

**Effect and Underlying Mechanisms of Cultivar Mixtures on Weed and  
Disease Suppression in Field Pea (*Pisum sativum*)**

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For the Degree of Master of Science  
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By

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## ABSTRACT

Field pea is an important annual crop due to its contribution to soil fertility and other rotational benefits. However, weeds and ascochyta blight limit pea yield, particularly in organic systems. Leafed and semi-leafless pea types differ in lodging resistance, and may affect weeds and disease through differences in canopy light penetration and air flow. Mixtures of the two leaf types may improve weed and disease suppression and yield compared with monocultures of the same cultivars. To test this hypothesis, replicated field experiments were conducted under organic and conventional management in Saskatoon and Vonda, SK, in 2011 and 2012. Mixtures of a leafed and semi-leafless cultivar, CDC Sonata and CDC Dakota, were sown in ratios of 0:100, 25:75, 50:50, 75:25, and 100:0 leafed to semi-leafless pea, at target seeding rates of 88 and 132 plants m<sup>-2</sup>. Conventionally managed plots were inoculated with ascochyta blight-infested pea straw and received overhead irrigation to encourage disease. Mixtures of 50% or more semi-leafless pea adopted the greater lodging resistance and weed suppression of the semi-leafless cultivar. Mixtures comprised of 25% leafed and 75% semi-leafless pea increased both seed and biomass yield compared with either cultivar grown alone. Yield enhancement was attributed to the leafed cultivar, whose seed yield was 76% higher in mixture than expected based on monoculture yield. Ascochyta blight epidemics were of moderate severity, and leafed and semi-leafless monocultures reached 36 and 43% necrosis in 2011, and 33 and 38% necrosis in 2012, respectively. The disease reaction of mixtures fell between the two component cultivars. At disease onset in 2012, lower light interception and shorter moisture durations coincided with the lower ascochyta blight severity of leafed monocultures. In 2011 and the later phase of the 2012 epidemic, disease severity was negatively associated with vine length, and positively associated with number of nodes and tissue senescence. Despite the advantages of leafed and semi-leafless pea mixtures, the limited selection of leafed cultivars impedes adoption of this technique by growers. For pea breeders, developing mixtures of pea lines isogenic for leaf type may increase yield compared with single cultivars.

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## **DEDICATION**

This thesis is dedicated to my parents, Brenda and Larry Syrový, who gave me my early memories of going for walks, to the lake, gardening, picking berries, and searching for small creatures to play with. It is my appreciation for the natural world and my place within it that guides my work.

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## LIST OF ABBREVIATIONS

AIC	Akaike's Information Criterion
ANOVA	Analysis of Variance
BF	Beginning of Flowering
BSF	Beginning of Seed Filling
CDC	Crop Development Centre
LAI	Leaf Area Index
LSD	Least Significant Difference
PAR	Photosynthetically Active Radiation
RGR	Relative Growth Rate
RIE	Radiation Interception Efficiency
RUE	Radiation Use Efficiency

## 1.0 INTRODUCTION

Field pea is an important rotational crop in annual cropping systems due to its ability to add nitrogen to the soil, and its benefits to yields of succeeding crops (Stevenson and van Kessel 1996; Mairl et al. 1996). However, techniques are needed to manage pests and disease, and increase pea yield, particularly in organic systems. Weeds are the primary pest concern for Saskatchewan's organic growers (Frick et al. 2008), and are particularly damaging to pea yield (Harker 2001). Yield loss due to weeds averaged 46% in a survey of conventional pea fields in central Alberta (Harker 2001), and yield loss as high as 94% can result from very high weed densities (Nelson and Nylund 1962). The foliar disease ascochyta blight, caused mainly by *Mycosphaerella pinodes*, can be problematic in both organic and conventional systems, particularly in seasons with high rainfall. Surveys in Saskatchewan and Manitoba found symptoms of the disease in virtually all fields (Dokken-Bouchard et al. 2010; McLaren et al. 2010). With severe symptoms, yield loss as high as 68% has been measured (Garry et al. 1998).

