(C)
(D)
(E)
(F)
1997
1998
1999
Cumulative percentage of aboveground biomass (%)
Cumulative percentage of the population (%)
0
20
40
60
80
100

Figure 4.12. The Lorenz curve as applied to aboveground biomass hierarchies in *Abutilon theophrasti* of not sprayed (A, B), sprayed with *Colletotrichum coccodes* alone (C, D), and in combination with bentazon (E, F) when grown in monospecific stands and in competition with soybean and harvested 118 days after seeding in 1997, 1998, and 1999. The area under the diagonal is equal to one-half the value of the Gini coefficients.

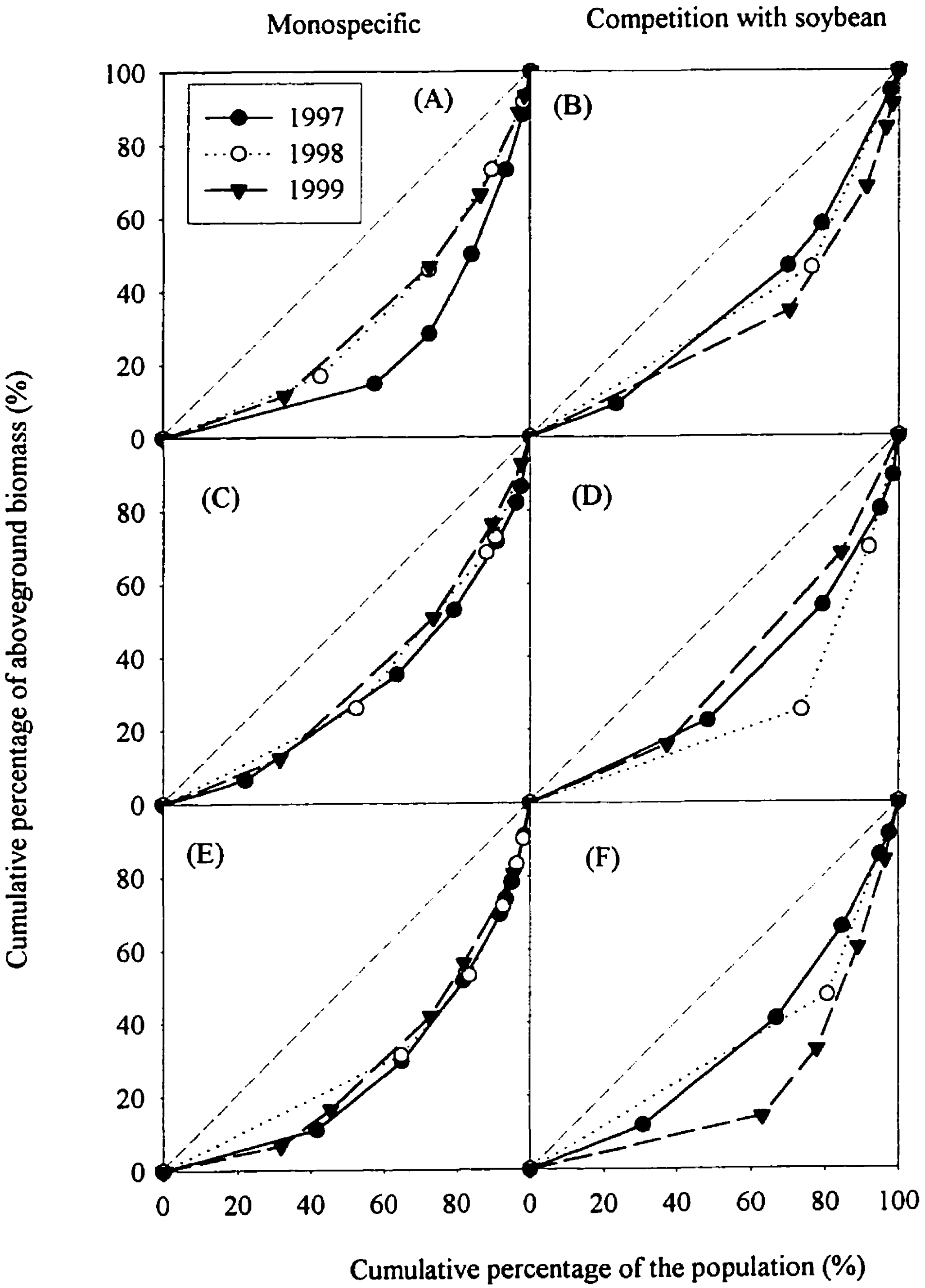
Monospecific
Competition with soybean
(A)
(B)
(C)
(D)
(E)
(F)
1997
1998
1999
Cumulative percentage of aboveground biomass (%)
Cumulative percentage of the population (%)
0
20
40
60
80
100

Figure 4.13. The Lorenz curve as applied to stem diameter hierarchies in *Abutilon theophrasti* of not sprayed (A, B), sprayed with *Colletotrichum coccodes* alone (C, D), and in combination with bentazon (E, F) when grown in monospecific stands and in competition with soybean and harvested 85 days after seeding in 1998 and 1999. The area under the diagonal is equal to one-half the value of the Gini coefficients. Stem diameter was not measured at 85 days after seeding in 1997.

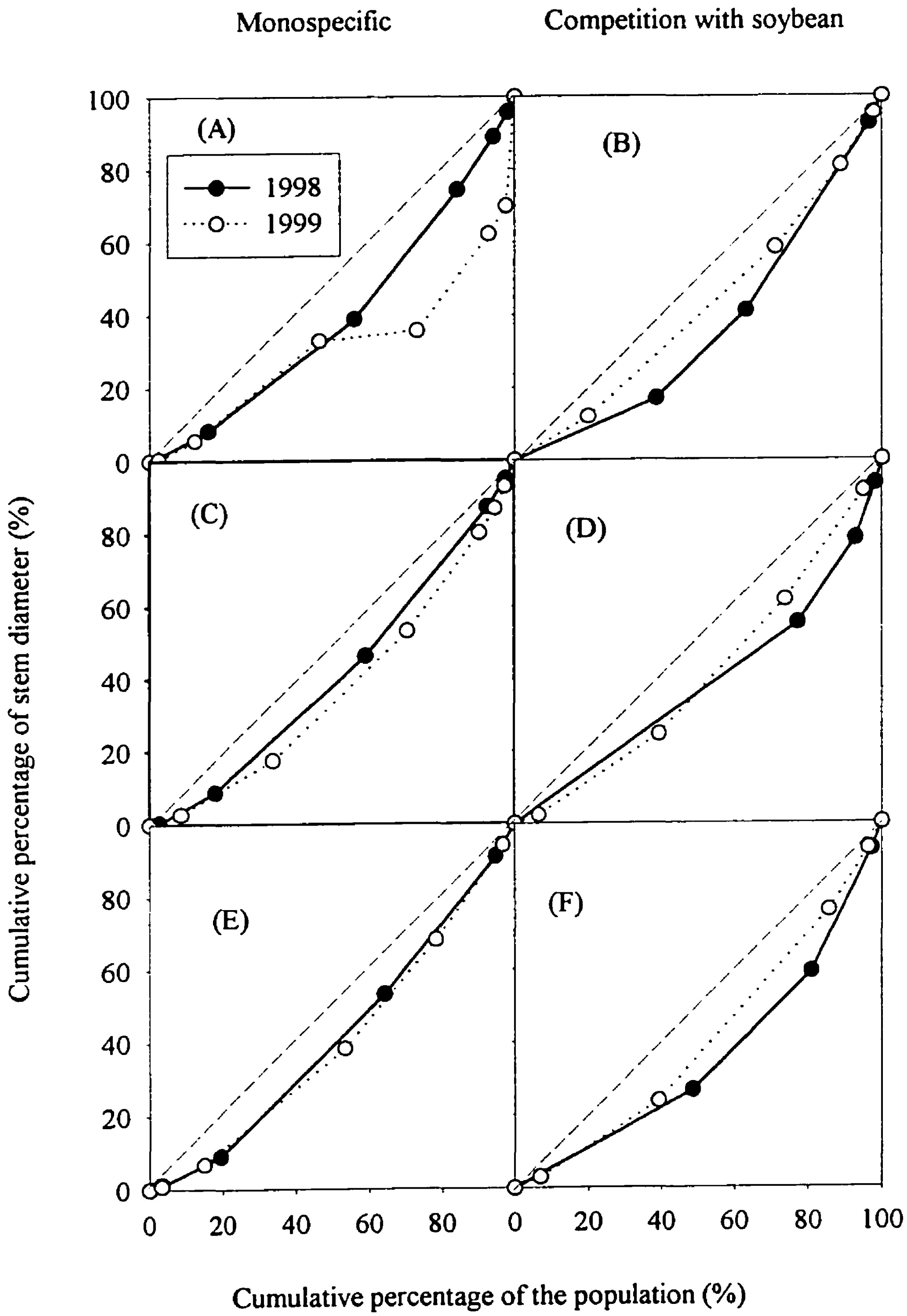
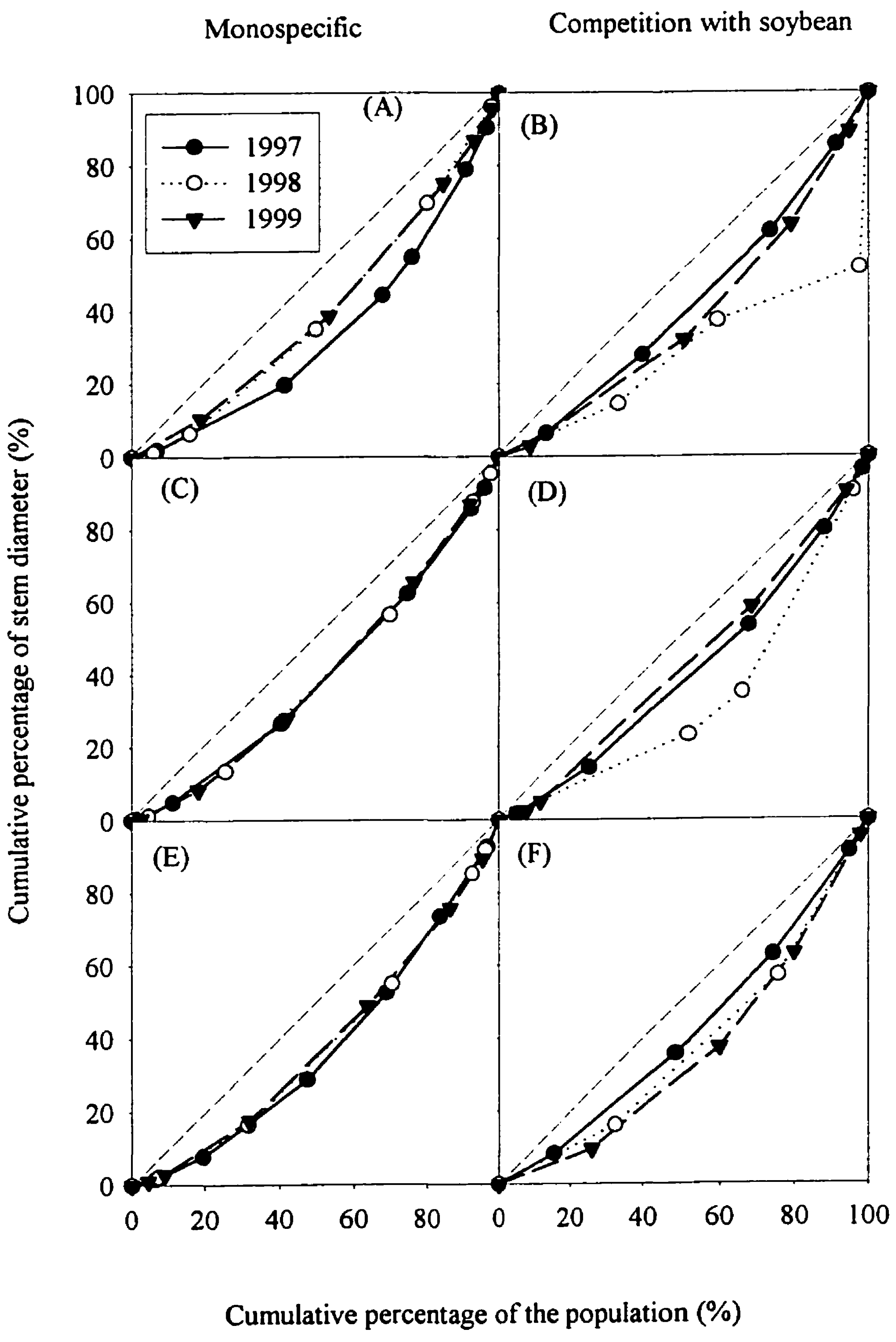

Monospecific
Competition with soybean
(A)
(B)
(C)
(D)
(E)
(F)
1998
1999
100
80
60
40
20
0
0
20
40
60
80
100
Cumulative percentage of stem diameter (%)
Cumulative percentage of the population (%)

Figure 4.14. The Lorenz curve as applied to stem diameter hierarchies in *Abutilon theophrasti* of not sprayed (A, B), sprayed with *Colletotrichum coccodes* alone (C, D), and in combination with bentazon (E, F) when grown in monospecific stands and in competition with soybean and harvested 118 days after seeding in 1997, 1998, and 1999. The area under the diagonal is equal to one-half the value of the Gini coefficients.



Monospecific
Competition with soybean
(A)
(B)
(C)
(D)
(E)
(F)
1997
1998
1999
Cumulative percentage of stem diameter (%)
Cumulative percentage of the population (%)
0
20
40
60
80
100

Connecting Text

In chapter 4, the effects of seed size, biotic and chemical stresses, and soybean interspecific competition on *A. theophrasti* plant height, aboveground biomass, and stem diameter were discussed. In this chapter, the allometric relationships between *A. theophrasti* plant height, aboveground biomass and stem diameter are studied, using the vegetative data collected over the three year duration of the project.

Chapter 5

The allometry of height, diameter, and aboveground biomass of *Abutilon theophrasti* in stress environments

5.1. Abstract

The allometry of plant height with respect to the aboveground biomass and stem diameter and the allometry of the aboveground biomass with respect to stem diameter were determined in velvetleaf (*Abutilon theophrasti*) in a monospecific stand and in competition with soybeans in the relatively short growing season area of southeastern Québec, Canada. The foliar application of a fungal pathogen, *Colletotrichum coccodes*, and the herbicide, bentazon, decreased the mean height and aboveground biomass of *A. theophrasti* due to premature defoliation when applied at the 2- to 3-leaf growth stage. The rapid recovery of *A. theophrasti* from defoliation resulted in a significantly higher aboveground biomass and plant height in a monospecific stand as compared to those in competition with soybean. The allometric relationships of *A. theophrasti* aboveground biomass and stem diameter in comparison with plant height were curvilinear in monospecific stands and in competition with soybean. However, aboveground biomass and stem diameter showed a simple linear relationship on a log-log scale in both monospecific stands and in competition with soybean. These results revealed that competition for light enhanced the higher inequality in *A. theophrasti* plant heights as compared with aboveground biomass and stem diameter when grown in unstressed and stress conditions. The response of height, stem diameter, and above ground biomass to stress conditions illustrated the opportunist strategy and ability of *A. theophrasti* to

escape weed management practices and to reproduce. From a weed management perspective these results explain, in part, the successful establishment and persistence of *A. theophrasti* in soybean cropping systems.

5.2. Introduction

The effect of competition for light on the size hierarchies in *Abutilon theophrasti*, a weedy Malvaceae species, when grown in a soybean cropping system has been analyzed (Baloch *et al.* 2001). The size hierarchy of *A. theophrasti* was positively skewed when it competed with soybean and was subsequently treated with the fungal pathogen, *Colletotrichum coccodes* and the herbicide, bentazon. Similarly, the aboveground biomass and stem diameter of *A. theophrasti* showed more variability in hierarchies as compared with plant height. However, it was unclear from these results as to how size parameters were correlated with each other. The most appropriate methodology for such comparison is the application of allometric analysis to determine the relationship between size parameters (Weiner and Thomas 1992, Nagashima and Terashima 1995). Allometry is the study of the change in proportion of the various parts of an organism as a consequence of growth (Gould 1966). According to this definition, the changes are measured in individuals over time, but in most of the cases, the data used to determine allometric relationships are normally from individuals of different sizes measured at one point of time (Weiner and Thomas 1992). This is due to convenience and because some of the most valuable data such as aboveground biomass can only be evaluated destructively. Allometry of resource allocations to the different organs is important for the fitness of a plant in a competitive environment (Anten and Hirose 1998). Application of allometry in size hierarchies can aid in the understanding of the competitive interaction between plants for light based on the aboveground allometric growth pattern of a plant which determines its pattern of light interception (Weiner and Thomas 1992). Plant allometry has a strong effect on the dynamics of population structure and the nature of plant-plant interactions within populations (Thomas and Weiner 1989).

The allometry of size can provide a quantitative means to draw broad comparisons among *A. theophrasti* individuals grown under stress conditions and can be determined by the following general assumption: $Y = aX^b$ where X and Y are organs or size matrices and a and b are constants (Huxley 1932). It was observed that the allometric relationship of annual plants in a stand changed with time and stand density (Weiner and Thomas 1992). The relationship between stem diameter, height, and plant mass showed a simple allometry when grown in isolation (Weiner and Thomas 1992; Weiner and Fishman 1994). However, crowded populations showed a complex allometry between height, stem diameter, and aboveground biomass and relationships were curvilinear or discontinuous (on a log-log scale).

The specific objectives of this research were to determine (a) the allometric relationships between *A. theophrasti* height, stem diameter, and aboveground biomass and (b) the effect of split application of *C. coccodes* and bentazon on these parameters in a monospecific population and in a mixed population with soybean. The results of previous research suggested that *A. theophrasti* size hierarchies were positively skewed and showed higher Gini coefficient values in the presence of soybean despite the application of *C. coccodes* and bentazon (Baloch *et al.* 2001). However, *A. theophrasti* plant height and stem diameter were negatively skewed (J-shaped) and the aboveground biomass was positively skewed (L-shaped) in monospecific stands. Based on those results, a curvilinear or discontinuous allometry in a monospecific stands and a linear allometry in a population competing with soybean are expected.

5.3. Materials and Methods

5.3.1. Study site, 5.3.2. Experimental design, 5.3.3. Establishment of planting densities, 5.3.4. Inoculum production, 5.3.5. Inoculum and herbicide application, and 5.3.6. Harvest procedures were same as described in section 4.3.1-4.3.6.

5.3.7. Statistical analyses. *A. theophrasti* plants were divided into two size groups depending upon their growth stages. Plants that showed continuous growth until the final harvest were classified as the 'tall' plants, while the 'short' plants were those that terminated (stunted) their growth during the growing season. Plants that possessed a height above 100 cm were classified as 'tall' and those below 100 cm were classified as 'short' plants. Stem diameter categories of 'thin' and 'thick' and aboveground biomass categories of 'light' and 'heavy' were separated by a median of 5 mm and 5 g, respectively. Differences in the allometric relationships between log size were determined by using a second-order polynomial regression, $Y = b_o + b_1X + b_2X^2$ on log-transformed data, to determine if the relationship was curvilinear or discontinuous between height, stem diameter, and aboveground biomass. A significant second-order polynomial term indicates that the relationships between growth parameters was curvilinear or discontinuous (Weiner and Thomas 1992). Whereas, a non significant second-order polynomial suggests that the relationships between the growth parameters were linear.

5.4. Results

5.4.1. Size distribution. Size distribution varied among *A. theophrasti* plants when grown in monospecific stands in 1997, 1998, and 1999 (Figs. 5.1 to 5.3). The differences in response from year to year demonstrated the variability in size distribution among *A. theophrasti* plants associated with fluctuations in the environmental conditions. For example, a uniform height distribution among *A. theophrasti* plants in 1997 suggested a favorable growing season (Fig. 5.1A). In contrast, the inequality in height among *A. theophrasti* plants was evident throughout the growing seasons of 1998 and 1999 (Figs. B and C). However, the overall percentage of extreme height classes (< 30 and ≥ 180 cm) of *A. theophrasti* individuals were relatively low (1.2 %) as compared with the midsize (120 cm), which comprised 63% of the *A. theophrasti* plants in all three years (Fig. 5.1). Despite the application of *C. coccodes* and bentazon the higher proportion of larger individuals in monospecific stands indicated that most of the *A. theophrasti* plants continued to grow until the end of the growing season (details in preceeding chapter).

When grown in competition with soybean, the number of small *A. theophrasti* plants (<60 cm) was relatively high (27.5 %) (Fig. 5.1). However, in 1998, a greater percentage (67%) of *A. theophrasti* plants was smaller than in 1997 and 1999 (Fig. 5.1B). Soybean competition did reduce *A. theophrasti* plant height in 1998 and 1999 as compared with 1997, resulting in a positive (L-shaped) skewedness in height frequency distribution in 1998 and 1999 and a negative (J-shaped) skewedness in 1997 (Fig. 5.1). Despite the competitive ability of soybean and the application of *C. coccodes* and bentazon, 59.4% of *A. theophrasti* individuals were in the height classes of 120-180 cm in 1997 (Fig. 5.1A). Most of the *A. theophrasti* plants escaped the shading effect by the soybean canopy structure thus, were able to captured maximum light. In contrast to height, stem diameter of *A. theophrasti* demonstrated positive (L-shape) skewedness distributions when grown in monospecific stands and in competition with soybean in the three growing seasons (Fig. 5.2). However, the aboveground biomass of *A. theophrasti* were demonstrated a uniform distributions among the frequency classes when grown in monospecific stands (Fig. 5.3), and a positive (L-shape) skewedness distributions when grown in competition with soybean in 1998 and 1999 and a uniform frequency distributions in 1997 (Fig. 5.3).

5.4.2. Cessation of height-growth of *A. theophrasti* plants under stress conditions.

Changes in the proportion of *A. theophrasti* plant height in the three successive growing seasons are shown in Table 5.1. The application of *C. coccodes* alone and in combination with bentazon and soybean interspecific competition did not affect the number of tall and short *A. theophrasti* plants in 1997 (Table 5.1). Similar results were found when not sprayed and sprayed *A. theophrasti* plants were grown in monospecific stands in 1997. However, when *A. theophrasti* plants were grown in competition with soybean and sprayed with *C. coccodes* alone and in split application with bentazon, the number of tall and short plants were significantly ($P<0.05$) varied as compared with sprayed and non sprayed plants in monospecific stands in 1998 (Table 5.1). Similarly in 1999, the split application of *C. coccodes* and bentazon did not affect the number of tall and short *A. theophrasti* plants when grown in monospecific stands as compared with plants, non sprayed and sprayed with *C. coccodes*, grown in competition with soybean (Table 5.1).

5.4.3. Relationships between allometry of size measures in *A. theophrasti.* Changes in allometric relationships between height, aboveground biomass, and stem diameter of *A. theophrasti* plants were examined for both the monospecific stands and population competing with soybean. Figures 5.4 to 5.6 illustrate the relationships of these growth parameters of *A. theophrasti* ('tall' and 'short') using the log-transformed pooled data of three successive years in the monospecific stands and population competing with soybean. These results demonstrated that the relationships between height-diameter and height-biomass showed a significant ($P < 0.01$) curvilinear or discontinuous allometry in both monospecific stands and population competing with soybean, in 1997 and 1999 (Figs. 5.4 and 5.5, Tables 5.2, 5.3, 5.8, and 5.9). Whereas, in six of the twelve cases in 1998, *A. theophrasti* plants in both monospecific stands and populations competing with soybean tended to show simple allometric relations between height-diameter and height-biomass (Tables 5.5 and 5.6). The allometric relationship between biomass-diameter was a simple linear among *A. theophrasti* plants grown under intra- and interspecific competition (Fig. 5.6). The application of *C. coccodes* alone did not affect the allometric relationships between height, aboveground biomass, and stem diameter in *A. theophrasti* (Tables 5.2 to 5.10). However, when bentazon was applied with *C. coccodes*, simple linear allometric relationships between height, biomass, and stem diameter in 1997 and 1998 were observed when *A. theophrasti* was growing in competition with soybean. In 1999, the application of *C. coccodes* and bentazon resulted in curvilinear allometric relationships between height-diameter and height-biomass (Tables 5.8 and 5.9).

5.5. Discussion

The results demonstrate that the allometric relationships between *A. theophrasti* height-diameter and height-biomass were curvilinear while biomass-diameter was a strong linear allometric relationship in 1997, 1998, and 1999. The application of *C. coccodes* along with bentazon on *A. theophrasti* plants growing in competition with soybean, resulted in simple linear allometric relationships between height, biomass, and stem diameter of *A. theophrasti* plants in the all growing seasons. However, the split application of *C. coccodes* and bentazon on *A. theophrasti* in monospecific stands and *C. coccodes* alone on competing populations with soybean showed curvilinear allometric relationships in 1997 and 1999 while, most of the growth parameters exhibited linear allometric distributions in 1998. In general, there was no difference between the allometry of *A. theophrasti* plants when grown in monospecific stands versus populations competing with soybean.

In preceeding chapter it was reported that the higher disease incidence and herbicide activities in 1998 enhanced the number of 'short' plants in both monospecific stands and populations competing with soybean (Baloch *et al.* 2001). The higher percentage of these 'short' plants showed an architectural similarity that strongly affected the allometric relationships between growth parameters in *A. theophrasti*. These results demonstrated that the allometric relationships between height, stem diameter, and biomass were more linear in 'short' plants as compared with 'tall' ones. For example, the numbers of 'tall' plants were higher in 1997 and 1999, resulting in higher curvilinear allometric relationships when height was compared with biomass and stem diameter. The higher number of 'short' plants in 1998 exhibited linear allometric relationships among the different growth parameters.

In the present study it was revealed that the combined effects of *C. coccodes*, bentazon, and soybean interspecific competition resulting in inequality in allometric relationships between growth parameters in *A. theophrasti*. The curvilinear allometry between growth parameters *in A. theophrasti* in 1997 and 1999 was the result of poor disease incidence of *C. coccodes* and minor impacts of bentazon resulting in increased competitiveness of *A. theophrasti* in both monospecific stands and in competition with soybean. Weiner and Thomas (1992) and Weiner and Fishman (1994) have reported that at low densities, the relationships between height, stem diameter, and biomass in *Tagetes patula* and *Kochia scoparia* populations showed a simple linear allometry. However, in crowded populations the relationships between log height-log diameter and log height-log biomass were curvilinear and log biomass-log diameter was a simple linear allometric relationship. It is therefore highly probable that the relationships between log height-log stem diameter and log height-log biomass were highly sensitive to the intensity of competition for light as compared with log diameter-log biomass. Moreover, the higher reduction (5x) in *A. theophrasti* aboveground biomass in competition with soybean, did not affect the allometry between log height-log diameter and log height-log biomass relationships among *A. theophrasti* plants competing with soybean. From these results, it is clear that despite the higher competitive ability of soybean, and the split application of *C. coccodes* and bentazon, the partitioning of biomass on aerial parts in *A. theophrasti* plants grown in competition with soybean plots were similar with plants grown in monospecific stands. The interspecific competition between *A. theophrasti* and soybean did enhance the inequality in the growth parameters amongst *A. theophrasti* individuals that resulted in few 'tall' and many 'short' plants.

The competitive interactions between *A. theophrasti* and soybean were based upon the architectural differences and plant density. Under intraspecific competition, most of the *A. theophrasti* plants produced a main central stem along with lateral branches, but in competition with soybean plots, *A. theophrasti* produced only a central stem. In contrast to *A. theophrasti*, soybean produced a three-dimensional architectural structure that enabled soybean to shade *A. theophrasti* plants at later growth stages (personal observations). Interspecific competition increased the number of 'short' *A. theophrasti* plants as compared with 'tall' ones. The higher number of 'short' plants also influenced the allometric correlation among height, biomass, and stem diameter. The biomass allocation in 'short' plants was mostly concentrated at the lower portion of the stem resulting in the log biomass-log diameter being a linear allometric relationship. Similarly, the biomass allocation in 'tall' plants decreased with increasing plant height resulting in a linear allometric distribution between log biomass-log diameter. These results were with those reported by Givnish (1982) and Gaber (1989).

Plant density also affected the allometric distribution between growth parameters. It has been suggested that, under a light limiting environment, the higher number of individuals per unit area increased the intensity of competition due to decreasing light penetration at the lower strata (Anten and Hirose 1998). Under those circumstances, plant height is more important than other parameters because taller plants have an advantage over shorter ones, intercepting greater light intensities than shorter ones (McMahon 1973, Anten and Hirose 1998). However, soybean interspecific competition increased the discontinuity in *A. theophrasti* plant height and the number of 'tall' plants was relatively short due to intense competition resulting in a higher inequality in size and disruptive (curvilinear) allometric distribution, particularly when height was correlated with stem diameter and aboveground biomass. Similar results as above were also reported by Yokozawa and Hara (1992).

The split applications of *C. coccodes* and bentazon also affected the allometric distribution between the height-biomass and height-diameter relationships. Premature defoliation caused by *C. coccodes* provided enough time for the soybean plants to overtop the infected *A. theophrasti* plants, resulting in a higher number of 'short' plants as compared with 'tall' ones in competition with soybean. The higher disease incidence also aided in increasing the number of subordinate *A. theophrasti* plants in both monospecific stands and populations competing with soybean that resulted in simple linear allometric relationships between height, biomass, and stem diameter.

The plasticity in resource allocation between the different growth parameters of *A. theophrasti* plants under stress conditions clearly indicated the successful strategy of this robust weedy species in cropping systems. The allometric relationships between height, stem diameter, and biomass suggest that the resource allocation of *A. theophrasti* plants was compromised between the different growth parts under stress conditions and more resources were allocated for height as compared with the aboveground biomass and stem diameter. The application of *C. coccodes* at the 2- to 3-leaf stage of *A. theophrasti* under favorable environmental conditions decreased the competitive ability of *A. theophrasti* due to the large number of 'short', less competitive plants resulting in higher soybean yield. The efficacy of *C. coccodes* is highly dependent upon environmental condition, especially moisture and temperature. In this study, environmental conditions were favourable for *C. coccodes* to cause disease on *A. theophrasti* only in 1998. Additional experiments are necessary to adequately test the efficacy of *C. coccodes* on allometric relationships in *A. theophrasti* plants grown in competition with other crops.

5.6. References

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Table 5.1. Effects of *Colletotrichum coccodes* and bentazon on *Abutilon theophrasti* plant height (%) when grown in monospecific stands and in competition with soybean during three growing seasons.

Treatment	1997		1998		1999	
	Tall	Short	Tall	Short	Tall	Short
†Cont. Mon.	13.2a (±1.9)	45 .0a (±9.8)	27.8b (±1.3)	6.9b (±1.9)	27.2a (±1.9)	16.2ab (±2.3)
Cont. Mix.	15.6a (±2.1)	5.0a (±0.8)	11.5ab (±1.7)	19.3ab (±1.4)	14.2bc (±1.1)	35.4a (±3.8)
C. c., Mon.	24.8a (±3.8)	14.1a (±0.7)	23.1b (±2.2)	6.9b (±0.5)	15.5b (±1.1)	14.1ab (±0.8)
C.c., Mix.	17.2a (±1.2)	13.3a (±1.3)	11.5a (±2.1)	25.5a (±1.4)	24.1a (±1.5)	14.1ab (±1.7)
C. c., b, Mon.	16.4a (±3.1)	15.8a (±1.4)	21.1ab (±1.2)	17.8ab (±1.2)	11.6bc (±0.8)	4.4b (±0.4)
C. c., b, Mix.	12.4a (±2.1)	6.6a (±0.9)	4.7a (±1.1)	23.2a (±1.8)	7.1c (±1.1)	16.2ab (±2.7)

† Cont. = not sprayed, *C. c.* = sprayed with *Colletotrichum coccodes*, b = treated with the herbicide, bentazon, Mon. = monospecific stands of *Abutilon theophrasti*, Mix. = *A. theophrasti* plants grown in competition with soybean. Number in parenthesis indicates standard error.

Mean in the same column followed by a different letter differ significantly ($P<0.05$) using an ANOVA protected Least Significant Differences (LSD) test.

Three years are significantly different based on Barttlet's test.

Data were combined for the two seed size classes.

Table 5.2. Tests for non-linearity of allometric relationships between height and stem diameter of *Abutilon theophrasti* sprayed with *Colletotrichum coccodes* alone and in combination with bentazon, in monospecific stands and in competition with soybean in 1997.

Entry	n	Mean height (x)	Mean diameter (y)	r^2	b_o	b_1	b_2	P*	rMSE
Monospecific									
Control	88	95.8	5.44	0.77	2.65	-3.29	1.15	<0.01	0.13
C. coccodes (C.c)	46	125.2	6.58	0.85	5.05	-5.87	1.82	<0.01	0.06
C. c./ bentazon	80	121.4	6.71	0.70	2.59	-3.09	1.07	<0.01	0.09
Competition with soybean									
Control	60	112.2	5.33	0.73	4.38	-5.27	1.69	<0.01	0.09
C. coccodes (C.c)	61	109.6	6.48	0.92	0.34	-1.14	0.67	0.01	0.07
C. c./ bentazon	40	122.9	6.47	0.71	4.42	-4.95	1.53	ns	0.08

**P*: significance of second-order term in regression: $y = b_0 + b_1X + b_2X^2$ (on log-transformed data). ns: not significant in the second-order term. Significance is evidence for curvilinearity; non significance is consistent with linear allometric relationship (Weiner and Thomas 1992). r^2 is for the polynomial regression model. rMSE: root of mean square error of the regression model. n = number of *A. theophrasti* plants.

Data were combined for two seed size classes and two harvests.

Table 5.3. Tests for non-linearity of allometric relationships between height and aboveground biomass of *Abutilon theophrasti* sprayed with *Colletotrichum coccodes* alone and in combination with bentazon, in monospecific stands and in competition with soybean in 1997.

Entry	n	Mean height (x)	Mean biomass (y)	r^2	b_o	b_1	b_2	P*	rMSE
Monospecific									
Control	88	95.8	6.97	0.89	3.93	-6.19	2.27	<0.01	0.18
C. coccodes (C.c)	46	125.2	8.60	0.86	7.89	-9.92	3.13	<0.01	0.11
C. c./ bentazon	80	121.4	10.51	0.88	4.01	-5.94	2.13	<0.01	0.12
Competition with soybean									
Control	60	112.2	6.81	0.84	2.13	-4.48	1.85	0.01	0.14
C. coccodes (C.c)	61	109.6	9.67	0.94	5.77	-8.22	2.83	<0.01	0.11
C. c./ bentazon	40	122.9	9.06	0.86	0.95	-3.09	1.46	ns	0.11

*P: significance of second-order term in regression: $y = b_O + b_1X + b_2X^2$ (on log-transformed data). ns: not significant in the second-order term. Significance is evidence for curvilinearity; non significance is consistent with linear allometric relationship (Weiner and Thomas 1992). r^2 is for the polynomial regression model. rMSE: root of mean square error of the regression model. n = number of *A. theophrasti* plants.

Data were combined for two seed size classes and two harvests.

Table 5.4. Tests for non-linearity of allometric relationships between aboveground biomass and stem diameter of *Abutilon theophrasti* sprayed with *Colletotrichum coccodes* alone and in combination with bentazon, in monospecific stands and in competition with soybean in 1997.

Entry	n	Mean biomass (x)	Mean diameter (y)	r^2	b_o	b_1	b_2	P*	rMSE
Monospecific									
Control	88	6.97	5.44	0.89	0.41	0.49	-0.04	ns	0.09
C. coccodes (C.c)	46	8.60	6.58	0.93	0.33	0.56	-0.01	ns	0.04
C. c./ bentazon	80	10.51	6.71	0.79	0.31	0.64	-0.09	0.04	0.08
Competition with soybean									
Control	60	6.81	5.33	0.80	0.38	0.39	0.06	ns	0.08
C. coccodes (C.c)	61	9.67	6.48	0.91	0.34	0.62	-0.08	0.03	0.07
C. c./ bentazon	40	9.06	6.47	0.84	0.31	0.62	-0.08	ns	0.06

**P*: significance of second-order term in regression: $y = b_0 + b_1X + b_2X^2$ (on log-transformed data). ns: not significant in the second-order term. Significance is evidence for curvilinearity; non significance is consistent with linear allometric relationship (Weiner and Thomas 1992). r^2 is for the polynomial regression model. rMSE: root of mean square error of the regression model. n = number of *A. theophrasti* plants.

Data were combined for two seed size classes and two harvests.

Table 5.5. Tests for non-linearity of allometric relationships between height and stem diameter of *Abutilon theophrasti* sprayed with *Colletotrichum coccodes* alone and in combination with bentazon, in monospecific stands and in competition with soybean in 1998.

Entry	n	Mean height (x)	Mean diameter (y)	r^2	b_o	b_1	b_2	P*	rMSE
Monospecific									
Control	51	124	6.02	0.84	-0.21	-0.82	0.61	ns	0.1
C. coccodes (C.c)	43	72.8	3.13	0.93	-0.89	0.47	0.14	ns	0.07
C. c./ bentazon	44	111.4	5.23	0.90	1.37	-2.31	0.96	<0.01	0.06
Competition with soybean									
Control	51	67.6	2.91	0.95	-1.11	0.67	0.09	ns	0.07
C. coccodes (C.c)	55	103.5	5.12	0.92	0.36	-0.94	0.55	<0.01	0.06
C. c./ bentazon	38	60.5	2.79	0.79	-0.92	0.72	0.03	ns	0.11

*P: significance of second-order term in regression: $y = b_0 + b_1X + b_2X^2$ (on log-transformed data). ns: not significant in the second-order term. Significance is evidence for curvilinearity; non significance is consistent with linear allometric relationship (Weiner and Thomas 1992). r^2 is for the polynomial regression model. rMSE: root of mean square error of the regression model. n = number of *A. theophrasti* plants.

Data were combined for two seed size classes and two harvests.

Table 5.6. Tests for non-linearity of allometric relationships between height and aboveground biomass of *Abutilon theophrasti* sprayed with *Colletotrichum coccodes* alone and in combination with bentazon, in monospecific stands and in competition with soybean in 1998.

Entry	n	Mean height (x)	Mean biomass (y)	r^2	b_o	b_1	b_2	*P**	rMSE
Monospecific									
Control	51	124	7.65	0.92	7.42	-9.52	3.1	<0.01	0.1
C. coccodes (C.c)	43	72.8	2.82	0.95	-1.39	-0.02	0.51	ns	0.11
C. c./ bentazon	44	111.4	5.93	0.93	4.08	-6.62	2.42	<0.01	0.1
Competition with soybean									
Control	51	67.6	2.87	0.86	1.31	-3.38	1.50	<0.01	0.23
C. coccodes (C.c)	55	103.5	5.99	0.93	1.99	-3.93	1.62	<0.01	0.11
C. c./ bentazon	38	60.5	2.53	0.92	-3.81	2.74	-0.24	ns	0.14

**P*: significance of second-order term in regression: $y = b_0 + b_1X + b_2X^2$ (on log-transformed data). ns: not significant in the second-order term. Significance is evidence for curvilinearity; non significance is consistent with linear allometric relationship (Weiner and Thomas 1992). r^2 is for the polynomial regression model. rMSE: root of mean square error of the regression model. n = number of *A. theophrasti* plants.

Data were combined for two seed size classes and two harvests.

Table 5.7. Tests for non-linearity of allometric relationships between aboveground biomass and stem diameter of *Abutilon theophrasti* sprayed with *Colletotrichum coccodes* alone and in combination with bentazon, in monospecific stands and in competition with soybean in 1998.

Entry	n	Mean biomass (x)	Mean diameter (y)	r^2	b_o	b_1	b_2	P*	rMSE
Monospecific									
Control	51	7.65	6.02	0.92	0.18	1.00	-0.31	<0.01	0.06
C. coccodes (C.c)	43	2.82	3.13	0.96	0.30	0.55	-0.3	ns	0.1
C. c./ bentazon	44	5.93	5.23	0.97	0.33	0.63	-0.09	<0.01	0.04
Competition with soybean									
Control	51	2.87	2.91	0.88	0.31	0.47	0.02	ns	0.11
C. coccodes (C.c)	55	5.99	5.12	0.89	0.36	0.56	-0.05	ns	0.07
C. c./ bentazon	38	2.52	2.79	0.85	0.32	0.42	0.02	ns	0.09

**P*: significance of second-order term in regression: $y = b_0 + b_1X + b_2X^2$ (on log-transformed data). ns: not significant in the second-order term. Significance is evidence for curvilinearity; non significance is consistent with linear allometric relationship (Weiner and Thomas 1992). r^2 is for the polynomial regression model. rMSE: root of mean square error of the regression model. n = number of *A. theophrasti* plants.

Data were combined for two seed size classes and two harvests.

Table 5.8. Tests for non-linearity of allometric relationships between height and stem diameter of *Abutilon theophrasti* sprayed with *Colletotrichum coccodes* alone and in combination with bentazon, in monospecific stands and in competition with soybean in 1999.

Entry	n	Mean height (x)	Mean diameter (y)	r^2	b_o	b_1	b_2	P*	*rMSE*
Monospecific									
Control	59	111.4	6.05	0.83	4.19	-4.83	1.54	<0.01	0.1
C. coccodes (C.c)	58	88.9	4.31	0.72	3.07	3.85	1.32	<0.01	0.12
C. c./ bentazon	39	108.9	6.34	0.81	-3.95	3.46	-0.55	ns	0.08
Competition with soybean									
Control	53	101.8	5.28	0.75	-1.83	1.72	-0.22	ns	0.09
C. coccodes (C.c)	23	119.1	7.08	0.92	2.88	-3.60	1.25	<0.01	0.06
C. c./ bentazon	28	79.4	4.53	0.88	1.27	-1.88	0.81	<0.01	0.09

**P*: significance of second-order term in regression: $y = b_0 + b_1X + b_2X^2$ (on log-transformed data). ns: not significant in the second-order term. Significance is evidence for curvilinearity; non significance is consistent with linear allometric relationship (Weiner and Thomas 1992). r^2 is for the polynomial regression model. rMSE: root of mean square error of the regression model. n = number of *A. theophrasti* plants.

Data were combined for two seed size classes and two harvests.

Table 5.9. Tests for non-linearity of allometric relationships between height and aboveground biomass of *Abutilon theophrasti* sprayed with *Colletotrichum coccodes* alone and in combination with bentazon, in monospecific stands and in competition with soybean in 1999.