Morphological traits of field pea canopies can moderate interactions between the crop, weeds, and disease. In interactions between a crop and weeds, competitive ability refers to both the ability of the crop to suppress weeds, and the ability of the crop to maintain yield in the presence of weeds (Jordan 1993). Strong competitive ability of field pea with weeds is associated with high leaf area (Wall and Townley-Smith 1996) and high crop biomass in the presence of weeds (Spies et al. 2011), as these traits aid the crop in diverting sunlight away from weeds. Ascochyta blight severity, in contrast, increases with canopy leaf area (Le May et al. 2009). Severe canopy lodging also encourages disease development (Banniza et al. 2005; Wang et al. 2006). Links between plant traits and disease may be caused by differences in canopy microclimates or spore dispersal (Le May et al. 2009; Tivoli et al. 2013).

Due to their contrasting traits, pea cultivars of different leaf types may impact weeds and disease. Semi-leafless pea was developed from wild type (leafed) pea by expressing the recessive *afaf* (afila) gene, which converts all leaflets to tendrils (Snoad and Gent 1976; Kielpinski and Blixt 1982). The larger tendrils make semi-leafless cultivars more resistant to lodging, which directly increases their seed yield relative to leafed pea in seasons where lodging occurs (Schouls and Langelaan 1994). Their higher lodging resistance, in addition to their

reduced leaf area, may also indirectly increase yield by limiting ascochyta blight development. In contrast, leafed pea cultivars in Saskatchewan were developed to produce high biomass yield for forage (Saskatchewan Pulse Growers 2012), which may aid in weed suppression. In several studies the most competitive cultivars shared the leafed characteristic (Tofinga et al. 1993; Semere and Froud-Williams 2001; Harker et al. 2008; Spies et al. 2011).

Growing two or more cultivars with contrasting traits can improve canopy characteristics and increase yield compared with growing the component cultivars alone. It is not uncommon for pathogen inoculum levels or disease severity of mixtures to be lower than the mean of the same cultivars grown as monocultures. For example, growing a low leaf area bean cultivar in mixture with one that had high leaf area reduced *Sclerotinia sclerotiorum* apothecia production under the canopy to the same levels as the low leaf area cultivar alone (Coyne et al. 1978). Similarly, symptoms caused by the splash-dispersed pathogen *Stagonospora nodorum* on two wheat cultivars classified as “very susceptible” and “very resistant” when grown alone, were reduced to similar levels to the “very resistant” cultivar in mixture (Jeger et al. 1981b). Yields of some cultivar combinations can also exceed expectations based on single cultivar yield (Jeger et al. 1981b; Mundt et al. 1994; Newton et al. 1997; Jedel et al. 1998).

Mixtures of pea cultivars of contrasting leaf types may increase yield under organic conditions compared with single cultivars. Under weed-free conditions, both seed (Schouls and Langelaan 1994) and biomass yield (Ćupina et al. 2010) of leafed and semi-leafless pea mixtures were higher than monoculture yield of the component cultivars grown alone. The magnitude of yield increase was 4-8% above the higher-yielding cultivar in both cases. Leafed pea yield showed greater increases in mixture than semi-leafless pea yield (Schouls and Langelaan 1994; Ćupina et al. 2010), and yield increases were associated with reduced lodging in mixture relative to leafed canopies (Schouls and Langelaan 1994). While leafed and semi-leafless mixtures can have higher yields under conventional conditions, however, their yields under organic conditions may differ due to their competitive interactions with weeds, and the presence of disease. In addition, the effects of different leaf type pea mixtures on weed and disease suppression are unknown. Intercrops of pea with other crop species show that changing pea canopy composition can affect pest suppression. Combining pea with cereals reduced biomass of competing weeds (Poggio 2005; Hauggaard-Nielsen et al. 2006), created a microclimate less conducive to

ascochyta blight (Schoeny et al. 2010), and reduced ascochyta blight severity (Fernández-Aparicio et al. 2010; Schoeny et al. 2010) compared with growing pea alone. By altering the characteristics of pea canopies through cultivar composition, it may be possible to alter weed suppression, canopy microclimate, and ascochyta blight severity.

This thesis is guided by the hypothesis that mixtures of leafed and semi-leafless pea will have higher yields, lodging resistance, weed and disease suppression, and a canopy microclimate less conducive to disease than either of the component cultivars grown alone. The two experiments designed to test this hypothesis each address a specific objective: the first, to identify a ratio of leafed to semi-leafless pea that maximizes yield and agronomic benefits under organic conditions, and the second, to identify plant and canopy traits associated with disease suppression in field pea. This information will aid producers in growing pea crops that are more pest suppressive and higher yielding. It will also aid pea breeders in selecting cultivars or mixtures of cultivars suitable for organic and low-input management.