Entry	n	Mean height (x)	Mean biomass (y)	r^2	b_o	b_1	b_2	P*	rMSE
Monospecific									
Control	59	111.4	8.22	0.93	2.3	-4.53	1.85	<0.01	0.09
C. coccodes (C.c)	58	88.9	4.49	0.84	5.0	-7.74	2.77	<0.01	0.20
C. c./ bentazon	39	108.9	8.48	0.77	19.7	-21.1	5.78	<0.01	0.15
Competition with soybean									
Control	53	101.8	6.11	0.89	-2.14	0.24	0.59	ns	0.15
C. coccodes (C.c)	23	119.1	11.69	0.75	7.01	-9.88	3.33	ns	0.29
C. c./ bentazon	28	79.4	5.43	0.95	1.87	-4.54	1.98	<0.01	0.15

**P*: significance of second-order term in regression: $y = b_0 + b_1X + b_2X^2$ (on log-transformed data). ns: not significant in the second-order term. Significance is evidence for curvilinearity; non significance is consistent with linear allometric relationship (Weiner and Thomas 1992). r^2 is for the polynomial regression model. rMSE: root of mean square error of the regression model. n = number of *A. theophrasti* plants.

Data were combined for two seed size classes and two harvests.

Table 5.10. Tests for non-linearity of allometric relationships between aboveground biomass and stem diameter of *Abutilon theophrasti* sprayed with *Colletotrichum coccodes* alone and in combination with bentazon, in monospecific stands and in competition with soybean in 1999.

Entry	n	Mean biomass (x)	Mean diameter (y)	r^2	b_o	b_1	b_2	P*	rMSE
Monospecific									
Control	59	8.22	6.05	0.91	0.42	0.33	0.08	0.03	0.05
C. coccodes (C.c)	58	4.49	4.31	0.83	0.39	0.36	0.07	ns	0.09
C. c./ bentazon	39	8.48	6.34	0.53	0.26	0.77	-0.19	ns	0.13
Competition with soybean									
Control	53	6.11	5.28	0.75	0.48	0.41	-0.08	ns	0.08
C. coccodes (C.c)	23	11.69	7.08	0.84	0.52	0.18	0.14	0.02	0.09
C. c./ bentazon	28	5.43	4.53	0.90	0.46	0.41	-0.04	ns	0.09

*P: significance of second-order term in regression: $y = b_0 + b_1X + b_2X^2$ (on log-transformed data). ns: not significant in the second-order term. Significance is evidence for curvilinearity; non significance is consistent with linear allometric relationship (Weiner and Thomas 1992). r^2 is for the polynomial regression model. rMSE: root of mean square error of the regression model. n = number of *A. theophrasti* plants.

Data were combined for two seed size classes and two harvests.

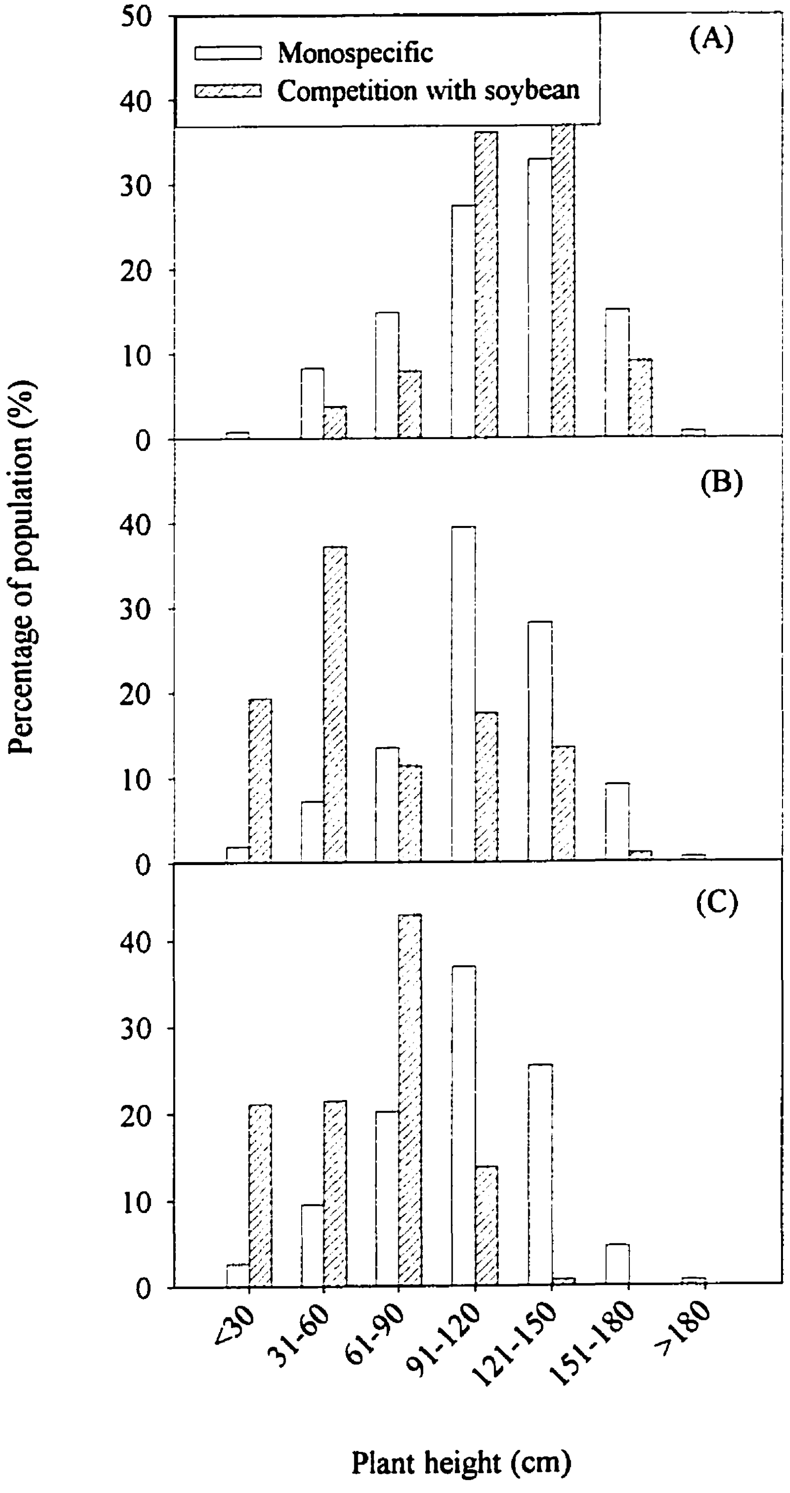


Figure 5.1. Overall height structure of *Abutilon theophrasti* grown in monospecific stands and in competition with soybean in 1997 (A), 1998 (B), and 1999 (C). Data were combined for the two seed size classes and two harvests.

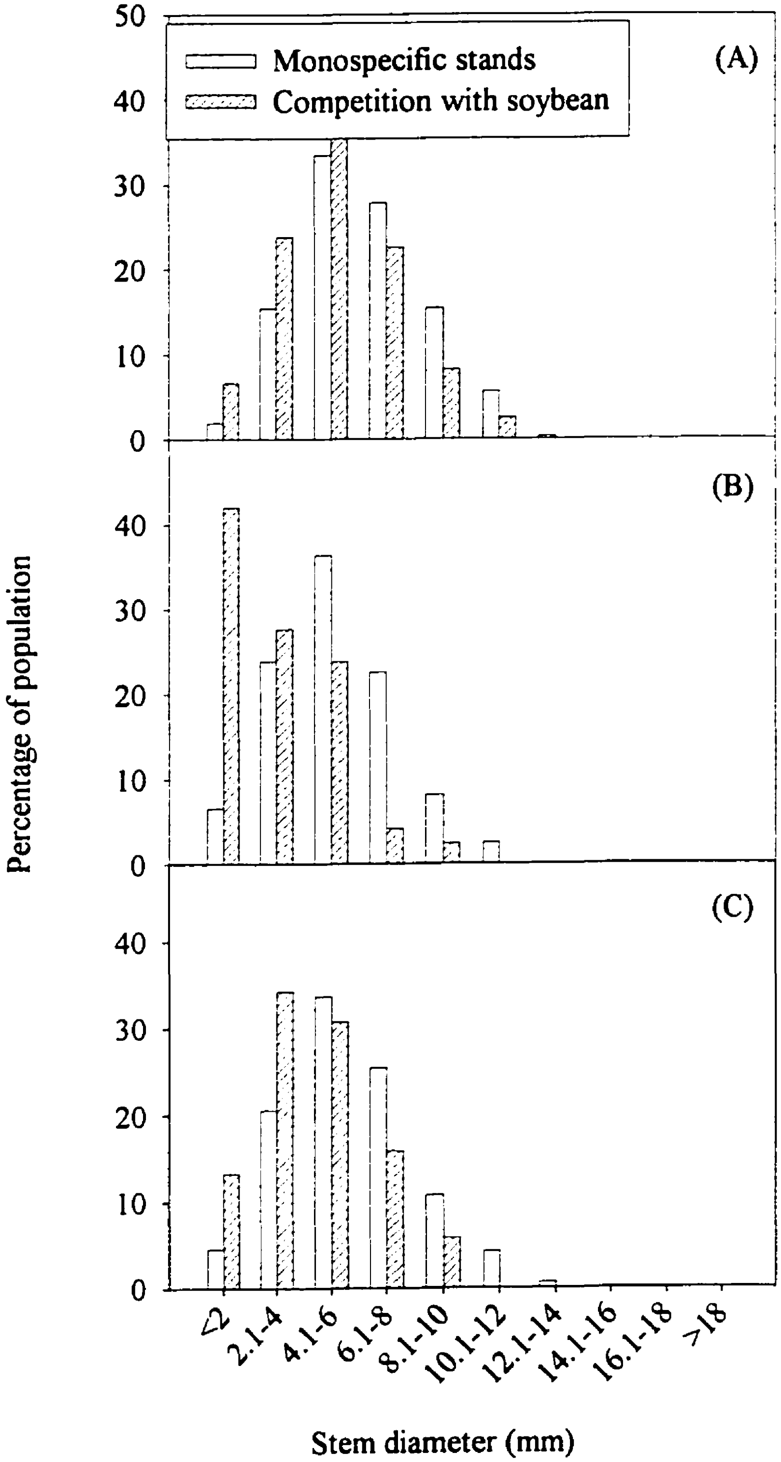


Figure 5.2. Overall stem diameter structure of *Abutilon theophrasti* grown in a monospcefic stand and in competition with soybean in 1997 (A), 1998 (B), and 1999 (C). Data were combined for the two seed size classes and the two harvests.

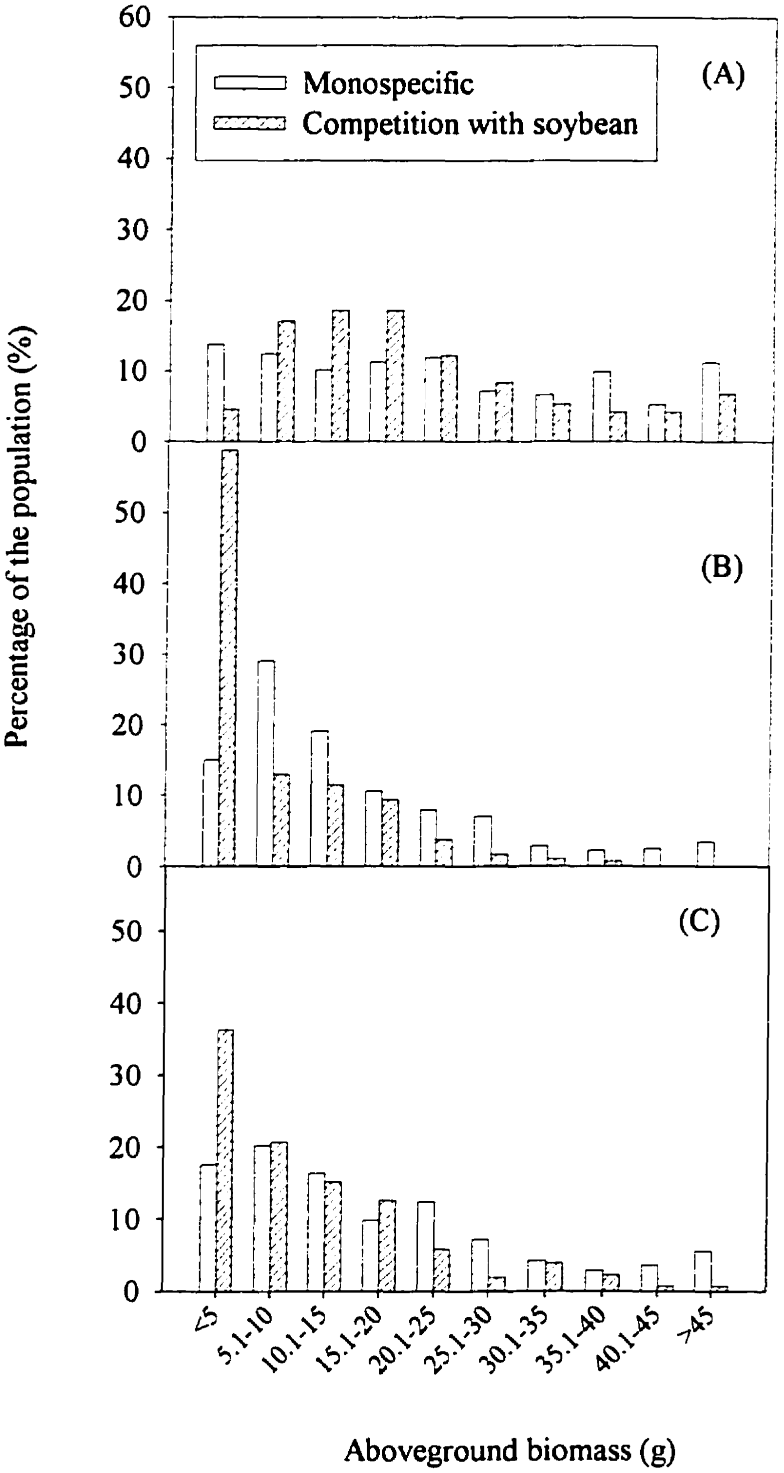


Figure 5.3. Overall aboveground biomass structure of *Abutilon theophrasti* grown in a monospecific stand and in competition with soybean in 1997 (A), 1998 (B), and 1999(C). Data were combined for the two seed size classes and the two harvests.

Figure 5.4. Final allometric relationships between height and aboveground biomass of *Abutilon theophrasti* unsprayed (A, B), sprayed *with Colletotrichum coccodes* alone (C, D) and in combination with bentazon (E, F), in monospecific stands and in competition with soybean. Data were combined for the two seed size classes, the two harvests and the three growing seasons.

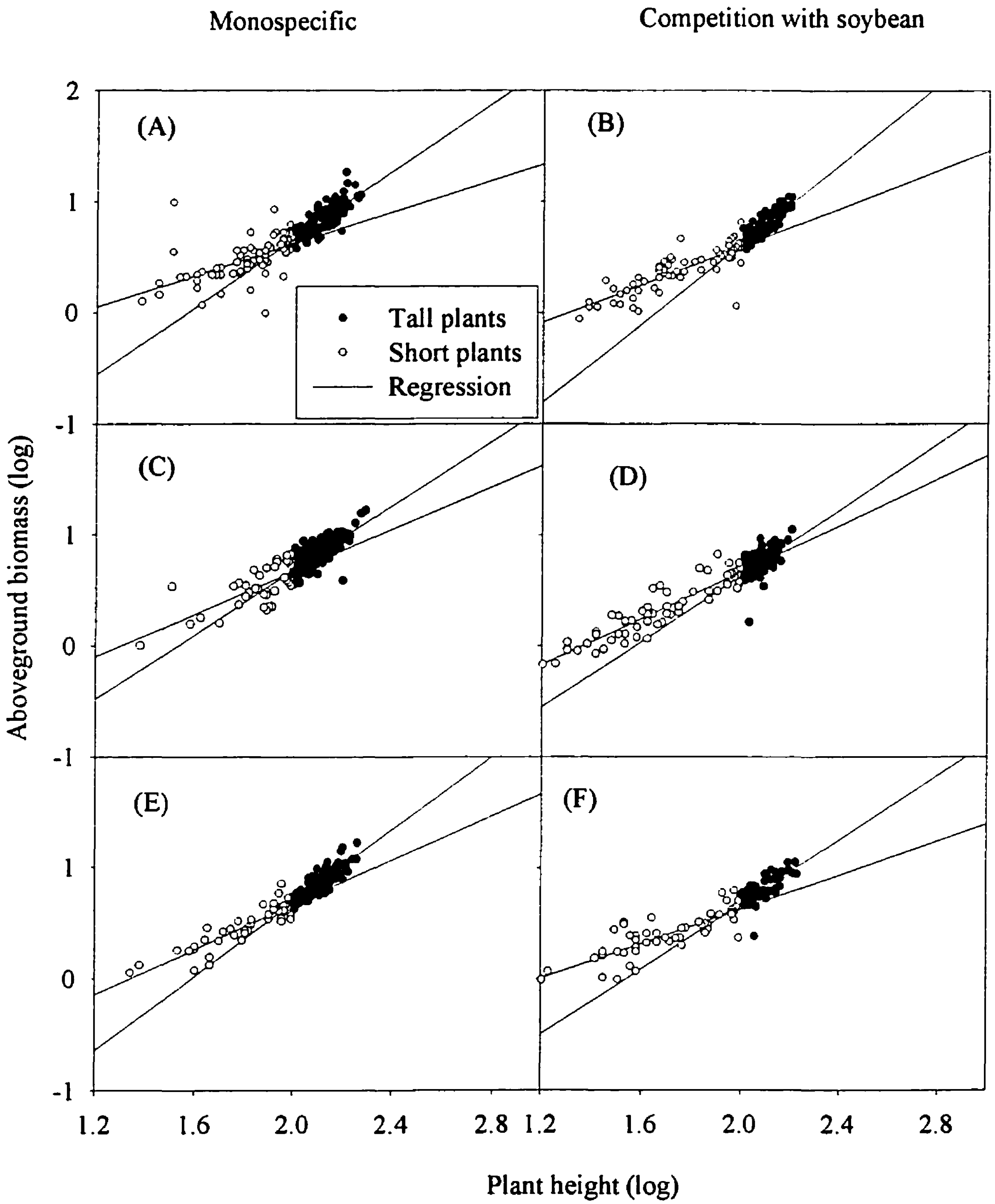
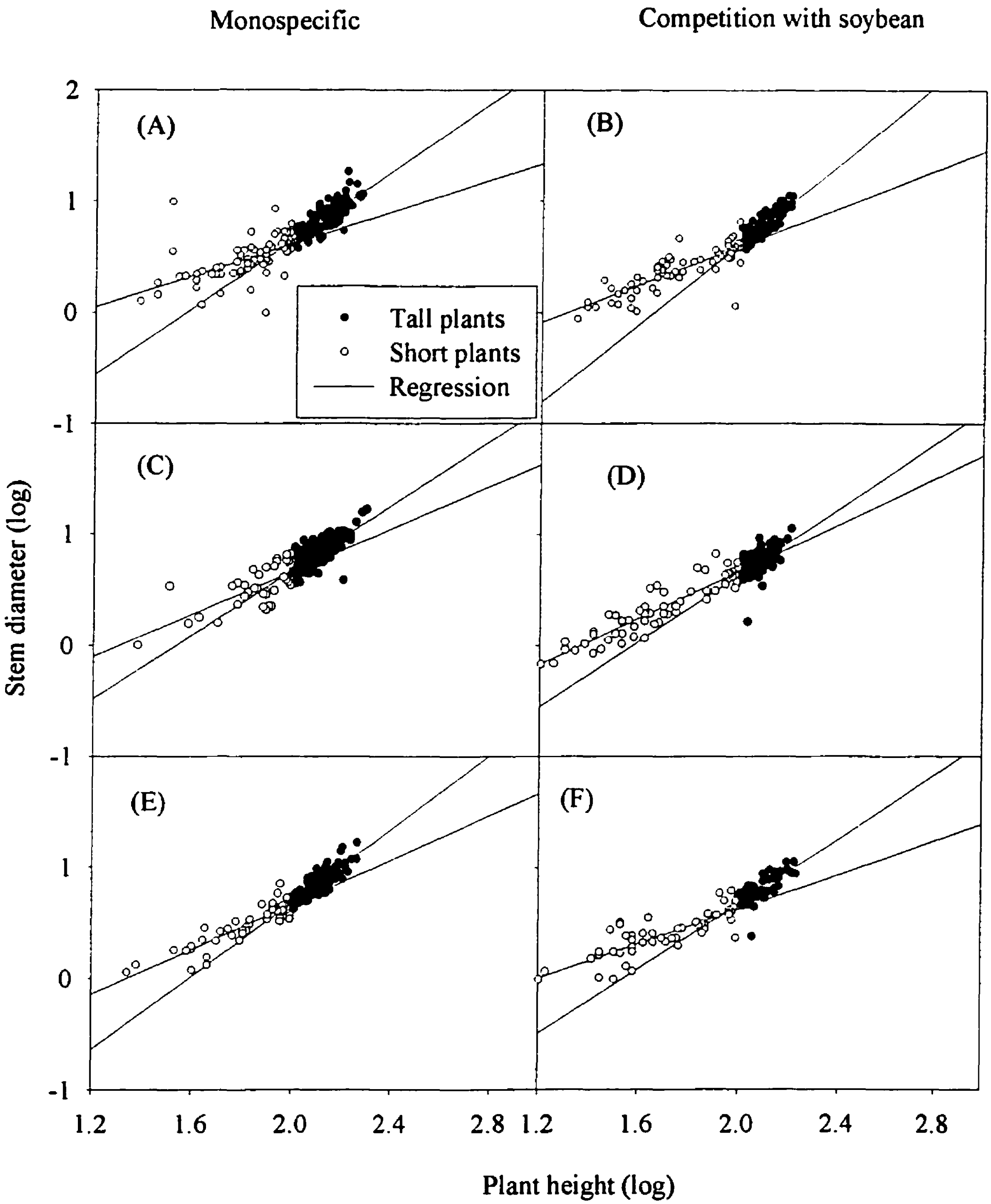
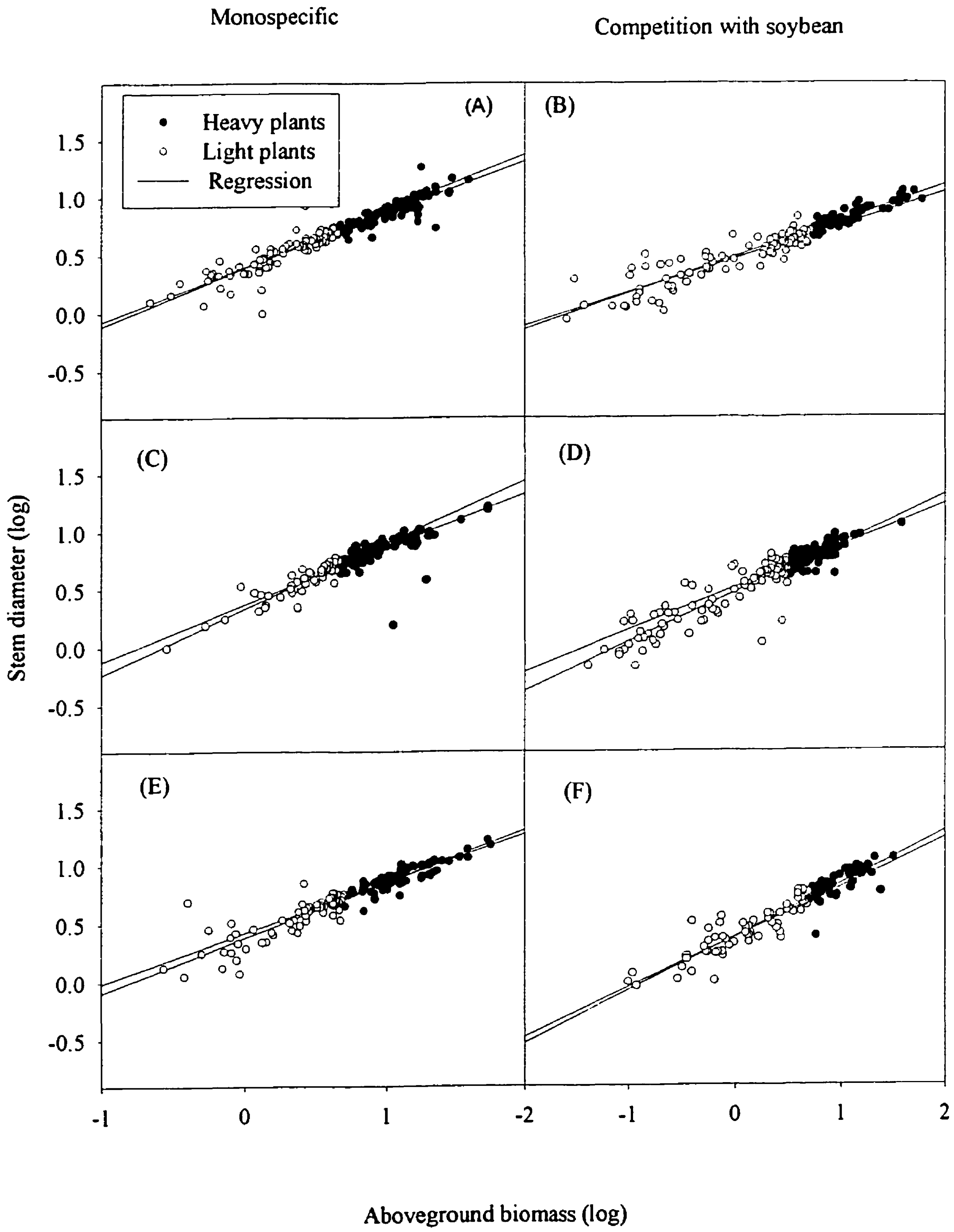