## 2.0 LITERATURE REVIEW

### 2.1 Canopy Effects on Weeds

#### 2.1.1. Crop Yield Loss due to Weeds

Weed management ranks in the top three overall concerns of Saskatchewan organic farmers, and is their number one pest issue (Frick et al. 2008). The spending patterns of conventional farmers show that weeds are no less a concern in conventional systems, considering that herbicide sales account for 76% of pesticide sales in Canada (CropLife Canada 2009). Field pea yield is particularly sensitive to competition from weeds compared with other field crops. In a study in central Alberta, field pea suffered significant yield loss when weeds were present 75% of the time, compared with 25 and 33% of the time for barley and canola, respectively (Harker 2001). At sites where yield loss occurred, the reductions averaged 46%. While yield loss due to weeds in field pea is common, factors such as the timing and duration of weed interference, weed density, weed species, and growing environment have profound effects on the magnitude of yield loss. In practice, yield loss in field pea may range from negligible to virtually 100% depending on all of these elements.

##### *2.1.1.1 Factors Affecting the Magnitude of Yield Loss in Field Pea*

###### 2.1.1.1.1 Timing and Duration of Weed Interference

The time of weed emergence relative to the crop, and how long competition persists before weeds are removed, both affect the magnitude of crop yield loss for field pea.

Weeds that emerge prior to or with the crop cause greater yield loss than weeds emerging after the crop. In studies with fresh market pea, white mustard (*Brassica hirta* Moench) that emerged three days ahead of the crop reduced yield by 52% compared with the weed-free check, while weeds that emerged four days after the crop had no significant impact on yield (Nelson and Nylund 1962). Other studies indicate that while earlier-emerging weeds cause greater yield damage, weeds that emerge as late as four weeks after the crop may still harm yield. Yield loss ranged from 23-60% with weeds emerging with the crop, and 11-44% with weeds emerging four weeks after the crop, for fresh market pea competing with black nightshade (*Solanum ptycanthum* Dun.) (Croster and Masiunas 1998).

The studies on time of weed removal in field pea are fairly consistent in concluding that early-emerging weeds should be removed within the first two weeks of crop growth to prevent yield loss. In a 14 site-year study in Saskatchewan, herbicide application one or two weeks after crop emergence benefited pea yield 64% of the time compared with later applications, due to improved weed control in seven site-years, and due to reduced crop herbicide injury in an additional two (May et al. 2003). Yield loss occurring within the first two weeks of competition falls in the range of 5-11% compared with weed-free controls (Gargouri and Seely 1972a; Harker et al. 2001). After the onset of yield loss, the rate of yield decline follows a linear trend (Gargouri and Seely 1972a; Harker et al. 2001). Daily yield loss ranged from 61-103 kg ha<sup>-1</sup> per day, depending on location, weed species, and season in a study in central Alberta (Harker et al. 2001). Yield loss due to early-emerging weeds approached a maximum of 32 to 77% approximately four to five weeks after crop emergence (Gargouri and Seely 1972a; Harker et al. 2001). In contrast with other studies, one study found inconsistent effects of time of weed removal with redstem filaree (*Erodium cicutarium* (L.) L'Her.) and wild oat (*Avena fatua* L.) removed at either the two or six leaf pair stage in pea. At one site, yield increased if weeds were removed at the earlier stage in one year, and if weeds were removed at the later stage in the other, while at a second site there was no significant effect of time of removal (Harker et al. 2007).

#### 2.1.1.1.2 Weed Density

Yield loss in pea frequently exceeds 50% when high weed densities are present. The percentage yield loss with increasing weed density typically increases following a hyperbolic curve (Nelson and Nylund 1962; Gargouri and Seely 1972b; Wall et al. 1991; O'Donovan and Blackshaw 1997), but in some cases yield loss increases linearly (Wall et al. 1991). Initial crop yield loss with each added weed per square metre has been reported to range from 0.1-6.5% for wild mustard (*Sinapis arvensis* L. = *Brassica kaber* (DC.) Wheeler), volunteer barley (*Hordeum vulgare* L.), and wild oat competing with pea (Gargouri and Seely 1972b; Wall et al. 1991; O'Donovan and Blackshaw 1997). As a result, thresholds for integrated weed management in field pea can be quite low; herbicide application is recommended when volunteer barley densities exceed two to six plants per square metre (O'Donovan and Blackshaw 1997). Maximum reported or predicted yield loss in pea competing with weeds is 58% for foxtail millet

(*Setaria italica* (L.) Beauv.) (Nelson and Nylund 1962), 71 to 94% for wild or white mustard (Nelson and Nylund 1962; Wall et al. 1991), 86% for volunteer barley (O'Donovan and Blackshaw 1997), and 70% for wild oat (Gargouri and Seely 1972b), at maximum weed densities of approximately 290, 125 to 290, 120, and 80 plants m<sup>-2</sup>, respectively.