Monospecific
Competition with soybean
(A)
(B)
(C)
(D)
(E)
(F)
Tall plants
Short plants
Regression
Aboveground biomass (log)
2
1
0
-1
1
0
-1
1
0
-1
1.2
1.6
2.0
2.4
2.8
1.2
1.6
2.0
2.4
2.8
Plant height (log)

Figure 5.5. Final allometric relationships between height and stem diameter of *Abutilon theophrasti* unsprayed (A, B), sprayed *with Colletotrichum coccodes* alone (C, D) and in combination with bentazon (E, F), in monospecific stands and in competition with soybean. Data were combined for two the seed size classes, the two harvests and the three growing seasons.



Monospecific
Competition with soybean
(A)
(B)
(C)
(D)
(E)
(F)
Tall plants
Short plants
Regression
Stem diameter (log)
Plant height (log)
2
1
0
-1
1.2
1.6
2.0
2.4
2.8

Figure 5.6. Final allometric relationships between aboveground biomass and stem diameter of *Abutilon theophrasti* unsprayed (A, B), sprayed *with Colletotrichum coccodes* alone (C, D), and in combination with bentazon (E, F) in monospecific stands and in competition with soybean. Data were combined for the two seed size classes, the two harvests and the three growing seasons.


Monospecific
Competition with soybean
Heavy plants
Light plants
Regression
(A)
(B)
(C)
(D)
(E)
(F)
Stem diameter (log)
1.5
1.0
0.5
0.0
-0.5
-1
0
1
-2
-1
0
1
2
Aboveground biomass (log)

Connecting Text

In the previous chapter, the effects of seed size, biotic and chemical stresses, and soybean interspecific competition on *A. theophrasti* growth and size hierarchies were studied. Amongst the factors, interspecific competition with soybean had the greatest impact on the size hierarchy development of *A. theophrasti* plants.

In this chapter the vegetative and reproductive data of *A. theophrasti* collected over three years are analyzed using desirability function for the estimation of *A. theophrasti* plant fitness grown in stress conditions. The applications and limitations of these methods for the estimation of *A. theophrasti* fitness are discussed.

Chapter 6

Effects of biotic and chemical stresses on the reproductive output of *Abutilon theophrasti*

6.1. Abstract:

Reproductive output in annual plants has received much attention over the last century and different methodologies have been applied to predict the successful establishment of a plant in an environment. A computer-based program was developed to calculate the reproductive potential and desirability function (*D*) of *Abutilon theophrasti* (velvetleaf) when grown under different stress environments. The fitness of *A. theophrasti* depends upon prolific seed production with high viability (>90%). Application of the fungal pathogen, *Colletotrichum coccodes*, along with a selective herbicide, bentazon, not only reduced the reproductive potential of *A. theophrasti*, but also delayed capsule production when grown in the presence of soybean. The number of capsules per plant varied among the growing seasons. It was high in 1997 due to higher temperatures than in 1998 and 1999, as cooler conditions in those years delayed capsule production. Height and aboveground biomass were positively correlated with reproductive output in *A. theophrasti*. Seed germination and dormancy, however, were not affected by *C. coccodes* and bentazon, but the time of capsule maturity was positively correlated with seed germination. The cumulative effects of all these parameters were determined by using the desirability function. The desirability values *(D)* were positively correlated with the adverse effects of *C. coccodes*, bentazon, and soybean interspecific competition which reduced *A. theophrasti* growth and reproduction. High *D* values (>0.6)

were obtained for *A. theophrasti* grown under stress conditions exhibited by *C. coccodes*, bentazon, and soybean interspecific competition. However, sprayed *A. theophrasti* in monospecific stands did not show higher D values as compared with non-sprayed *A. theophrasti* grown in competition with soybean. This is the first report of using the desirability function method for the estimation of fitness in plants.

6.2. Introduction

The fitness of plants depends upon their survival, growth, and fecundity. These factors determine the relative contribution of a plant to future generations in the gene pool of a population (Clay 1990). The biotic and abiotic factors surrounding a plant's microenvironment, including competition, level of herbivory, and infection by pathogenic microorganism influence plant fitness (Clay 1990). The effects of herbivory and pathogens on plant fitness are more pronounced in annuals as compared with perennials. Perennials can compensate for damage due to defoliation by compromising between reproductive and vegetative output. In the case of annuals, they must reduce their reproductive output to compensate for the defoliation. For example, Koptur *et al.* (1998) reported that defoliation significantly reduced the number of pods, number of seeds, total seed mass, and individual seed weight in *Vicia sativa*. Germination and dormancy of these seeds however, was not affected by the defoliation. Similarly, the reproductive output of *Senecio vulgaris* was reduced by 60% due to a rust infection caused by *Puccinia lagenophorae* when compared with the non-sprayed plants (Paul and Ayres 1986). Seed weight and seed viability, however, were not affected by the rust infection. Similar results were obtained when *Senecio vulgaris* was infected by *Verticillium albo-*

altrum (Matta and Kerling 1964) and by *Erysiphe fischeri* (Ben-Kalio and Clarke 1979). In contrast, the reproductive output and mean seed weight in *Plantago aristata* were not reduced by defoliation since the bracts surrounding the flowers compensated for the damage (Horton and Lacey 1994).

To understand plant fitness, the potential to allocate resources between biomass and reproduction is important. Therefore, the combination of reproductive parameters along with vegetative parameters such as plant height, aboveground biomass, and stem diameter may be helpful to quantify the fitness of a plant under stress conditions. For this purpose, Harrington's (1965) desirability function, which was initially used as a quality control procedure, may have utility in combing these parameters. Thus, the application of the desirability function may be helpful in understanding plant fitness under stress conditions.

To examine the effects of different stresses on the fitness of a plant, a host-pathogen interaction was studied in a cropping system. Velvetleaf (*Abutilon theophrasti* Medic.) is a major weed of corn and soybean crops in Canada and the United States (Spencer 1984, Warwick and Black 1988). *A. theophrasti* is a strong competitor for light and generally overtops most crops. Most of the leaves of *A. theophrasti* are concentrated in the upper portion of the stems, while the lower leaves are readily abscised.

Colletotrichum coccodes (Wallr.) Hughes is a foliar fungal pathogen, which selectively infects *A. theophrasti* and causes gray-brown foliar lesions. The lesions become necrotic, the infected leaves desiccated prematurely and then abscise. When *C. coccodes* was applied at the cotyledon stage, *A. theophrasti* was killed (Wymore *et al.* 1988). When *C. coccodes* was applied at later stages, the infected leaves abscised and the plants continued to grow. The disease caused by *C. coccodes* significantly reduces the growth and competitive ability of *A. theophrasti* in soybean, resulting in lower reproductive output (DiTommaso *et al.* 1996).

The specific objectives in this study were: 1) to determine the effect of intraspecific and soybean interspecific competition on *A. theophrasti* reproductive parameters using the desirability function; 2) to determine if these effects were modified by *C. coccodes* and the herbicide bentazon; and 3) to examine the relationship of these factors on *A. theophrasti* fitness. Based on the results of previous work (Baloch *et al.* 2001), it is hypothesized that the disease caused by *C. coccodes* and bentazon would drastically reduced *A. theophrasti* fitness when grown in competition with soybean. Furthermore, disease severity would be intensified on *A. theophrasti* plants when competing with soybean because the crop canopy would provide a microenvironment for increased infection, resulting in a lower fitness of *A. theophrasti*.

6.3. Materials and Methods

6.3.1. Study site, 6.3.2. Experimental design, 6.3.3. Establishment of planting densities, and 6.3.4. Inoculum and herbicide application were the same as described in section 4.31-4.3.4.

6.3.5. Harvest procedures. Throughout the fruit maturation period, capsules (black in colour) from each tagged *A. theophrasti* plant were hand harvested. Capsules were collected on a weekly basis with five to seven visits per year depending upon the weather conditions. All mature capsules were air-dried at room temperature for three weeks and then weighed. The number of capsules, capsule weight, seed number, and seed weight were determined. Seeds from each plant were placed in 9-cm diameter plastic Petri dishes containing 8 ml of distilled water. Seeds were incubated at 4°C in the dark for one week, followed by 20/14°C for 14/10h day/night for three weeks for the germination and dormancy tests. The single tagged *A. theophrasti* plants were harvested at 118 days after seeding. At harvest, the main stem diameter (between cotyledon and first pair of true leaves), the height from the cotyledonary node to the apical meristem, and the aboveground biomass were recorded.

6.3.6. Statistical analyses. The number of capsules per plant, the number of seeds per plant, and the capsule weight per plant were analyzed for each plant. The analysis of variance (ANOVA) procedure was modified in order to take into account the potential of the temporal repeated measures of reproductive parameters (Dutilleul 1998). The model used for the modified univariate ANOVA was derived by adding time effects plus all interactions to the terms of the standard ANOVA model and using the MANOVA and REPEATED of the GLM procedure of SAS version 6.12 (SAS 1990) followed Moser and Saxton (1990) and Dutilleul (1998). Changes in mean seed weight in time were fitted linear functions of the form

$$Y = b_0 + b_1 X$$

where Y was the mean seed weight and X represented the days after seeding, b_0 and b_1 being regression coefficients.

6.3.7. Desirability Function. Based on Harrington's (1965) desirability function (*D*), a general assessment of *A. theophrasti* fitness was constructed. The measured responses of plant height, stem diameter, aboveground biomass, seed weight, and seed viability were combined into one desirability value. The basis for constructing a desirability function is to convert all of these important fitness parameters of *A. theophrasti* into a dimensionless desirability scale (d_k). The d_k ranges from 0 to 1; a d_k value of 0 corresponds to the absence of influence of the studied parameter and conversely a d_k value of 1 corresponds to the maximum influence of the studied parameter on the fitness of *A. theophrasti*. In this study all vegetative and reproductive parameters together produced a d_k weight of 0.9 based on their influences on the fitness of *A. theophrasti*. An overall D is defined as a geometric combination of the desirability d_k of each response variable and calculated from the individual values according to the following formula defined by Larré *et al.* (1997):

$$D = \sqrt[\sum_{j=1}^{n} a_j]{\prod_{j=1}^{n} da_j j}$$

where, d are the dimensionless desirability that ranges from 0 to 1 and the corresponding weight α ranges from 0 to 1 based on importance of a parameter. The uncertainty associated with the desirability function as a generalized index was assessed by using the bootstrapping method for the estimation of the variance and standard error along with the 95% confidence interval by using 1000 iterations of the corresponding parameters. The desirability function and bootstrapping method were calculated by using a computer program written in BASIC (Miron Teshler, personal communication).

6.4. Results

6.4.1. Effects of *C. coccodes* and bentazon on *A. theophrasti* capsule production. The seed size differences in *A. theophrasti* did not have significant effects on capsule number, capsule weight, and seed number per capsule in 1997, 1998, and 1999 (Table 6.1).

Similarly, the split application of *C. coccodes* and bentazon did not affect capsule production in the monospecific stands of *A. theophrasti* in any of the three growing-seasons. In monospecific stands, the effects of *C. coccodes* and bentazon were not evident 26 days after spraying since the affected leaves had dropped, and *A. theophrasti* continued to grow (data not shown). However, the soybean interspecific competition drastically reduced capsule production (over 60%) in two out of the three growing-seasons (Fig. 6.1). The results of the repeated measure ANOVA suggested that the presence of soybean significantly ($P<0.001$) reduced the capsule production per plant in 1997, 1998, and 1999, (Table 6.1). Similarly, capsule weight and seed number were significantly ($P<0.05$) reduced due to the soybean interspecific competition in 1997, 1998, and 1999 (Table 6.1). Environmental conditions also affected capsule production in *A. theophrasti*. For example, the prolonged dry weather in 1997 did not only enhance capsule production due to early maturing of capsules, but also decreased the efficacy of *C. coccodes*, resulting in a higher reproductive output (Fig. 6.1). The growing season started earlier in 1998 due to the mild winter, but the prolonged wet summer of 1998 enhanced the efficacy of *C. coccodes*, resulting in higher disease level and a delay in capsule production of *A. theophrasti* in 1998 as compared with 1997 and 1999 (Fig. 6.1). The inconsistency in capsule production was the main reason for the significant temporal effect ($P< 0.01$) on the reproductive output across the three growing seasons (Table 6.1). In 1997 and 1998 the significant interaction ($P<0.05$) between the Time factor and soybean competition was the result of the architectural differences between *A. theophrasti* and soybean. The soybean canopy over topped *A. theophrasti* resulting in delayed capsule production.

6.4.2. Effects of *C. coccodes* and bentazon on mean seed weight of *A. theophrasti.* The split application of *C. coccodes* and bentazon and soybean interspecific competition drastically reduced the mean seed of *A. theophrasti* plants over time in three growing seasons (Table 6.2 and Figs. 6.2-6.4). The slopes (b_1) of the linear functions fitted on the linear phase of mean seed weight against days after seeding is presented in Table 6.2 and Figs. 6.2-6.4. There was a relatively decrease in the slopes (mean seed weights per days after seeding) for sprayed *A. theophrasti* plants grown in competition with soybean in three growing seasons (Table 6.2). Significantly higher r^2 (>0.90) values were obtained for different treatments (Table 6.2).

6.4.3. Effects of *C. coccodes* and bentazon on *A. theophrasti* using the desirability function (*D*). The application of the desirability function (*D*) explained the overall effects of *C. coccodes* and bentazon on both the vegetative and the reproductive outputs of *A. theophrasti* plants when grown in the presence or in the absence of soybean. The effects of *C. coccodes* and bentazon on *A. theophrasti* height and aboveground biomass strongly influenced the reproductive output. In monospecific stands, the negative affects caused by the fungal pathogen and the herbicide were compensated by *A. theophrasti*. However, seed weight and seed viability were not influenced by these factors, but depended upon the floral position (data not shown). The *D* values were higher in 1998 and 1999 (0.61 and 0.63, respectively) as compared with 1997 (0.18) (Tables 6.3 to 6.5). The application of *C. coccodes* and bentazon and the interspecific competition with soybean severely affected both the vegetative and reproductive parameters of *A. theophrasti* resulting in considerably higher *D* values in 1998 and 1999 as compared with 1997. Soybean interspecific competition had similar impacts on the vegetative and reproductive parameters of non-sprayed *A. theophrasti* resulting in a *D* value of 0.56 in 1998 (Table 6.4). The maximum *D* value (0.39) for *C. coccodes* sprayed *A. theophrasti* plants in monospecific stands was observed in 1998. In general, *D* values were lower when *C. coccodes* and bentazon were applied on monospecific stands of *A. theophrasti* (0.15 and 0.10, for 1998 and 1999 respectively). Due to the broad ranges of *CI* values for *D*, it was difficult to estimate any differences between treatments. The *D* values showed similar trends among treatments when different weights were assigned to the growth and reproductive parameters (Appendices Tables 1 to 15).

6.5. Discussion

This study showed that the application of the desirability function were helpful means to determine *A. theophrasti* fitness in a competitive environment. Results also showed that *A. theophrasti* fitness was not affected by the application of *C. coccodes* and bentazon in monospecific stands. However, the application of *C. coccodes* alone was more effective than with the split application of *C. coccodes* and bentazon on *A. theophrasti* reproductive output when grown in monospecific stands. This might be due to the negative effects of *C. coccodes* on *A. theophrasti* growth and reproduction which have resulted into a comparatively lower reproductive and higher desirability values of *A. theophrasti* than with the split application of the pathogen and the herbicide. The presence of soybean played a vital role on the fitness of *A. theophrasti*. The results of a previous study indicated that the architectural differences between soybean and *A. theophrasti* were more important for the determination of hierarchy differences than plant density alone (DiTommaso and Watson 1997). Similarly, these structural differences between soybean and *A. theophrasti* also influenced *A. theophrasti* fitness based on reproduction.

The integration of all these biological parameters suggested that the split application of *C. coccodes* and bentazon influenced primarily the fitness of *A. theophrasti* when grown in soybean interspecific competition. Similar results were reported by Lee and Bazzaz (1981) when *A. theophrasti* was artificially defoliated. At a low density in monospecific stands, the reproductive output of *A. theophrasti* was not affected by the 75% defoliation, however at a higher density, the defoliation drastically reduced the reproductive output and the above ground biomass (Lee and Bazzaz 1981). Similarly, Paul and Ayres (1986) reported that the infection by *Puccinia lagenophorae* reduced the seed production of *Senecio vulgaris* by 60% as compared with the non-sprayed plants, and the infected plants were more vulnerable when grown under interspecific competition with *Trifolium subterraneum*.

The application of *C. coccodes* alone, the split application of *C. coccodes* and bentazon, and soybean interspecific competition reduced the seed set in *A. theophrasti* plants. However, the seeds collected from both sprayed and non-sprayed *A. theophrasti* plants had a high viability (>90 %). In contrast, De Clerk-Floate (1999) reported that the powdery mildew fungus, *Erysiphe cynoglossi* had a negative impact on the growth and reproduction of *Cynoglossum officinale* and seed viability was reduced up to 65% in seeds from sprayed plants. The results of this study suggest that the time of *A. theophrasti* capsule maturation have a significant effect on seed size. The early-maturing capsules typically produced heavier seeds than late-maturing capsules. Application of *C. coccodes* and bentazon and soybean interspecific competition drastically reduced mean seed of *A. theophrasti* plants as compared with not sprayed one.

The high *D* (>0.6) of the sprayed *A. theophrasti* grown in soybean, showed the strong influence of stress in 1998 and 1999. The *D* value was helpful to predict the survival rate of *A. theophrasti* in the cropping system. The higher *D* under stress conditions does not, however, appear to reflected the overall fitness in *A. theophrasti* since a single escaped plant from weed management practices has the potential to produced enough seeds to ensured the persistence of *A. theophrasti* into the next generation. In addition to vegetative and reproductive parameters, other important factors such as soil seed bank, soil depth, soil microorganisms, soil temperature, and cultural practices might aid in the estimation of *A. theophrasti* fitness using the *D*. Despite these limitations, the desirability function is a good approach for the estimation of plant fitness in a competitive environment as the desirability function combines several integrated variables into a single value.

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Table 6.1 Probability values from the ANOVA table for the effect of seed size, *Colletotrichum coccodes* and the herbicide, bentazon (weed control treatment) and soybeans interspecific competition on *Abutilon theophrasti* reproductive output.

Source	1997			1998			1999		
	Capsule number per plant	Capsule weight per plant	Seed number per plant	Capsule number per plant	Capsule weight per plant	Seed number per plant	Capsule number per plant	Capsule weight per plant	Seed number per plant
Between subject effects									
Block	0.9373	0.8696	0.8143	0.3611	0.0572	0.0437	0.0753	0.1891	0.2412
Seed size	0.2900	0.2361	0.2700	0.5584	0.2533	0.3758	0.7127	0.6659	0.9258
Competition	0.0009	0.0011	0.4257	0.0001	0.0001	0.0001	0.001	0.0084	0.0046
Weed control treatment (Trt)	0.3168	0.2381	0.4257	0.9382	0.7535	0.7594	0.1775	0.6659	0.1609
Within subject effects									
Time	0.0001	0.0001	0.0001	0.1180	0.0307	0.1256	0.0450	0.0173	0.0159
Time x Seed size	0.0025	0.0048	0.0065	0.9047	0.3516	0.2969	0.1809	0.4352	0.2608
Time x Competition	0.0001	0.0011	0.0004	0.0006	0.0001	0.0001	0.2762	0.4626	0.4489
Time x Trt	0.0448	0.2547	0.0515	0.2913	0.3178	0.4972	0.0017	0.0227	0.0011
Time x Block	0.5356	0.7469	0.8313	0.0525	0.001	0.0035	0.9472	0.8380	0.7881

Table 6.2. The slopes (b_l) of linear functions fitted to the linear phase of *Abutilon theophrasti* mean seed weight increase against the number of days in 1997, 1998 and 1999.

Treatment	1997		1998		1999	
	b_l	r^2	b_l	r^2	b_l	r^2
Small seed size						
[†]Cont. Mon.	29.2 ± 2.3[*]	0.96	32.7 ± 1.5	0.99	20.8 ± 1.7	0.98
Cont. Mix.	21.4 ± 2.1	0.95	29.1 ± 2.4	0.97	19.5 ± 2.7	0.96
C.c. Mon.	38.4 ± 0.4	0.99	30.2 ± 1.6	0.98	21.9 ± 1.3	0.99
C.c. Mix.	28.8 ± 2.5	0.96	21.7 ± 0.8	0.99	17.3 ± 2.8	0.94
C.c. b. Mon.	32.2 ± 1.3	0.99	32.3 ± 2.1	0.98	34.5 ± 1.4	0.99
C.c. b. Mix.	27.8 ± 0.9	0.99	15.2 ± 2.3	0.91	21.7 ± 1.7	0.98
Large seed size						
Cont. Mon.	36.1 ± 1.9	0.98	22.9 ± 1.6	0.98	31.5 ± 1.6	0.99
Cont. Mix.	30.5 ± 2.6	0.96	21.4 ± 2.2	0.95	26.1 ± 2.9	0.97
C.c. Mon.	29.7 ± 1.6	0.98	30.3 ± 2.2	0.97	18.9 ± 4.5	0.89
C.c. Mix.	25.6 ± 2.1	0.96	28.9 ± 1.5	0.98	18.9 ± 2.5	0.96
C.c. b. Mon.	27.4 ± 2.3	0.96	35.9 ± 0.5	0.99	26.1 ± 0.5	0.99
C.c. b. Mix.	16.9 ± 1.7	0.95	23.0 ± 1.3	0.98	10.7 ± 3.6	0.81

All b_l values significant ($P < 0.001$), [*]standard error (SE) of coefficient, [†]Cont. = not sprayed, C.c. = sprayed with *Colletotrichum coccodes*, b = sprayed with bentazon, Mon. = *A. theophrasti* in monospecific stands, Mix = *A. theophrasti* in competition with soybean. *A. theophrasti* were separated into two seed size groups, small (<10 mg) and large (>10 mg) prior to seeding in each year.

Table 6.3. The Desirability function (D) for the fitness of *Abutilon theophrasti* as affected by *Colletotrichum coccodes* and bentazon in monospecific stands and in competition with soybean in 1997.

Parameters	weight	Treatment†					
		Ct.Mon	Ct.Mix	C. Mon	C. Mix	C. b.Mon	C. b.Mix
Height	0.9	150.5	150	151	149.5	153.5 (6.7)	136.7
		(12.9)	(4.2)	(15.8)	(5.6)		(12.3)
Diameter	0.9	9.0	10.1	10.7	9.3	10.2	8.5
		(1.1)	(0.5)	(1.9)	(0.6)	(0.2)	(1.4)
Biomass	0.9	16.5	18.2	25.6	22.5	18.9	13.5
		(1.7)	(0.8)	(9.8)	(6.6)	(2.7)	(3.5)
Capsule no.	0.9	28.5	24.8	33.8	25.0	29.3	21.3
		(2.8)	(4.7)	(11.5)	(7.5)	(3.9)	(8.5)
Seed mass	0.9	41.2	41.5	65.3	53.9	56.6	48.3
		(3.5)	(4.7)	(2.4)	(3.3)	(6.6)	(8.1)
Germination	0.9	30.6	10.1	15.6	34.5	28.7	16.6
		(7.2)	(6.1)	(6.2)	(6.7)	(7.5)	(6.0)
Dormancy	0.9	69.4	89.9	84.5	65.5	71.3	83.4
		(7.2)	(6.1)	(6.2)	(6.7)	(7.5)	(6.0)
Desirability function	---	0.13	0.09	0.05	0.14	0.11	0.18
CI‡ (lower)		0.1	0.1	0.01	0.05	0.07	0.08
(upper)		0.23	0.13	0.1	0.24	0.12	0.22

† Ct = not sprayed, C = sprayed with *Colletotrichum coccodes*, b = treated with the herbicide, bentazon Mon = monospecific stands, Mix.= competition with soybean, CI = Confidence interval. Data of two seed size classes were pooled.

Number in parenthesis indicates standard error

Table 6.4. The Desirability function (D) for the fitness of *Abutilon theophrasti* as affected by *Colletotrichum coccodes* and bentazon in monospecific stands and in competition with soybean in 1998.

Parameters	weight	Treatment†					
		Ct.Mon	Ct.Mix	C. Mon	C. Mix	C. b.Mon	C. b.Mix
Height	0.9	153.7 (10.3) †	104.5 (19.1)	137.5 (9.1)	116.0 (20.0)	154.0 (14.3)	100.5 (16.8)
Diameter	0.9	8.6 (0.9)	5.2 (0.7)	7.8 (0.9)	5.2 (0.9)	9.0 (1.3)	4.5 (0.7)
Biomass	0.9	17.4 (4.4)	6.5 (1.7)	10.1 (2.5)	8.4 (2.5)	18.3 (5.6)	5.5 (1.5)
Capsule no.	0.9	17.0 (4.3)	6.8 (1.2)	12.0 (3.6)	6.5 (2.5)	20.5 (6.9)	4.1 (1.1)
Seed mass	0.9	51.4 (4.2)	34.6 (5.9)	44.8 (3.9)	26.6 (10.5)	47.4 (2.3)	16.6 (5.8)
Germination	0.9	3.2 (1.9)	23.6 (10.2)	0.4 (0.36)	1.2 (24.6)	7.1 (3.6)	26.0 (24.6)
Dormancy	0.9	76.9 (1.9)	76.4 (10.2)	99.6 (3.6)	73.8 (3.6)	92.9 (3.6)	74.1 (0.4)
Desirability function	---	0.18	0.56	0.38	0.58	0.15	0.61
CI‡ (lower)		0.11	0.33	0.17	0.27	0.10	0.37
(upper)		0.24	0.74	0.49	0.78	0.29	0.79

† Ct = not sprayed, C = sprayed with *Colletotrichum coccodes*, b = treated with the herbicide, bentazon Mon = monospecific stands, Mix = competition with soybean, CI = Confidence interval. Data of two seed size classes were pooled.

Number in parenthesis indicates standard error

Table 6.5. The Desirability function (D) for the fitness of *Abutilon theophrasti* as affected by *Colletotrichum coccodes* and bentazon in monospecific stands and in competition with soybean in 1999.

Parameters	weight	Treatment†					
		Ct.Mon	Ct. Mix	C. Mon	C. Mix	C. b.Mon	C. b.Mix
Height	0.9	136	121	134	125	152	110
		(9.6) †	(9.4)	(10.3)	(7.3)	(10.4)	(19.5)
Diameter	0.9	9.4	6.9	8.8	7.6	11.5	6.3
		(1.7)	(0.5)	(0.8)	(0.4)	(1.7)	(1.6)
Biomass	0.9	15.2	0.9	12.0	11.7	24.8	9.6
		(5.3)	(1.9)	(2.8)	(1.6)	(8.6)	(4.2)
Capsule no.	0.9	15.3	9.0	12.3	7.3	14.5	7.0
		(4.9)	(3.7)	(2.8)	(1.1)	(2.4)	(2.7)
Seed mass	0.9	25.5	21.7	25.7	17.3	32.8	19.2
		(4.6)	(7.9)	(2.3)	(4.3)	(2.3)	(7.2)
Germination	0.9	39.1	25.0	48.7	42.0	56.7	44.6
		(2.5)	(8.7)	(6.5)	(14.1)	(8.2)	(20.8)
Dormancy	0.9	80.5	75.7	60.5	42.2	57.7	45.6
		(2.5)	(8.7)	(6.5)	(14.1)	(8.2)	(20.8)
Desirability function	------	0.16	0.35	0.19	0.39	0.10	0.62
CI‡ (lower)	-----	0.16	0.30	0.21	0.30	0.10	0.30
(upper)	------	0.38	0.50	0.33	0.50	0.23	0.79

† Ct = not sprayed, C = sprayed with *Colletotrichum coccodes*, b = treated with the herbicide, bentazon Mon = monospecific stands, Mix = competition with soybean, CI = Confidence interval. Data of two seed size classes were pooled.

Number in parenthesis indicates standard error

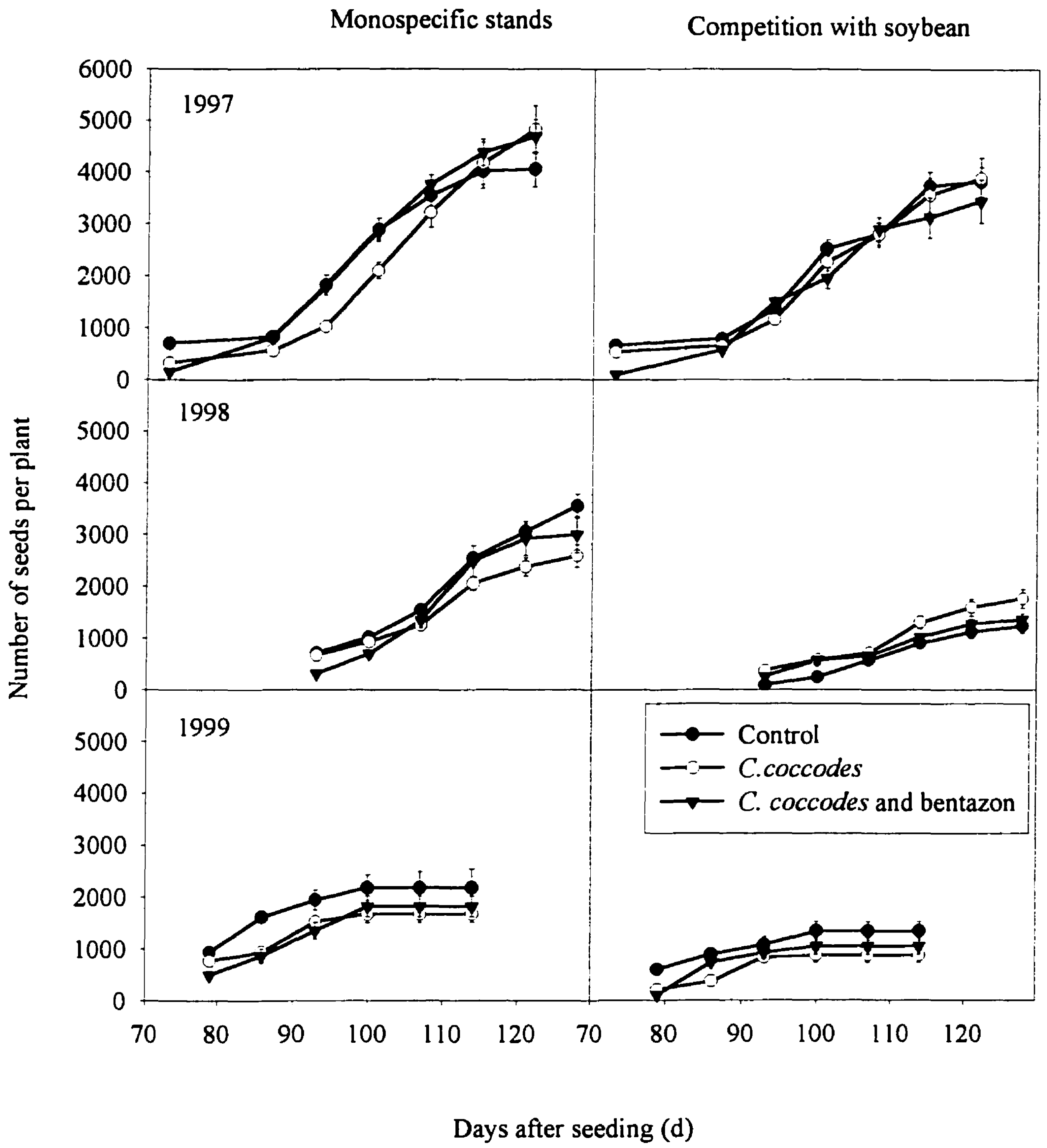

Figure 6.1. The effects of *Colletotrichum coccodes* and bentazon on the cumulative number of *A. theophrasti* seed (± SE) in monospecific stands and in competition with soybean over three growing seasons.

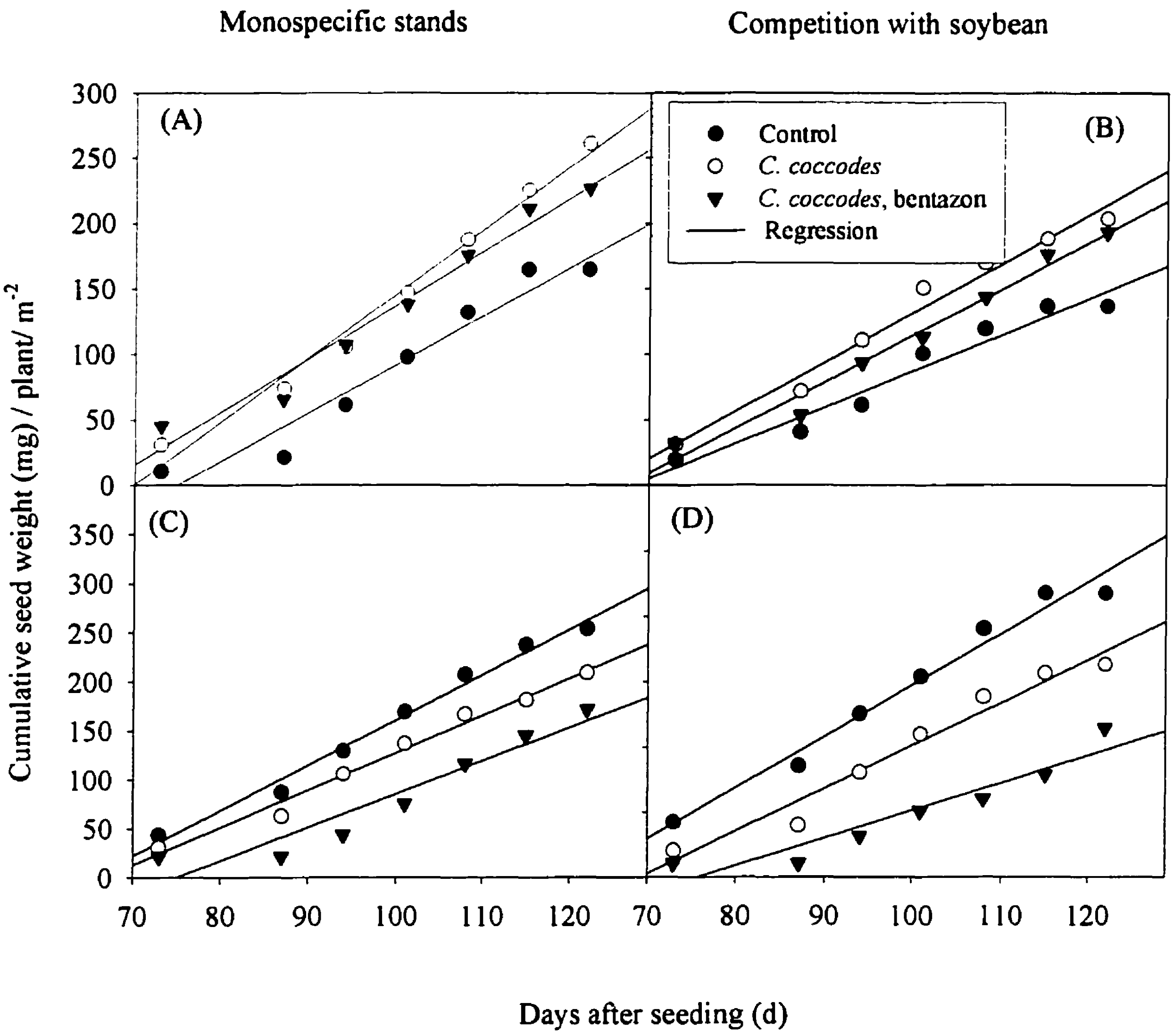

Figure 6.2. The effects of *Colletotrichum coccodes* and bentazon on mean seed weight of *Abutilon theophrasti* originated from small (A and B) and large (C and D) seed size groups grown in monospecific stands and in competition with soybean in 1997.

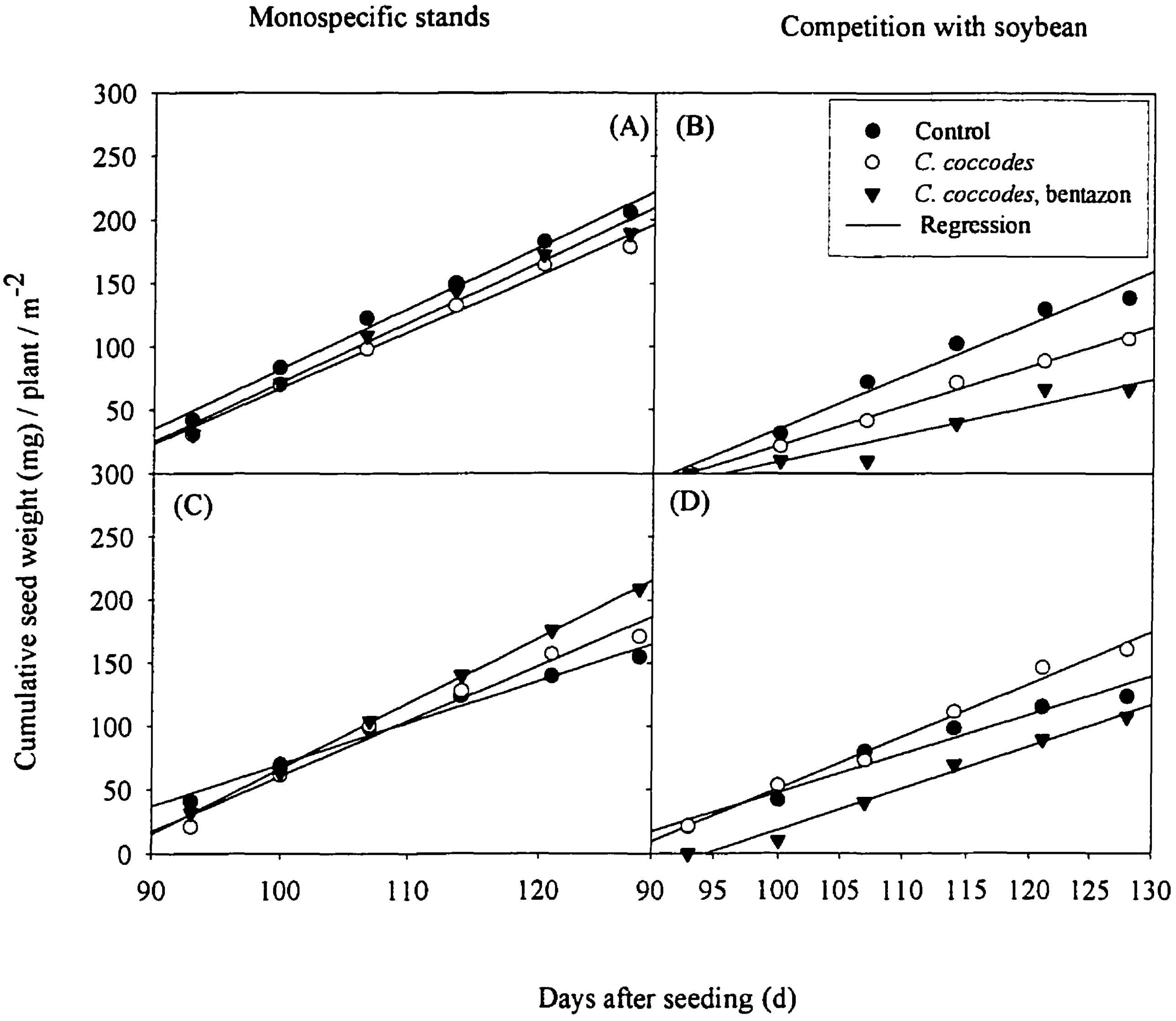

Figure 6.3. The effects of *Colletotrichum coccodes* and bentazon on mean seed weight of *Abutilon theophrasti* originated from small (A and B) and large (C and D) seed size groups grown in monospecific stands and in competition with soybean in 1998.