#### 2.1.1.1.3 Weed Species

Different weed species have different abilities to cause yield loss in crop plants or other weeds. Plant size and investment in leaf material are very important factors in the competitive ability of annual species. The aggressivity of a plant species relative to another, an index measuring whether individuals of each species gain or lose biomass through interspecific competition, can be predicted with high precision ( $R^2 = 0.98$ ) using a regression model that includes plant dry weight, the rate of increase in plant dry weight per unit leaf area, and the ratio of leaf area to plant dry weight (Roush and Radosevich 1985). In contrast, relative growth rate (RGR), a measure of total plant productivity, is a relatively poor predictor of competitive ability (Roush and Radosevich 1985).

In field pea, few studies have directly compared the impact of different weed species on crop yield. One study evaluated the relative importance of controlling wild oat or redstem filaree with grass or broadleaf herbicides, respectively. The authors found that controlling wild oat alone reduced yield loss (31% yield loss) compared with controlling redstem filaree only (47% yield loss), leading to the conclusion that controlling wild oat was more critical than controlling redstem filaree (Harker et al. 2007). It was highlighted, however, that yield loss was further reduced to 11% when both weeds were controlled. Another study comparing yield loss at different densities of two weeds, foxtail millet and white mustard, found that field pea could tolerate greater populations of foxtail millet than white mustard. Approximately 32 white mustard plants m<sup>-2</sup> caused the same yield loss as 290 foxtail millet plants m<sup>-2</sup> in fresh market pea (Nelson and Nylund 1962). To further investigate these results, the authors compared the RGR of pea with white and wild mustard, rough (i.e. redroot) pigweed (*Amaranthus retroflexus* L.), ladysthumb (*Polygonum persicaria* L.), barnyardgrass (*Echinochloa crusgalli* (L.) Beauv.), foxtail millet, green (*Setaria viridis* (L.) Beauv.) and yellow foxtail (*Setaria glauca* (L.) Beauv.), grown in the absence of competition. Despite the weak relationship between RGR and competitive ability noted earlier, the relatively strong competitive ability of white mustard, and

weak competitive ability of foxtail millet, correlated well with RGR. Additionally, wild mustard and barnyardgrass were predicted to be strong competitors with field pea based on RGR.

#### 2.1.1.1.4 Environmental Effects

The growing environment, which includes growing season temperatures and precipitation as well as site characteristics, directly impacts crop growth. Pea is a cool-season legume, accumulating maximum dry matter at 21°C/10°C to 24°C/16°C daytime/nighttime temperatures up to the sixth node, 16°C/10°C to 21°C/16°C up to the tenth node, 16°C/10°C to 21°C/13°C up to flowering, and 16°C/10°C to 18°C/13°C up to maturity (Stanfield et al. 1966). Pea is also sensitive to waterlogged soils, and is susceptible to root rot pathogens under conditions of high soil moisture. Low soil oxygen due to waterlogging for five days reduced crop biomass and seed yield by more than 50% regardless of crop growth stage (Cannell et al. 1979), although pea was most sensitive to waterlogging just prior to flowering (Cannell et al. 1979; Belford et al. 1980). Standing water also increases incidence of fusarium root rot (*F. oxysporum* f. sp. *pisi* and *F. solani* f. sp. *pisi*) by as much as 85%, and severity as much as 75%, compared with well-drained soil (Tu 1994).

In addition to its direct impacts, the growing environment may also affect competitive dynamics between crop and weeds, since different species may have different optimal growing conditions. In controlled environment studies of pea competing with maize, under the same water stress conditions pea leaf area was reduced by 40%, whereas maize leaf area was reduced by 62% (Semere and Froud-Williams 2001). Under field conditions, the same wild mustard densities caused greater pea yield loss in a season of high rainfall (15-35%) compared with a season of low rainfall (4-22%) (Wall et al. 1991). Different pea cultivars may also show differential responses to environmental conditions. When 17 pea cultivars were grown in environments with increasing levels of weed competition, the yield loss of some cultivars decreased relative to the average, whereas others increased (McDonald 2003). Other examples where significant site-year x treatment effects on weed control or yield loss under weed competition were observed (e.g. O'Donovan and Blackshaw 1997; Harker et al. 2001, 2007; May et al. 2003) highlight the importance of growing environment on competition between crop and weed species.