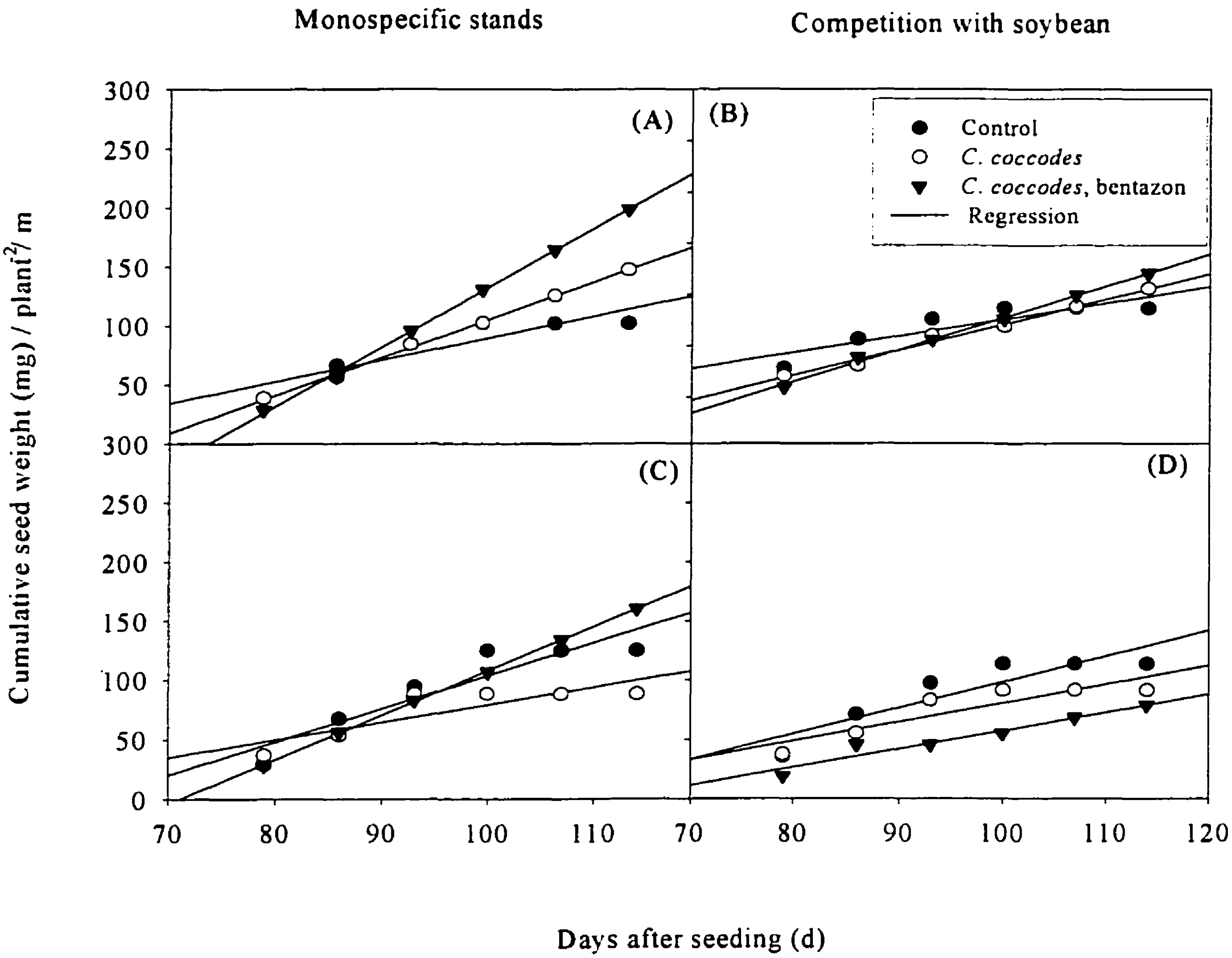

Figure 6.4. The effects of *Colletotrichum coccodes* and bentazon on mean seed weight of *Abutilon theophrasti* originated from small (A and B) and large (C and D) seed size groups grown in monospecific stands and in competition with soybean in 1999.

Connecting Text

In chapter 6, the reproductive output of *A. theophrasti* was significantly reduced by interspecific competition with soybean, however the impact of the competition on soybean grain yield was not considered.

In this chapter, the effect of seed size and biotic and chemical stresses and soybean interspecific competition on the reproductive output of soybean and *A. theophrasti* are examined.

Chapter 7

Effect of seed size and the fungal pathogen *Colletotrichum coccodes* infection on velvetleaf (*Abutilon theophrasti*)–soybean competition in the field

7.1. Abstract

The competitive ability of velvetleaf (*Abutilon theophrasti* Medic.) was evaluated in a soybean cropping system in 1997, 1998, and 1999. *A. theophrasti* was planted at a density of 100 m^2 alone, and in competition with soybean with 40 cm in 1997 and 20 and 40 cm row spacing in 1998 and 1999. The fungal pathogen *Colletotrichum coccodes* (Wallr.) Hughes, and a reduced rate of the herbicide, bentazon, were applied alone and as a split application on *A. theophrasti* at the 2- to 3-leaf stage. Seed size did not affect emergence or competitive ability of *A. theophrasti* in both pure stand and soybean mixture plots. Interspecific competition between *A. theophrasti* and soybean had a deleterious effect on *A. theophrasti* and soybean reproduction. *C. coccodes* and bentazon alone or in combination did not have a significant impact on *A. theophrasti* reproductive yield when grown in monospecific stands. However, when *A. theophrasti* was grown with soybean, *C. coccodes* and bentazon significantly reduced reproduction in this weed. The complex architecture of soybean significantly reduced the level of photosynthetically active solar radiation (PAR) reaching *A. theophrasti* plants and resulted in a trade-off between reproductive and vegetative biomass allocation when *A. theophrasti* was shaded by soybean. The number of *A. theophrasti* capsules was drastically reduced (60%) when *A. theophrasti* was grown in mixture with soybean as compared with monospecific

stands, however the number of seeds per capsule and weight per capsule were not affected.

7.2. Introduction

Competition is a major factor determining the composition and structure of plant communities in both natural and disturbed habitats (Pfleeger *et al.* 1999). In natural environments, plant communities generally exhibit relatively stable plant species associations and interactions. In annual crop production systems, however, plant communities are unstable with weeds and crops competing for shared resources during a relatively short growing period (Radosevich *et al* 1997). It is generally recognized that under competitive conditions weeds typically show greater plasticity in the allocation of resources to either growth or reproductive structures than crops (Lindquist *et al* 1995, Mabry and Wayne 1997, Sugiyama and Bazzaz 1997). Resource allocation to growth and reproductive structures in weedy species is affected by several factors including density and herbivory (Lee and Bazzaz 1981), plant pathogens (Charudattan 1991), and the competitive ability of crops (Lindquist *et al* 1995). Herbivory has an adverse effect on the longevity of undamaged leaves and causes major shifts in the allocation of stored carbohydrate reserves from roots to shoots. Stafford (1989) reported that *A. theophrasti* plants grown at low population densities were able to compensate for defoliation such that net reproductive output remained unchanged. At high planting densities however, severe defoliation resulted in substantial decreases in *A. theophrasti* reproductive output (Lee and Bazzaz 1981).

The negative impact of weeds on crops can be alleviated by altering crop row spacing (Lindquist and Mortensen 1998). The use of narrow row spacing (19 cm) in soybean increases the interception of incoming photosynthetic photon flux (PPF). Similarly, the canopy architecture of soybean is effective in shading weeds and reducing growth and reproductive output (Board *et al.* 1992).

Chemical herbicides are a major component of current weed control strategies in many cropping systems of the world. Unfortunately over the last 15 years, the benefits of herbicides have often been offset by the increased prevalence of difficult to control herbicide-tolerant weed species because of the continuous use of herbicides having similar modes of action (Lindquist *et al* 1995, Heap 2001).

Various fungal plant pathogens are known to have negative effects on the growth and reproduction of weeds. Several selective pathogens of troublesome weeds have been successfully used for their control in crop production systems (Charuddattan 1991, TeBeest 1996).

The integration of an agrochemical and of a selective fungal pathogen was tested in an *Abutilon theophrasti*-soybean cropping system during the 1997, 1998, and 1999 growing season. *A. theophrasti* plants were subjected to a split application of the fungal pathogen *Colletotrichum coccodes*, and the herbicide, bentazon in a soybean crop within a 40 cm crop row spacing. *C. coccodes* is a selective fungal pathogen that causes gray brown foliar lesions on *A. theophrasti*. Application of spore suspensions of this fungal pathogen can kill plants when applied at the cotyledon or 1-leaf stage but causes extensive necrosis and premature leaf senescence when applied at later growth stages of the weed. DiTommaso *et al.* (1996) reported reduced growth and competitive ability of *A.*

theophrasti in mixture plots with soybean when *C. coccodes* was applied at the 2- to -3 leaf stage. The integration of the biological control agent *C. coccodes* that has been shown to reduce the growth and competitive ability of *A. theophrasti*, and reduced rates of the selective herbicide, bentazon should provide more effective control of this troublesome agricultural weed in a soybean cropping system than either tactic used alone. Hence, the specific objectives of this research were: (1) to determine the effects of *A. theophrasti* seed size, *C. coccodes* infection and soybean competition on growth and reproduction of *A. theophrasti*; and (2) to assess whether a split application of *C. coccodes* and bentazon would provide more effective control of *A. theophrasti* in a soybean crop than either treatment used alone.

7.3. Materials and Methods

7.3.1-7. Study site, Experimental design, Establishment of planting densities, Inoculum production inoculum and herbicide application, Disease rating and Environmental data as described in Section 4.3.

7.3.8. Light measurement. The quantity of PAR (photosynthetically active solar radiation, 390-700 nm wavelengths) was measured once in mid-August of 1998 and 1999 under full-sun conditions in each *A. theophrasti* monospecific and soybean mixture plot. Light measurements were taken at the top of the velvetleaf canopy and at ground level using a horizontal quantum sensor (Li-191SB, LI-COR, Inc. Lincoln, Nebraska) and a data logger (Li-Cor 1000, LI-COR, Inc. Lincoln, Nebraska). Two measurements were taken at the canopy, one by inverting the sensor upward and the second by pointing downward towards the soil. Light measurement above the canopy provided a measurement of the total light falling on the canopy and the measurement with the sensor facing downward provided an estimate of light reflected by both the canopy and the soil surface. The light measurement at ground level provided an estimate of the amount of light penetrating the entire canopy. The data collected were used to calculate several radiation parameters for monospecific and soybean mixture plots (Varlet-Grancher *et al.* 1989).

$$PAR_a = PAR_o - PAR_{ts} - PAR_{rsvg} \qquad (1)$$

$$\varepsilon_a = PAR_a / PAR_o \qquad (2)$$

$$PAR_i = PAR_o - PAR_{ts} \qquad (3)$$

$$\varepsilon_i = PAR_i / PAR_o \qquad (4)$$

in which: PAR_a = absorbed radiation; PAR_o = photosynthetic active radiation; PAR_{ts} = radiation transmitted to the soil; PAR_{rsvg} = radiation reflected from soil and vegetation; ε_a = absorption efficiency; PAR_I = intercepted radiation; ε_i = interception efficiency.

7.3.9. Harvest procedure

7.3.9.1. *A. theophrasti.* Throughout the growing season (i.e. from early August onwards), mature *A. theophrasti* capsules (black in colour) from all plants within each 0.25 m^2 subplot were harvested by hand and stored at room temperature (20 ± 1°C). For each plant, the number of capsules per plant, number and weight of seeds per plant, capsule weight per plant, number and weight of seeds per fruit, mean weight per seed, and ratio of seed weight to capsule weight were determined.

7.3.9.2. Final harvest of soybean. Soybean was harvested by hand 120 days after sowing. All soybean plants located along a 1 m transect within each central row were harvested. Each 1 by 2 m plot encompassed three rows for the 40-cm spacing. The total number of pods, seeds per pod, and seed yield per plant for each of the treatment combinations were determined. No vegetative data were collected for soybean.

7.3.10. Statistical analyses. Reproductive data for each year were analyzed using a factorial analysis of variance (ANOVA) (SAS 1990) to determine the effects of seed size, *C. coccodes*, and soybean interspecific competition on the number of *A. theophrasti* capsules/plant, number of seeds/capsule, and seed weight. To correct for heterogeneity of variances, data involving counts (such as number of capsule per plant, number of seeds per plant, and mean number of seeds per fruits) were arcsine square root transformed before analyses (SAS 1990). Simple mean comparisons were made using a GLM protected LSD test at the 0.05 level of probability (SAS 1990).

7.4. Results

7.4.1 Environment. Climatic conditions for the 1997, 1998, and 1999 growing seasons are presented in Figs. 7.1 and 7.2. Total precipitation (from April to September) was greater in 1997 (610.3 mm) compared with 1998 (422.8 mm) and 1999 (518.9 mm). The total rainfall received in 1997 was relatively greater than the 30-year average of 518 mm and was evenly distributed through the growing season (Fig. 7.1). In contrast, the 1998 and 1999 growing seasons showed higher fluctuations in rainfall as compared with 1997. The months of June through August were relatively warmer in 1997 and 1999 than in 1998 (Fig. 7.2).

7.4.2. Relationship between seed size and seedling emergence. The effect of seed size on *A. theophrasti* seedling emergence varied for the monospecific and soybean mixture plots in all three years. Seedling emergence increased with seed size in both monospecific and mixture plots in 1998 and 1999 compared with 1997 (Fig. 7.3). However, overall emergence of *A. theophrasti* seedlings was lower in soybean mixture plots than monospecific plots despite differences in initial seed size in all three years (Fig. 7.3). For both seed size fractions, the average number of days required for seedlings to emerge ranged from 4 days in 1997 and 1999, to 8 days in 1998. In all three years, no *A. theophrasti* seedling emergence was recorded 12 days after seeding (Fig. 7.3).

7.4.3. Effects of seed size and *C. coccodes*/bentazon application on *A. theophrasti* reproduction. The presence of soybean significantly ($P < 0.001$) reduced *A. theophrasti* reproductive output in all three years compared with *A. theophrasti* plants grown in pure stand (Table 7.1 and 7.2). However, initial differences in *A. theophrasti* seed size and inoculation with *C. coccodes* alone or in a split application with bentazon had no effect on *A. theophrasti* reproductive output (Table 7.1). In general, *A. theophrasti* reproductive output was greater in 1997 compared with 1998 and 1999 (Table 7.1).

7.4.4. Effects of seed size and *C. coccodes*/bentazon application on soybean reproduction The interspecific competition between soybean and *A. theophrasti* significantly ($P<0.05$) affected soybean yield in 1998 and 1999 (Table 7.3). Soybean yield was significantly decreased in all three years within mixture plots with *A. theophrasti* compared with plants grown in the absence of the weed (Table 7.3). However, inoculating mixture plots with *C. coccodes* alone or in a split application with bentazon significantly increase soybean yield as compared with non-treated stands in 1999 (Table 7.3).

7.4.5. Relationship between *A. theophrasti* height and light interception. At ground level, the amount of photosynthetically active solar radiation (PAR, 390-700 nm wavelengths) was reduced by up to 98% due to interception of PAR by the canopies of soybean and *A.*

theophrasti plants. In both 1998 and 1999 however, the level of PAR reaching the ground in *A. theophrasti* monospecific plots was greater (13.8 and 12.9%) than the level reaching the ground within soybean mixture plots (< 3 %). Soybean interspecific had no effect on the amount of PAR (3%) reaching the ground in mixture plots. At canopy level, the PAR_a was similar within both monospecific and soybean mixture plots (Table 7.4). However, absorbed efficiency (ε_a) was greater in mixture plots because of higher leaf area and more complex canopy structure that allowed more incoming light to be trapped compared with the relatively scattered canopy orientation *A. theophrasti* plants pure stand plots. Similarly, levels of intercepted radiation (PAR_i) and interception efficiency were relatively greater (> 0.90) in soybean mixture plots than *A. theophrasti* monospecific plots (< 0.82) because of the greater light reflection in mixture plots.

7.5. Discussion

The initial seed size differences in *A. theophrasti* plants did not have a significant impact on the competitive ability of these plants when grown in pure stand or in competition with soybean. This may have been due to the narrow range of differences in seed size fraction (small <9.9 mg and large seed size >10mg) such that reproductive output in *A. theophrasti* plants remained unchanged for these seed size categories. Despite the narrow range of seed size fractions used in the present study, there is general agreement that the initial advantage of a larger seed size in terms of carbohydrate reserves and early emergence does not persist to later plant growth stages (Marshall *et al.* 1985). However, Zhang and Hamill (1997) observed that seed size differences in *A. theophrasti* significantly affected the growth of target plants in a competitive environment with larger-seeded plants experiencing less severe reductions in growth than smaller-seeded plants.

Seed size differences and the split application of *C. coccodes* and bentazon did not affect *A. theophrasti* reproductive output when plants were grown in pure stands. Despite substantial foliar damage and necrosis on *A. theophrasti* plants inoculated with *C. coccodes* and sprayed with bentazon, most plants survived and reproduced particularly in the monospecific plots. Lee and Bazzaz (1981) reported that partial defoliation in *A. theophrasti* did not affect plant performance due to a rapid compensatory response in this species. At low densities, *A. theophrasti* plants were able to compensate for up to 75% of the leaf biomass removed, however at higher densities, severe defoliation caused significant reductions in *A. theophrasti* reproductive output (Lee and Bazzaz 1981). Similarly, Mabry and Wayne (1997) indicated that the compensatory response of *A. theophrasti* following defoliation was influenced by the intensity of competition and type of neighbouring species. These factors might explain the effectiveness of the *C. coccodes* and bentazon applications on *A. theophrasti* when grown in a competitive environment with soybean versus in monospecific stands. When competing with soybean, the reproductive output of *A. theophrasti* plants was significantly reduced compared with plants grown in pure stand likely because of the higher competitive ability of soybean. Munger *et al.* (1987) reported that inter-specific competition between soybean and *A. theophrasti* resulted in a 40-50% reduction in the reproductive output of these plants. However, findings in the present study show that reproductive losses in *A. theophrasti* were greater than for soybean. Despite inconsistent results in *A. theophrasti* reproduction over the three growing seasons, it is clear that density-dependent plasticity was the main reason for lower capsule production in *A. theophrasti* when grown in the presence of soybean. The number of *A. theophrasti* seeds remained constant in both monospecific and soybean mixture plots regardless of the increased overall planting density in mxture plots (i.e. 100 *A. theophrasti* + 35 soybean plants m^{-2}). The lower total density and more uniform architectural structure in *A. theophrasti* pure stand resulted in less intense competitive interactions and increased allocation of resources to reproductive structures. From these findings, it is also clear that space availability played an important role in explaining the reproductive plasticity observed in *A. theophrasti* plants grown in pure stand. In the preceding chapter, it was reported that architectural differences between *A. theophrasti* and soybean canopies resulted in higher reproductive plasticity in *A. theophrasti* plants. In monospecific plots, the availability of more space allowed *A. theophrasti* plants to produce several lateral branches along the central stem with each branch producing an indeterminate number of capsules thus resulting in higher reproductive output (Zanin and Sattin 1987). In contrast to the growth pattern observed in pure stand, *A. theophrasti* plants grown in mixture plots with soybean produced no lateral branching off the central stem presumably because of more intense competitive interactions for shared resources such as light and space pre-emption by the soybean crop. Research by Benvenuti *et al.* (1994) also demonstrated that when *A. theophrasti* plants are subjected to various degrees of shading, reproductive output is drastically reduced because of a decrease in the allocation of resources to reproductive organs. The deleterious effects of inter-specific competition on *A. theophrasti* reproduction appear to be more severe than in pure stand. For instance, DiTommaso *et al.* (1996) reported that the reproductive output of *A. theophrasti* plants grown at monospecific planting densities of 350 plant m^{-2} was similar to that of plants grown at planting densities of 125 plants m^{-2}.

As canopy thickness and complexity of structure in soybean increased at later growth stages, penetration of solar radiation was largely prevented thereby permitting low levels of light to reach the soil surface. Correspondingly, the complex branching pattern and more complete coverage of inter-row spaces by soybean plants resulted in greater light interception levels and absorption efficiency for soybean than *A. theophrasti* plants. In soybean mixture plots, PAR levels at the soil surface were reduced by up to 97% as compared with the 87% reductions found in *A. theophrasti* monospecific plots.