## **2.1.2 Mechanisms of Competition between Field Pea and Neighbouring Plants**

Yield reduction occurs when resources needed for vegetative and reproductive development are inadequate to support optimal growth of both the crop and weeds. Limitation of one or more resources may negatively impact the crop, weeds, or both. Competition between plants for resources can be divided into above-ground and below-ground interactions. Competition above-ground occurs as foliage of crop and weeds intercept sunlight, while competition below-ground occurs as roots draw water and nutrients from the soil.

### ***2.1.2.1 Above-Ground Interactions (Competition for Light)***

Shading pea plants under field conditions decreases crop yield. Applying shade treatments that reduced light intensity by 50% produced an approximately equal percentage reduction in crop yield in fresh market pea (Meadley and Milbourn 1971). When light intensity was varied during reproductive growth field pea yield declined linearly with light intensity, although the rate of yield loss was much smaller than the rate at which light was reduced (Gubbels 1980). The yield loss due to shading occurs during reproductive growth rather than vegetative crop growth. Plants shaded only during reproductive growth yielded similarly to plants that were shaded throughout the entire growing season, whereas plants shaded only during vegetative growth yielded similarly to plants that were unshaded (Meadley and Milbourn 1971). Plants unshaded prior to flowering were able to equalize their yield by producing pod-bearing branches at upper plant nodes, and retaining a greater number of flowers and pods.

Yield loss in shaded plants is primarily due to increased abscission of formed flowers and pods, and secondarily due to a reduction in the number of seeds per pod. In the above-noted study on fresh market pea, the percentage of aborted flowers and pods in reproductive-shaded treatments ranged from 36-53%, compared with 7-17% in plants that were unshaded or shaded during vegetative growth only (Meadley and Milbourn 1971). The number of peas per pod was also reduced, but seed weight was unaffected. The same yield components were affected in studies where shoot competition was isolated from root competition: above-ground competition reduced the number of pods per plant by 15%, and weight per pod by 20%, but did not affect seed weight (Tofinga et al. 1993). Under intense levels of shading however, seed weight may also be affected. Seed weight declined linearly when light intensity was reduced from full sunlight, to 39 and 11% of available sunlight (Gubbels 1980).

Although it is clear that low light levels are detrimental to pea productivity, experiments where shoot competition was isolated from root competition suggest that shading by neighbouring plants does not limit pea productivity during early growth, and may not be the major limiting factor during later crop growth. Additive mixtures of pea with maize (Semere and Froud-Williams 2001) or cereals (Tofinga et al. 1993) were grown with soil and aerial partitions, which allowed study of separate and combined effects of above- and below-ground competition on both crops. Shoot competition alone did not significantly reduce pea biomass, plant or leaf area in plants harvested during vegetative growth (Semere and Froud-Williams 2001), or pea biomass and seed yield in plants grown to maturity (Tofinga et al. 1993). This implies that either neighbouring plants do not cause enough shading to limit yield in field pea, or that other resources such as water or nutrients become limiting factors before access to light. In contrast with pea, wheat and barley biomass and grain yield was stifled by shoot competition alone when grown in mixtures with pea (Tofinga et al. 1993), suggesting that pea was a stronger competitor for light in these mixtures.

While the isolated effects of above-ground competition on pea may be relatively small, the effects of shading may be either enhanced or subdued by root competition. Allowing both shoots and roots to compete reduced pea biomass more than expected based on additive effects in one case (Tofinga et al. 1993), and less than expected in another (Semere and Froud-Williams 2001). Liebman (1989) demonstrated how such an interaction might occur in a study of field pea-barley intercrops competing with white mustard. Nitrogen fertilizer increased the height of white mustard plants, reducing the amount of sunlight available to pea from 62-100%, to 28-85% of above-canopy levels.

#### ***2.1.2.2 Below-Ground Interactions (Competition for Water and Nutrients)***

Plant roots occupying the same space compete for water and nutrients. For field pea water is a particularly important limiting resource. Reducing water supply to field pea-cereal mixtures decreased pea plant height by 32%, biomass by 27%, leaf area by 34-54%, and seed yield by 35-65% (Liebman 1989; Semere and Froud-Williams 2001). In contrast, adding nitrogen to mixtures of pea with barley and white mustard benefited the competing crops and had either a neutral or detrimental effect on pea leaf area and seed yield (Liebman 1989).

Unlike shoot competition, root competition for below-ground resources alone reduces biomass yield, plant height, and leaf area of pea in its vegetative stage (Semere and Froud-Williams 2001), and crop biomass and grain yield in pea plants grown to maturity (Tofinga et al. 1993). Root competition with maize during vegetative growth decreased pea biomass by 43% (Semere and Froud-Williams 2001). Similar to light limitation, competing roots reduce the number of pods per plant, the number of seeds per pod, and to a lesser extent seed weight. The number of pods per plant and weight per pod decreased by 25% and 20% due to root competition, respectively, while individual seed weights decreased by 5% for semi-leafless, but not leafed pea (Tofinga et al. 1993).

There is evidence that the rooting profile and patterns of nitrogen uptake for field pea respond to root competition with other species. These physiological responses can minimize yield loss by allowing pea to only partially overlap with competing plants in below-ground resource use. In studies using lithium as a marker for root activity, Tofinga and Snaydon (1992) demonstrated that in pea and cereal monocultures lithium uptake was highest close to the soil surface, and decreased as soil depth increased. In same-row or cross-drilled mixtures of the two crops however, field pea roots took up significantly more lithium from 15 cm depth or deeper, while cereals continued to extract lithium from the upper 15 cm of the soil profile. Likewise, pea relies less on fertilizer N when competing with weeds or cereals than when grown with little or no competition. Allowing weed competition to persist for four weeks after pea emergence increased the amount of nitrogen fixed from the atmosphere to 81%, compared with 51% for pea with weeds removed one week after emergence (Soon et al. 2004). Similarly, pea fixed 94% of its required nitrogen when grown in root competition with cereals, compared with 76% when grown in monocultures (Tofinga et al. 1993). The ability of pea to fix its own nitrogen while allowing competing plants to use fertilizer nitrogen may account for the higher productivity of pea-cereal mixtures compared with monocultures of the same crops (Tofinga et al. 1993).

### **2.1.3 Enhancing the Competitive Ability of Field Pea**

Under organic conditions, mechanical weed control is restricted to very early crop growth. Even when herbicides are used, control may be incomplete (for example due to unfavourable weather during application, improper timing, reduced rates, or presence of herbicide-resistant weeds), leaving weeds to compete with the crop for resources throughout the

season. Therefore it is valuable to identify characteristics associated with the ability of the crop to divert sunlight, water and nutrients from weeds, to suppress the biomass of weeds, and enhance its own yield. Competitiveness may refer to both of these attributes: the crop's ability to suppress weeds (suppression), and its ability to maintain yield in the presence of weeds (tolerance) (Jordan 1993). A more competitive crop may be achieved through modifying characteristics of the crop as a whole (for simplicity's sake referred to as the "canopy" level), or characteristics of individual plants ("cultivar" level). Characteristics of a competitive pea crop at each level (canopy and cultivar) are discussed below, in order of the strength of established links between the characteristic and competitive ability.

### ***2.1.3.1 Canopy Level***

#### **2.1.3.1.1 Crop Density**

Crop density results from a combination of seeding rate, the percentage of seeds that germinate, and the percentage of germinated seeds that emerge. While the seeding rate typically is adjusted to account for the tested germination rate of the seed, studies suggest that to achieve the targeted plant density, seeding rates should also account for crop emergence. Although emergence may be difficult to predict, the literature suggests that the percentage of viable field pea seeds that develop into emerged plants is generally quite low. On average 67% of viable seeds produce plants, based on studies conducted in Saskatchewan and Alberta (Townley-Smith and Wright 1994; Johnston et al. 2002; Baird et al. 2009; Spies et al. 2010). The rate of emergence may also be affected by the amount of seed sown or the presence of weeds. In the absence of weeds, pea crops sown at target densities of less than 50 plants m<sup>-2</sup> may have emergence rates of 90% or greater, while at higher densities emergence averages 65% (Johnston et al. 2002; Spies et al. 2010). Under competition from weeds, pea emergence rates are similar to, or slightly lower than, high density weed-free crops, regardless of sowing density (Townley-Smith and Wright 1994; Baird et al. 2009).