As expected, application of the selective fungal pathogen, *C. coccodes* alone at the 2-to-3 leaf stage of *A. theophrasti* did not effectively control this weed in a soybean cropping system in two out of three growing seasons. However, the split application of a reduced rate of bentazon and *C. coccodes* significantly reduced the competitive ability of *A. theophrasti* when grown in soybean planted at narrow row spacing. Hence, the integration of cultural, biological and chemical strategies could provide effective control of this troublesome agricultural weed in row crops thereby reducing our reliance on herbicides for control *A. theophrasti* in row crops.

7.6. References

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Table 7.1. Effects of *Colletotrichum coccodes* and bentazon on the capsule weight of *Abutilon theophrasti* grown in monospecific stands and in competition with soybean in 1997, 1998, and 1999.

Treatment*	1997	1998	1999
Small seed size		gm^{-2}	
Cont. Mon.	17.3 (±2.1)bc	15.5(±3.8)a	13.1 (±6.3)ab
Cont. Mix.	16.4 (±3.2)bc	4.6 (±1.6)cd	9.9 (±4.5)bc
C. coccodes, Mon.	22.5 (±7.9)bc	11.3(±2.8)ab	11.5 (±3.3)abc
C. coccodes, Mix.	17.6 (±5.5)bc	5.5 (±1.2)bcd	6.9 (±1.4)bc
C. coccodes, b. Mon.	19.3 (±3.4)bc	16.2 (±3.4)a	14.1(±1.8)ab
C. coccodes, b. Mix.	13.1 (±5.1)bc	3.1 (±0.8)cd	5.6 (±1.6)bc
Large seed size			
Cont. Mon.	41.8 (±9.4)a	10.8 (±1.6)abc	14.2 (±4.5)ab
Cont. Mix.	10.1 (±1.8)c	5.4 (±2.3)bcd	8.8 (±3.1)bc
C. coccodes, Mon.	27.42 (±3.4)ab	11.6 (±3.2)ab	7.5 (±0.6)bc
C. coccodes, Mix.	17.4 (±5.1)bc	7.5 (±2.3)bcd	7.3(±2.3)bc
C. coccodes, b. Mon.	22.3 (±4.1)bc	11.2 (±0.8)ab	20.7 (±3.4)a
C. coccodes, b. Mix.	9.9 (±4.3)c	3.5 (±1.4)cd	2.5 (±0.9)c

*Cont. = not sprayed, Mon. = monospecific stands, Mix. = competition with soybean, b = sprayed with bentazon.

Number in parenthesis indicates standard error

Means within a column followed by different letters are significantly different ($P < 0.05$).

Table 7.2. Probability values for the effects of seed size and biotic and chemical weed control treatments on reproductive out put of *Abutilon theophrasti* grown in monospecific stands and in competition with soybean in three growing seasons.

Source	Number of capsules			Weight of capsules			Number of seeds/capsule		
	97	98	99	97	98	99	97	98	99
Competition (C)	0.0004	0.0001	0.0002	0.0004	0.0001	0.1726	0.0004	0.0001	0.0175
Block (B)	0.5958	0.0533	0.0059	0.4992	0.0130	0.1558	0.4904	0.0161	0.1272
Seed size (S)	0.4571	0.7095	0.7438	0.3628	0.9373	0.1076	0.4044	0.9628	0.8209
Weed control treatments (T)	0.2523	0.5610	0.1640	0.2805	0.6263	0.3704	0.3297	0.5453	0.1609

Table 7.3. Reproductive yield of soybean as influenced by *Abutilon theophrasti* interspecific competition and chemical weed control treatments in 1997, 1998, and 1999.

Treatment*	1997	1998	1999
		gm^{-2}	
Weed free	157.6 (±16.8)a	142.5 (±18.7)a	112.9 (±7.3)a
Weedy, Small seed size			
Not sprayed	88.2 (±13.2)b	83.2 (±8.8)c	64.6 (±8.4)b
Sprayed with *C. coccodes*	86.3 (± 2.8)b	101.6 (±21.2)bc	113.9 (±25.2)a
Sprayed with *C. coccodes* and bentazon	85.1 (± 17.2)b	105.8 (±10.2)abc	117.5 (±21.9)a
Weedy, Large seed size			
Not sprayed	84.8 (± 17.2)b	100.1 (±7.1)bc	60.9 (±2.2)b
Sprayed with *C. coccodes*	106.1 (± 7.9)b	101.4 (±3.5)bc	112.2 (±5.5)a
Sprayed with *C. coccodes* and bentazon	118.4 (±18.9)ab	127.7 (±11.5)ab	106.7 (±15.8)a

Number in parenthesis indicates standard error

Means within a column followed by different letters are significantly different ($P < 0.05$)

Table 7.4. Light absorption and light interception (nm) in *Abutilon theophrasti* monospecific stands and in mixed soybean and *A. theophrasti* stands.

Light parameter	Monospecific stands (mean ± se)		Competition with soybean (mean ± se)	
	1998	1999	1998	1999
PAR_a*	1123.9 (34.9)†	1572.9 (113.3)	1131.3 (29.9)	1649.5 (123.5)
ε_a	0.82 (0.02)	0.82 (0.02)	0.93 (0.01)	0.91 (0.01)
PAR_i	1177.8 (36.0)	1708.6 (119.4)	1171.7 (31.6)	1778.9 (133.0)
ε_i	0.86 (0.02)	0.89 (0.02)	0.97 (0.01)	0.98 (0.004)

* PAR_a = absorbed light; ε_a = absorbed efficiency; PAR_I = intercepted radiation; ε_I = interception efficiency,

† number in parenthesis indicates Standard Error,

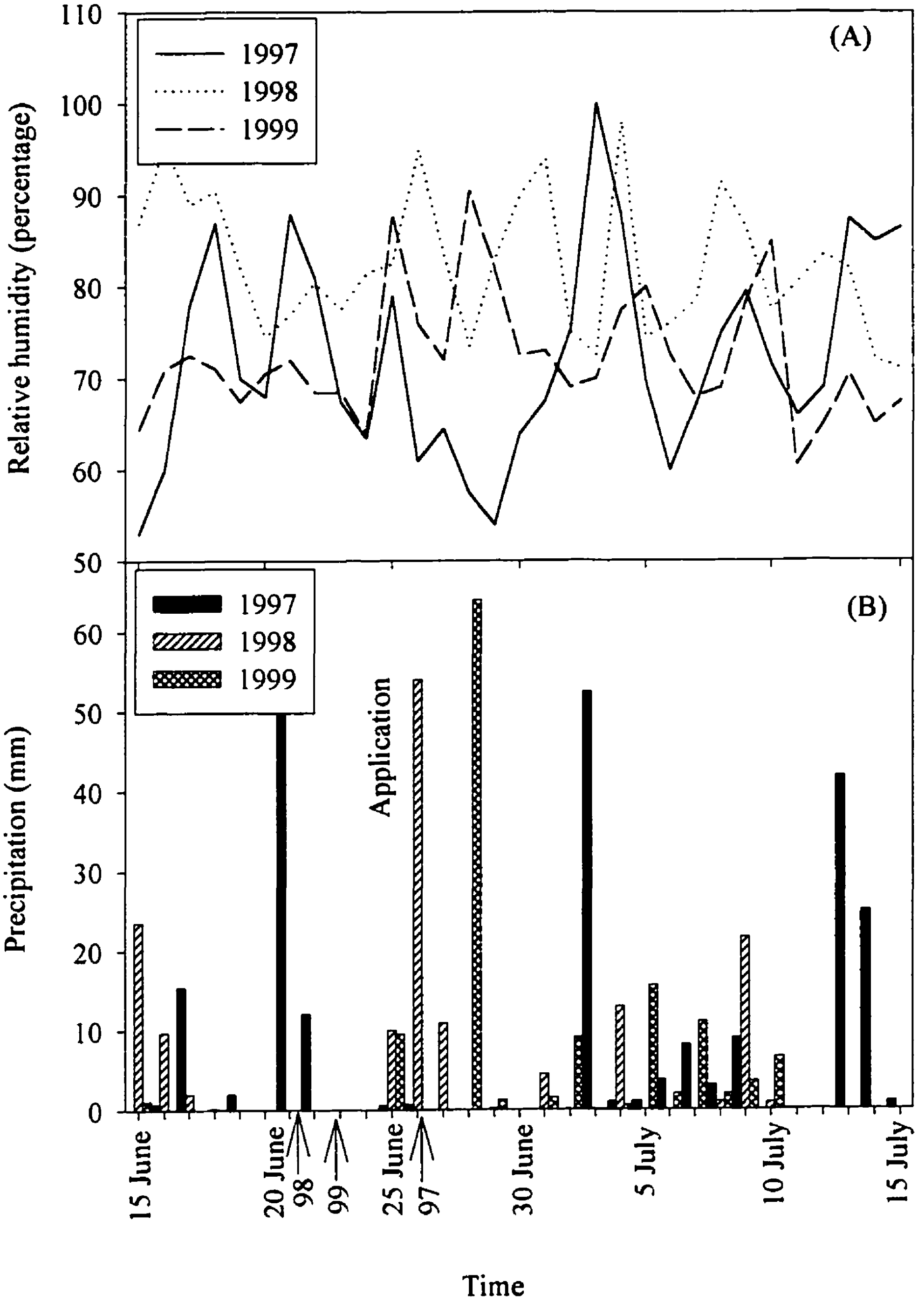


Figure 7.1. Relative humidity (A) and precipitation (B) at the time of *Colletotrichum coocodes* inoculation during 1997, 1998, and 1999 field trials Arrows indicate the application of the *C. coccodes.*

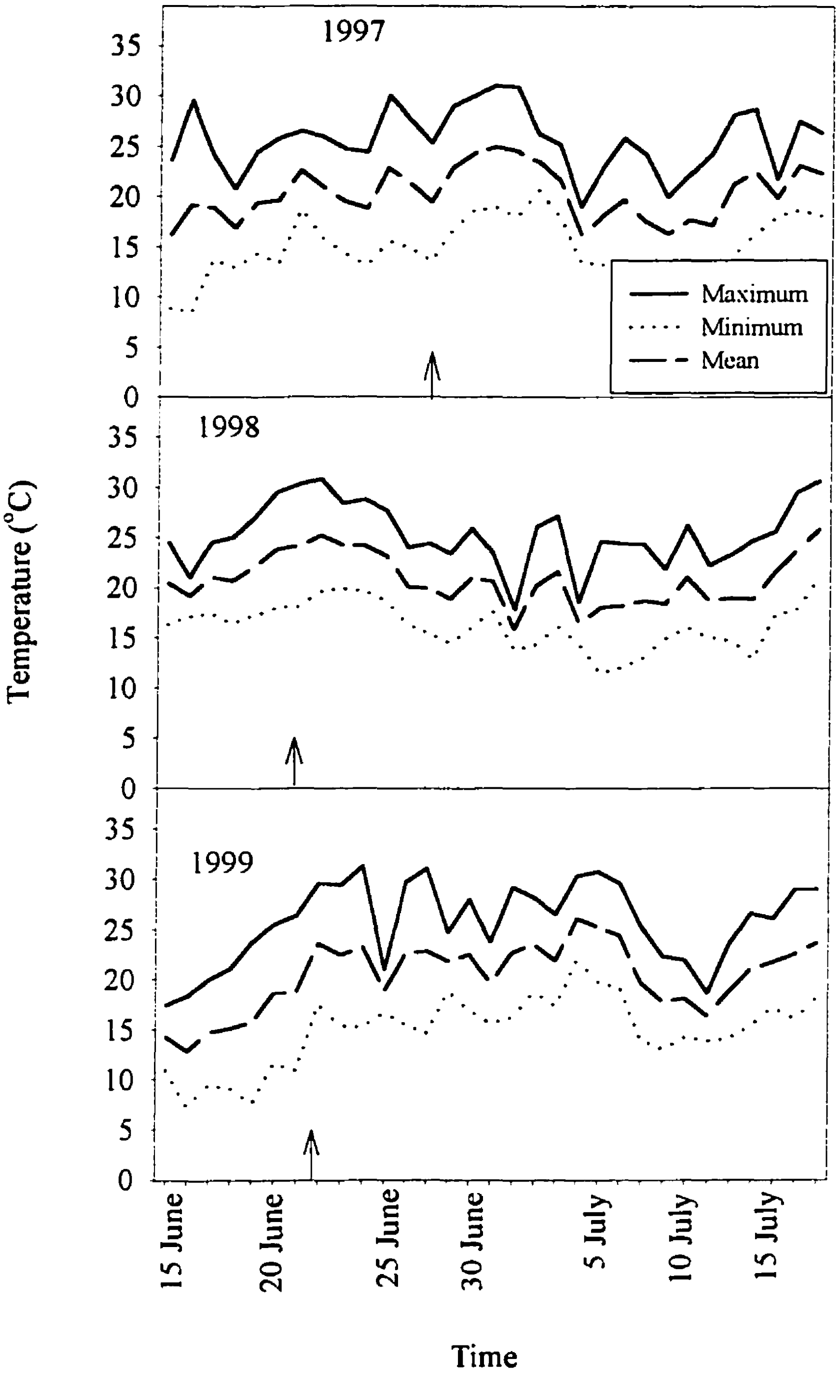
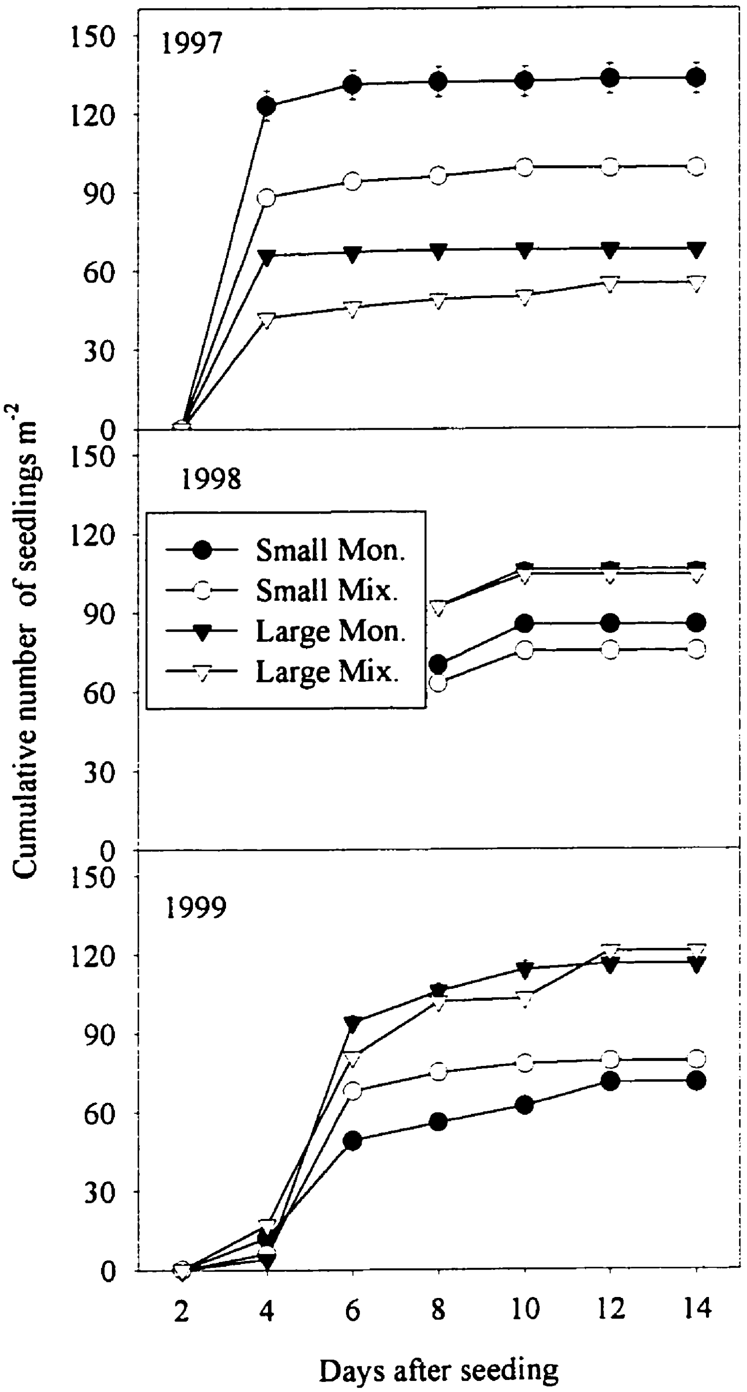


Figure 7.2. Air temperature (solid line: maximum, dotted lines, minimum: dashed, mean) during field trials of 1997, 1998, and 1999. Arrows indicate the application of *Colletotrichum coccodes*.

Figure 7.3. Seedling emergence of *Abutilon theophrasti* during 1997, 1998, and 1999. *A. theophrasti* plants originated from two seed size groups (small and large) grown in monospecific stands and in competition with soybean. Bars extending beyond the symbol denote SE.


1997
1998
1999
Small Mon.
Small Mix.
Large Mon.
Large Mix.
Cumulative number of seedlings m-2
0
30
60
90
120
150
2
4
6
8
10
12
14
Days after seeding

Chapter 8. General Conclusions

The research reported in this thesis examined the effect of seed size and the fungal pathogen, *Colletotrichum coccodes* on growth and reproduction of *Abutilon theophrasti* plants grown under stress environments.

Seed size distribution among ten *Abutilon theophrasti* plants significantly affected the seed germination and dormancy. Seeds from individual *A. theophrasti* plants exhibited a large degree of variation in their germinability (57% to 92%). Seed germination was low for the extreme seed size classes in ten *A. theophrasti* plants. Concomitantly, there was a positive linear relationship between dormancy and seed mass. *A. theophrasti* seeds of less than 7 mg were largely non-viable (96%), although the proportion of non-viable seeds for each *A. theophrasti* plant was very low.

Under field conditions, the intrinsic differences in plant growth due to initial seed size did not affect the growth or reproduction of *A. theophrasti*. Smaller sized seed had an advantage over larger seeds as they emerged earlier and occupied more space than the later emerging larger seeds. Despite the advantage of early emergence of small seed size groups there was no significant differences in *A. theophrasti* growth and reproduction between plants originating from small or large seeds. This may have been due to the small differences in the seed size classes, which were not sufficient to show inequality between these groups. Similarly, under controlled environments, the seed weight advantage of seedlings produced from heavier seeds was no longer apparent 15 days after germination and the differences in parental seed size did not persistent in the offspring in successive generations. However, the results of this study suggest that time of *A. theophrasti* capsule maturation has a significant effect on seed size, with the impact being more pronounced in later generations. The early-maturing capsules typically produced heavier seeds than late-maturing capsules regardless of *C. coccodes* inoculation.

The deleterious effect of *C. coccodes* infection was more pronounced in later generations as compared with the first generation indicating that this selective fungal pathogen did not stimulate transgenerational induced resistance in *A. theophrasti*. The effect of *C. coccodes* on *A. theophrasti* growth was significantly greater in the first month due to the defoliation of inoculated plants thus, resulting in reduced height and stem diameter. However, the indeterminate growth of *A. theophrasti* allowed plants to recover from the damage caused by earlier *C. coccodes* infection.

The distribution of *A. theophrasti* plant height in monospecific stands was negatively skewed (J-shaped) as compared with aboveground biomass and stem diameter, were positively skewed (L-shaped). Higher unbiased Gini values (G') were observed among *A. theophrasti* plants when grown in competition with soybean as compared with monospecific stands. This reflected the intensity of interspecific competition for light among plants that resulted in high inequality among the growth parameters. The application of *C. coccodes* alone and in combination with bentazon did not increase the inequality among the growth parameters of *A. theophrasti* in monospecific stands as compared with sprayed plants competing with soybean. The allometric relationships between *A. theophrasti* height-diameter and height-biomass were curvilinear while biomass-diameter was a strong linear allometric relationship. The application of *C. coccodes* along with bentazon on *A. theophrasti* competing with soybean, exhibited simple linear allometric relationships among height, biomass, and stem diameter in all three growing seasons. The split applications of *C. coccodes* and bentazon on *A.*

theophrasti in a monospecific stands and *C. coccodes* sprayed plants when competing with soybean, showed the curvilinear allometric relationships amongst height, aboveground biomass, and stem diameter in 1997 and 1999. While in 1998, most of the growth parameters exhibited linear allometric distributions.

In this study, *A. theophrasti* fitness was not affected by the application of *C. coccodes* and bentazon in monospecific populations. However, the presence of soybean played a vital role on the fitness of *A. theophrasti*. The cumulative effects of *C. coccodes*, bentazon, and soybean interspecific competition significantly reduced seed set in *A. theophrasti* plants, however, seed viability remained unchanged, when grown in both monospecific stands and in mixture with soybean.

From an agronomic perspective, the results of the present study shows that the reproductive losses in *A. theophrasti* were higher then those of soybean in a mixed stand. Intraspecific competition among *A. theophrasti* plants did not affect their reproductive output as compared with plants grown in competition with soybean. This may be the result of the uniform architectural structure among *A. theophrasti* plants in monospecific stands resulting in reduced competition and greater biomass allocation to reproduction as compared with resource allocation when grown in competition with soybean. The results of this study demonstrated that the application of the fungal pathogen, *C. coccodes* alone at the 2- to 3-leaf stage did not effectively control *A. theophrasti* in a soybean cropping system. However, the split application of a low rate of bentazon and the fungal pathogen significantly reduced the competitive ability of *A. theophrasti* when grown in competition with soybeans.