Achieving the target plant population is central to optimizing yield. Under weed-free conditions, pea yield increases asymptotically with increasing crop density (Heath et al. 1991; Johnston et al. 2002; Spies et al. 2010). Below the asymptote, linear yield increases are observed with increasing plant density. An increase in density from 20 to 80 plants m<sup>-2</sup> increased grain yield by 27 and 50% in the cultivars CDC Sonata and Courier, respectively (Spies et al. 2010).

The diminishing returns at high densities are caused by decreased branching (Heath et al. 1991; Spies et al. 2010), number of pods (Heath et al. 1991), and to a lesser extent seed weight (Heath et al. 1991; Johnston et al. 2002) on individual plants. Under weed-free conditions, economic returns are maximized between 50 and 100 plants  $m^{-2}$  (Heath et al. 1991; Johnston et al. 2002; Spies et al. 2010), consistent with the recommended target density of 88 plants  $m^{-2}$  in Saskatchewan (Saskatchewan Pulse Growers 2000). Only in one study on canning pea was the weed-free optimum density greater than 100, at 140 plants  $m^{-2}$  (Lawson 1982).

Under competition from weeds, the asymptotic relationship between crop density and yield is maintained. The mechanisms of leveling off of yield at increasing densities are similar under weed competition to weed-free conditions: individual plant biomass (Lawson 1982; Townley-Smith and Wright 1994), and the number of branches, flowers, and pods (Lawson 1982) decrease with increasing crop density. The presence of competing weeds affects pea plants physiologically in a similar manner to increasing crop density, particularly at low crop densities. At higher crop densities, branching and numbers of flowers and pods on individual plants are similarly reduced, regardless of weed presence or absence (Lawson 1982).

Since the declining productivity of individual plants is initiated at lower densities when plants are subjected to competition from weeds, optimal field pea densities are generally higher in the presence than in the absence of weeds. Unlike weed-free conditions, where yield began leveling off as early as at 50 plants  $m^{-2}$ , substantial yield increases were reported between pea densities of 50 and 100 plants  $m^{-2}$  when competing with weeds (Townley-Smith and Wright 1994; O'Donovan and Blackshaw 1997; Baird et al. 2009). Under weedy conditions, pea yield is optimized at 90 to 120 plants  $m^{-2}$  (Wall and Townley-Smith 1996; O'Donovan and Blackshaw 1997; Baird et al. 2009), a 20 to 80% seeding rate increase compared with weed-free conditions.

In addition to their improved tolerance to competition from weeds, higher density pea crops are more weed suppressive than lower density crops. High density versus low density pea has been observed to reduce weed emergence in some cultivars or seasons (Wall et al. 1991; Townley-Smith and Wright 1994; Wall and Townley-Smith 1996), and decrease number of weed species compared with uncropped, weedy control plots (Lawson and Topham 1985). However the most consistently recorded effect of pea density on weeds is a reduction in weed biomass production. The reduction may follow a linear (Lawson and Topham 1985; Wall and Townley-

Smith 1996) or asymptotic trend (Townley-Smith and Wright 1994; Baird et al. 2009), amounting to approximately a 2.3% reduction in weed dry weight with each additional crop plant  $\text{m}^{-2}$  (Lawson and Topham 1985). Between seeding rates of 10 to 250 (Baird et al. 2009), and 63 to 150 plants  $\text{m}^{-2}$  (Marx and Hagedorn 1961), weed biomass declined by approximately 70%. Only one study recorded inconsistent and marginal effects of increasing seeding rates from 50 to 150 plants  $\text{m}^{-2}$  on biomass and seed set of volunteer barley (O'Donovan and Blackshaw 1997).

Increasing seeding rate is the single most effective method to improve weed suppression and minimize crop yield loss due to weeds, since studies evaluating both seeding rate and cultivars found larger and/or more consistent effects for the former (Wall et al. 1991; Townley-Smith and Wright 1994; Wall and Townley-Smith 1996). However, since cultivar differences are frequently still observed at high seeding rates (Wall et al. 1991; Townley-Smith and Wright 1994; Wall and Townley-Smith 1996), seeding competitive cultivars may give added benefit for the same seed cost. Additionally, the cost of seeding at very high rates may be prohibitive, and necessitate other methods of enhancing crop competition.