Chapter 9. Contribution to Knowledge

The following are considered to be key contributions to original knowledge arising from the research described in this thesis:

1. This is the first report of the transgenerational effect of *Colletotrichum coccodes* and seed size on *Abutilon theophrasti* growth and reproductive parameters. The response of *A. theophrasti* to the pathogen did not change over the three generations suggesting that plants did not develop resistance to *C. coccodes* infection.
2. Chapter 4 of this study provides the first detailed presentation of size distributions of *A. theophrasti* plants when grown in monospecific stands and in competition with soybean.
3. This is the first attempt to characterize, in detail, the allometric relationships between plant height, aboveground biomass, and stem diameter of *A. theophrasti* plants.
4. This is the first study to have examined the application of the desirability function method for the estimation of fitness in *A. theophrasti*.
5. This study demonstrated the effectiveness of *C. coccodes* and bentazon to reduce the growth and reproduction of *A. theophrasti* plants when grown in competition with soybean.

Appendices

Table 1.1. The Desirability function (D) for the fitness of *Abutilon theophrasti* as affected by *Colletotrichum coccodes* and bentazon in monospecific stands and in competition with soybean in 1997.

Parameters	weight	Treatment†					
		Ct. Mon	Ct. Mix	C. Mon.	C. Mix.	C. b.Mon.	C. b.Mix.
Height	0.9	150.5	150	151	149.5	153.5	136.7
Diameter	0.9	9.0	10.1	10.7	9.3	10.2	8.5
Biomass	0.9	16.5	18.2	25.6	22.5	18.9	13.5
Capsule no.	0.9	28.5	24.8	33.8	25.0	29.3	21.3
Seed mass	0.9	41.2	41.5	65.3	53.9	56.6	48.3
Dormancy	0.9	69.4	89.9	84.5	65.5	71.3	83.4
D	---	0.18	0.16	0.08	0.15	0.12	0.32
SE		0.03	0.06	0.05	0.05	0.02	0.11
CI (lower)		0.09	0.12	0.02	0.11	0.07	0.31
(upper)		0.19	0.36	0.30	0.30	0.13	0.65

†Ct = not sprayed, C = sprayed with *Colletotrichum coccodes*, b = treated with the herbicide, bentazon, Mon = monospecific stands, Mix = competition with soybean, CI = confidence interval. Data of two seed size classes were pooled. Number in parenthesis indicates standard error.

Table 1.2. The Desirability function (D) for the fitness of *Abutilon theophrasti* as affected by *Colletotrichum coccodes* and bentazon in monospecific stands and in competition with soybean in 1997.

Parameters	weight	Treatment					
		Ct. Mon	Ct. Mix	C. Mon.	C. Mix.	C. b.Mon.	C. b.Mix.
Height	0.9	150.5	150	151	149.5	153.5	136.7
Diameter	0.7	9.0	10.1	10.7	9.3	10.2	8.5
Biomass	0.7	16.5	18.2	25.6	22.5	18.9	13.5
Capsule no.	0.9	28.5	24.8	33.8	25.0	29.3	21.3
Seed mass	0.9	41.2	41.5	65.3	53.9	56.6	48.3
Germination	0.5	30.6	10.1	15.6	34.5	28.7	16.6
Dormancy	0.8	69.4	89.9	84.5	65.5	71.3	83.4
D	---	0.18	0.15	0.06	0.15	0.10	0.26
SE		0.05	0.03	0.03	0.06	0.02	0.10
CI (lower)		0.14	0.09	0.01	0.14	0.06	0.23
(upper)		0.26	0.16	0.19	0.35	0.11	0.59

†Ct = not sprayed, C = sprayed with *Colletotrichum coccodes*, b = treated with the herbicide, bentazon, Mon = monospecific stands, Mix = competition with soybean, CI = confidence interval. Data of two seed size classes were pooled. Number in parenthesis indicates standard error.

Table 1.3. The Desirability function (D) for the fitness of *Abutilon theophrasti* as affected by *Colletotrichum coccodes* and bentazon in monospecific stands and in competition with soybean in 1997.

Parameters	weight	Treatment					
		Ct. Mon	Ct. Mix	C. Mon.	C. Mix.	C. b.Mon.	C. b.Mix.
Height	0.9	150.5	150	151	149.5	153.5	136.7
Diameter	0.7	9.0	10.1	10.7	9.3	10.2	8.5
Biomass	0.7	16.5	18.2	25.6	22.5	18.9	13.5
Capsule no.	0.9	28.5	24.8	33.8	25.0	29.3	21.3
Seed mass	0.9	41.2	41.5	65.3	53.9	56.6	48.3
Dormancy	0.8	69.4	89.9	84.5	65.5	71.3	83.4
D	---	0.20	0.19	0.08	0.17	0.11	0.33
SE		0.04	0.07	0.05	0.06	0.03	0.13
CI (lower)		0.13	0.17	0.05	0.15	0.09	0.31
(upper)		0.23	0.39	0.28	0.33	0.17	0.74

†Ct = not sprayed, C = sprayed with *Colletotrichum coccodes*, b = treated with the herbicide, bentazon, Mon = monospecific stands, Mix = competition with soybean, CI = confidence interval. Data of two seed size classes were pooled. Number in parenthesis indicates standard error.

Table 1.4. The Desirability function (D) for the fitness of *Abutilon theophrasti* as affected by *Colletotrichum coccodes* and bentazon in monospecific stands and in competition with soybean in 1997.

Parameters	weight	Treatment					
		Ct. Mon	Ct. Mix	C. Mon.	C. Mix.	C. b.Mon.	C. b.Mix.
Height	0.7	150.5	150	151	149.5	153.5	136.7
Diameter	0.6	9.0	10.1	10.7	9.3	10.2	8.5
Biomass	0.6	16.5	18.2	25.6	22.5	18.9	13.5
Capsule no.	0.9	28.5	24.8	33.8	25.0	29.3	21.3
Seed mass	0.9	41.2	41.5	65.3	53.9	56.6	48.3
Germination	0.5	30.6	10.1	15.6	34.5	28.7	16.6
Dormancy	0.8	69.4	89.9	84.5	65.5	71.3	83.4
D	---	0.18	0.13	0.05	0.15	0.10	0.25
SE		0.04	0.03	0.03	0.05	0.02	0.06
CI (lower)		0.13	0.10	0.04	0.13	0.07	0.20
(upper)		0.24	0.18	0.16	0.34	0.13	0.37

†Ct = not sprayed, C = sprayed with *Colletotrichum coccodes*, b = treated with the herbicide, bentazon, Mon = monospecific stands, Mix = competition with soybean, CI = confidence interval. Data of two seed size classes were pooled. Number in parenthesis indicates standard error.

Table 1.5. The Desirability function (D) for the fitness of *Abutilon theophrasti* as affected by *Colletotrichum coccodes* and bentazon in monospecific stands and in competition with soybean in 1997.

Parameters	weight	Treatment					
		Ct. Mon	Ct. Mix	C. Mon.	C. Mix.	C. b.Mon.	C. b.Mix.
Height	0.7	150.5	150	151	149.5	153.5	136.7
Diameter	0.6	9.0	10.1	10.7	9.3	10.2	8.5
Biomass	0.6	16.5	18.2	25.6	22.5	18.9	13.5
Capsule no.	0.9	28.5	24.8	33.8	25.0	29.3	21.3
Seed mass	0.9	41.2	41.5	65.3	53.9	56.6	48.3
Dormancy	0.8	69.4	89.9	84.5	65.5	71.3	83.4
D	---	0.20	0.24	0.08	0.14	0.13	0.31
SE		0.04	0.06	0.05	0.06	0.02	0.13
CI (lower)		0.11	0.19	0.05	0.13	0.08	0.30
(upper)		0.20	0.35	0.27	0.38	0.15	0.78

†Ct = not sprayed, C = sprayed with *Colletotrichum coccodes*, b = treated with the herbicide, bentazon, Mon = monospecific stands, Mix = competition with soybean, CI = confidence interval. Data of two seed size classes were pooled. Number in parenthesis indicates standard error.

Table 2.1. The Desirability function (D) for the fitness of *Abutilon theophrasti* as affected by *Colletotrichum coccodes* and bentazon in monospecific stands and in competition with soybean in 1998.

Parameters	weight	Treatment					
		Ct. Mon	Ct. Mix	C. Mon.	C. Mix.	C. b.Mon.	C. b.Mix.
Height	0.9	153.7	104.5	137.5	116.0	154.0	100.5
Diameter	0.9	8.6	5.2	7.8	5.2	9.0	4.5
Biomass	0.9	17.4	6.5	10.1	8.4	18.3	5.5
Capsule no	0.9	17.0	6.8	12.0	6.5	20.5	4.1
Seed mass	0.9	51.4	34.6	44.8	26.6	47.4	16.6
Dormancy	0.9	76.9	76.4	99.6	73.8	92.9	74.1
D	---	0.38	0.80	0.57	0.78	0.41	0.94
SE		0.09	0.06	0.10	0.08	0.13	0.02
CI (lower)		0.31	0.20	0.31	0.27	0.41	0.50
(upper)		0.57	0.90	0.60	0.94	0.77	0.99

†Ct = not sprayed, C = sprayed with *Colletotrichum coccodes*, b = treated with the herbicide, bentazon, Mon = monospecific stands, Mix = competition with soybean, CI = confidence interval. Data of two seed size classes were pooled. Number in parenthesis indicates standard error.

Table 2.2. The Desirability function (D) for the fitness of *Abutilon theophrasti* as affected by *Colletotrichum coccodes* and bentazon in monospecific stands and in competition with soybean in 1998.

Parameters	weight	Treatment					
		Ct. Mon	Ct. Mix	C. Mon.	C. Mix.	C. b.Mon.	C. b.Mix.
Height	0.9	153.7	104.5	137.5	116.0	154.0	100.5
Diameter	0.7	8.6	5.2	7.8	5.2	9.0	4.5
Biomass	0.7	17.4	6.5	10.1	8.4	18.3	5.5
Capsule no.	0.9	17.0	6.8	12.0	6.5	20.5	4.1
Seed mass	0.9	51.4	34.6	44.8	26.6	47.4	16.6
Germination	0.5	3.2	23.6	0.4	1.2	7.1	26.0
Dormancy	0.8	76.9	76.4	99.6	73.8	92.9	74.1
D	---	0.16	0.45	0.31	0.54	0.23	0.62
SE		0.05	0.13	0.05	0.15	0.08	0.12
CI (lower)		0.15	0.44	0.17	0.50	0.21	0.40
(upper)		0.31	0.81	0.32	0.91	0.44	0.73

†Ct = not sprayed, C = sprayed with *Colletotrichum coccodes*, b = treated with the herbicide, bentazon, Mon = monospecific stands, Mix = competition with soybean, CI = confidence interval. Data of two seed size classes were pooled. Number in parenthesis indicates standard error.

Table 2.3. The Desirability function (D) for the fitness of *Abutilon theophrasti* as affected by *Colletotrichum coccodes* and bentazon in monospecific stands and in competition with soybean in 1998.

Parameters	weight	Treatment					
		Ct. Mon	Ct. Mix	C. Mon.	C. Mix.	C. b.Mon.	C. b.Mix.
Height	0.9	153.7	104.5	137.5	116.0	154.0	100.5
Diameter	0.7	8.6	5.2	7.8	5.2	9.0	4.5
Biomass	0.7	17.4	6.5	10.1	8.4	18.3	5.5
Capsule no.	0.9	17.0	6.8	12.0	6.5	20.5	4.1
Seed mass	0.9	51.4	34.6	44.8	26.6	47.4	16.6
Dormancy	0.8	76.9	76.4	99.6	73.8	92.9	74.1
D	---	0.36	0.78	0.54	0.54	0.37	0.93
SE		0.09	0.07	0.10	0.09	0.13	0.02
CI (lower)		0.31	0.23	0.33	0.29	0.35	0.75
(upper)		0.56	0.80	0.61	0.76	0.77	0.99

†Ct = not sprayed, C = sprayed with *Colletotrichum coccodes*, b = treated with the herbicide, bentazon, Mon = monospecific stands, Mix = competition with soybean, CI = confidence interval. Data of two seed size classes were pooled. Number in parenthesis indicates standard error.

Table 2.4. The Desirability function (D) for the fitness of *Abutilon theophrasti* as affected by *Colletotrichum coccodes* and bentazon in monospecific stands and in competition with soybean in 1998.

Parameters	weight	Treatment					
		Ct. Mon	Ct. Mix	C. Mon.	C. Mix.	C. b.Mon.	C. b.Mix.
Height	0.7	153.7	104.5	137.5	116.0	154.0	100.5
Diameter	0.6	8.6	5.2	7.8	5.2	9.0	4.5
Biomass	0.6	17.4	6.5	10.1	8.4	18.3	5.5
Capsule no.	0.9	17.0	6.8	12.0	6.5	20.5	4.1
Seed mass	0.9	51.4	34.6	44.8	26.6	47.4	16.6
Germination	0.5	3.2	23.6	0.4	1.2	7.1	26.0
Dormancy	0.8	76.9	76.4	99.6	73.8	92.9	74.1
D	---	0.21	0.57	0.29	0.53	0.23	0.61
SE		0.05	0.10	0.05	0.15	0.07	0.12
CI (lower)		0.16	0.32	0.16	0.50	0.22	0.41
(upper)		0.29	0.59	0.31	0.91	0.41	0.75

†Ct = not sprayed, C = sprayed with *Colletotrichum coccodes*, b = treated with the herbicide, bentazon, Mon = monospecific stands, Mix = competition with soybean, CI = confidence interval. Data of two seed size classes were pooled. Number in parenthesis indicates standard error.

Table 2.5. The Desirability function (D) for the fitness of *Abutilon theophrasti* as affected by *Colletotrichum coccodes* and bentazon in monospecific stands and in competition with soybean in 1998.

Parameters	weight	Treatment					
		Ct. Mon	Ct. Mix	C. Mon.	C. Mix.	C. b.Mon.	C. b.Mix.
Height	0.7	153.7	104.5	137.5	116.0	154.0	100.5
Diameter	0.6	8.6	5.2	7.8	5.2	9.0	4.5
Biomass	0.6	17.4	6.5	10.1	8.4	18.3	5.5
Capsule no.	0.9	17.0	6.8	12.0	6.5	20.5	4.1
Seed mass	0.9	51.4	34.6	44.8	26.6	47.4	16.6
Dormancy	0.8	76.9	76.4	99.6	73.8	92.9	74.1
D	---	0.33	0.72	0.55	0.71	0.52	0.94
SE		0.10	0.12	0.13	0.12	0.07	0.02
CI (lower)		0.31	0.41	0.43	0.40	0.25	0.60
(upper)		0.63	0.75	0.79	0.75	0.55	0.99

†Ct = not sprayed, C = sprayed with *Colletotrichum coccodes*, b = treated with the herbicide, bentazon, Mon = monospecific stands, Mix = competition with soybean, CI = confidence interval. Data of two seed size classes were pooled. Number in parenthesis indicates standard error.

Table 3.1. The Desirability function (D) for the fitness of *Abutilon theophrasti* as affected by *Colletotrichum coccodes* and bentazon in monospecific stands and in competition with soybean in 1999.

Parameters	weight	Treatment					
		Ct. Mon	Ct. Mix	C. Mon.	C. Mix.	C. b.Mon.	C. b.Mix.
Height	0.9	136	121	134	125	152	110
Diameter	0.9	9.4	6.9	8.8	7.6	11.5	6.3
Biomass	0.9	15.2	0.9	12.0	11.7	24.8	9.6
Capsule no.	0.9	15.3	9.0	12.3	7.3	14.5	7.0
Seed mass	0.9	25.5	21.7	25.7	17.3	32.8	19.2
Dormancy	0.9	80.5	75.7	60.5	42.2	57.7	45.6
D	---	0.27	0.55	0.31	0.47	0.15	0.50
SE		0.07	0.04	0.13	0.09	0.04	0.06
CI (lower)		0.22	0.15	0.30	0.28	0.14	0.19
(upper)		0.41	0.60	0.79	0.52	0.26	0.53

†Ct = not sprayed, C = sprayed with *Colletotrichum coccodes*, b = treated with the herbicide, bentazon, Mon = monospecific stands, Mix = competition with soybean, CI = confidence interval. Data of two seed size classes were pooled. Number in parenthesis indicates standard error.

Table 3.2. The Desirability function (D) for the fitness of *Abutilon theophrasti* as affected by *Colletotrichum coccodes* and bentazon in monospecific stands and in competition with soybean in 1999.

Parameters	weight	Treatment					
		Ct. Mon	Ct. Mix	C. Mon.	C. Mix.	C. b.Mon.	C. b.Mix.
Height	0.9	136	121	134	125	152	110
Diameter	0.7	9.4	6.9	8.8	7.6	11.5	6.3
Biomass	0.7	15.2	0.9	12.0	11.7	24.8	9.6
Capsule no.	0.9	15.3	9.0	12.3	7.3	14.5	7.0
Seed mass	0.9	25.5	21.7	25.7	17.3	32.8	19.2
Germination	0.5	39.1	25.0	48.7	42.0	56.7	44.6
Dormancy	0.8	80.5	75.7	60.5	42.2	57.7	45.6
D	---	0.32	0.48	0.32	0.43	0.19	0.46
SE		0.05	0.06	0.04	0.05	0.04	0.05
CI (lower)		0.18	0.21	0.14	0.15	0.15	0.14
(upper)		0.34	0.58	0.34	0.45	0.29	0.54

†Ct = not sprayed, C = sprayed with *Colletotrichum coccodes*, b = treated with the herbicide, bentazon, Mon = monospecific stands, Mix = competition with soybean, CI = confidence interval. Data of two seed size classes were pooled. Number in parenthesis indicates standard error.

Table 3.3. The Desirability function (D) for the fitness of *Abutilon theophrasti* as affected by *Colletotrichum coccodes* and bentazon in monospecific stands and in competition with soybean in 1999.

Parameters	weight	Treatment					
		Ct. Mon.	Ct. Mix	C. Mon.	C. Mix.	C. b.Mon.	C. b.Mix.
Height	0.9	136	121	134	125	152	110
Diameter	0.7	9.4	6.9	8.8	7.6	11.5	6.3
Biomass	0.7	15.2	0.9	12.0	11.7	24.8	9.6
Capsule no.	0.9	15.3	9.0	12.3	7.3	14.5	7.0
Seed mass	0.9	25.5	21.7	25.7	17.3	32.8	19.2
Dormancy	0.8	80.5	75.7	60.5	42.2	57.7	45.6
D	---	0.33	0.64	0.31	0.49	0.18	0.52
SE		0.08	0.10	0.04	0.06	0.05	0.07
CI (lower)		0.26	0.32	0.14	0.21	0.17	0.23
(upper)		0.48	0.66	0.35	0.59	0.32	0.53

†Ct = not sprayed, C = sprayed with *Colletotrichum coccodes*, b = treated with the herbicide, bentazon, Mon = monospecific stands, Mix = competition with soybean, CI = confidence interval. Data of two seed size classes were pooled. Number in parenthesis indicates standard error.

Table 3.4. The Desirability function (D) for the fitness of *Abutilon theophrasti* as affected by *Colletotrichum coccodes* and bentazon in monospecific stands and in competition with soybean in 1999.

Parameters	weight	Treatment					
		Ct. Mon	Ct. Mix	C. Mon.	C. Mix.	C. b.Mon.	C. b.Mix.
Height	0.7	136	121	134	125	152	110
Diameter	0.6	9.4	6.9	8.8	7.6	11.5	6.3
Biomass	0.6	15.2	0.9	12.0	11.7	24.8	9.6
Capsule no.	0.9	15.3	9.0	12.3	7.3	14.5	7.0
Seed mass	0.9	25.5	21.7	25.7	17.3	32.8	19.2
Germination	0.5	39.1	25.0	48.7	42.0	56.7	44.6
Dormancy	0.8	80.5	75.7	60.5	42.2	57.7	45.6
D	---	0.29	0.44	0.31	0.36	0.19	0.42
SE		0.06	0.05	0.03	0.08	0.04	0.05
CI (lower)		0.21	0.16	0.12	0.12	0.15	0.16
(upper)		0.37	0.45	0.36	0.55	0.28	0.56

†Ct = not sprayed, C = sprayed with *Colletotrichum coccodes*, b = treated with the herbicide, bentazon, Mon = monospecific stands, Mix = competition with soybean, CI = confidence interval. Data of two seed size classes were pooled. Number in parenthesis indicates standard error.

Table 3.5. The Desirability function (D) for the fitness of *Abutilon theophrasti* as affected by *Colletotrichum coccodes* and bentazon in monospecific stands and in competition with soybean in 1999.

Parameters	weight	Treatment					
		Ct. Mon	Ct. Mix	C. Mon.	C. Mix.	C. b.Mon.	C. b.Mix.
Height	0.7	136	121	134	125	152	110
Diameter	0.6	9.4	6.9	8.8	7.6	11.5	6.3
Biomass	0.6	15.2	0.9	12.0	11.7	24.8	9.6
Capsule no.	0.9	15.3	9.0	12.3	7.3	14.5	7.0
Seed mass	0.9	25.5	21.7	25.7	17.3	32.8	19.2
Dormancy	0.8	80.5	75.7	60.5	42.2	57.7	45.6
D	---	0.32	0.59	0.39	0.34	0.18	0.46
SE		0.07	0.05	0.11	0.05	0.05	0.07
CI (lower)		0.25	0.18	0.36	0.18	0.16	0.25
(upper)		0.46	0.63	0.67	0.41	0.31	0.52

†Ct = not sprayed, C = sprayed with *Colletotrichum coccodes*, b = treated with the herbicide, bentazon, Mon = monospecific stands, Mix = competition with soybean, CI = confidence interval. Data of two seed size classes were pooled. Number in parenthesis indicates standard error.