#### 2.1.3.1.2 Crop Spatial Arrangement

In the absence of weeds, seed placement, row spacing, and planting pattern have inconsistent effects on pea yield. In studies of different seeder technologies, pea seed yield was similar whether seed was placed in narrow rows or dispersed in bands when the same intra-row spacing was used (Johnston et al. 2002), and improving uniformity of spacing within rows improved seed yield in only one of two cultivars, in one of two seasons (Wilkins et al. 1991). Seeding field pea in rows 23 versus 30 cm apart had no effect on seed yield (Johnston et al. 2002), while processing pea yield increased as the distance between rows decreased from 27 to 9 cm (Gritton and Eastin 1968). The latter discrepancy may be due to the larger range in row spacings tested in the study on processing pea. Trellised snow pea grown in double rows yielded better than pea grown in single rows, but the effect was only significant in one of two years (Kahn and Nelson 1991).

Very little work has been published on the effects of crop spatial characteristics on field pea competing with weeds. The existing work suggests that manipulating row spacing, but not row orientation, may improve the competitiveness of field pea. In studies on Austrian winter pea (*Pisum sativum* ssp. *arvense* (L.) Poir), weed biomass decreased by an average of 28%, and yield

increased by 37%, as intra-row spacings progressively narrowed from 36 to 18 cm (Heneise and Murray 1980). In contrast, crop row orientation had inconsistent effects on the competitiveness of field pea with weeds in a study in Western Australia. Orienting rows perpendicularly to the sun, or east-west in Western Australia, reduced weed biomass by 36% compared with north-south in one site-year, but had no significant effects in the remaining two site-years. Furthermore, row orientation had no effect on yield of pea competing with weeds (Borger et al. 2010).

### ***2.1.3.2 Cultivar Level***

Identifying characteristics of competitive pea cultivars is complicated by the fact that very few studies have been conducted using isogenic lines. In the absence of such studies, it is difficult to establish definitive links between individual morphological characteristics and competitive ability. In reality, cultivars tested may differ in multiple characteristics, some of them enhancing suppression and tolerance, and others lessening these attributes. Furthermore, the performance of cultivars in the presence of weeds may vary from season to season due to factors such as weed populations and climatic conditions (e.g. Wall et al. 1991; McDonald 2003). Despite these difficulties, the many studies conducted in this area have identified several characteristics that are associated with improved competitive ability in field pea. These, as well as several characteristics that have relatively weak or unestablished links with weed competition, are discussed in detail.

#### **2.1.3.2.1 Vine Length**

Vine length, or plant height, is the most widely recognized cultivar characteristic associated with competitiveness with weeds in field pea. Vine length is primarily genetically determined and is not responsive to the presence or absence of weeds at a crop density of 50 plants  $\text{m}^{-2}$  (Spies et al. 2011). However, vine length may increase by up to 10% as crop density increases over a range of 30 to 120 plants  $\text{m}^{-2}$  (Tivoli et al. 1996). Longer vines were moderately ( $r = -0.40$  to  $r = -0.75$ ) to strongly ( $r = -0.92$ ) correlated with reduced weed biomass in multi-site-year studies that included 12 or 10 cultivars, respectively (Wall and Townley-Smith 1996; Spies et al. 2011). The reduction in weed biomass was predicted to be between 3.77 and 5.58  $\text{g m}^{-2}$  for each added centimetre of vine length (Wall and Townley-Smith 1996). The majority of other studies are in agreement with this trend. In a study that included 21 cultivars, those with 100 cm

vine length or greater significantly decreased growth scores of volunteer wheat and annual ryegrass (*Lolium rigidum* Gaud.) compared with short (<75 cm) or medium cultivars, and reduced wheat seed set by 20 to 30% (McDonald 2003). Similarly, in mixtures of pea and barley competing with white mustard, mustard biomass was lowered by 50% in mixtures that included tall versus short pea (Liebman 1989). In one study however, a short cultivar (<70 cm vine length) lowered weed biomass by 42 and 51% compared with two tall cultivars (>100 cm vine length) (Townley-Smith and Wright 1994). This discrepancy highlights that other characteristics in addition to vine length are important for the competitive ability of field pea.

Longer vines may also improve crop tolerance to weeds, but this effect is less consistent than the weed suppression benefits. Two of the above studies were in agreement in finding that longer vines were significantly correlated with smaller yield loss ( $r = -0.76$ ; Spies et al. 2011), and that yield loss under weedy conditions was greatest in short cultivars (Wall and Townley-Smith 1996). In contrast, some authors have observed either that yield loss due to weeds was similar in tall and short cultivars (Townley-Smith and Wright 1994), or that taller cultivars were less sensitive to weeds in one experiment but not another (McDonald 2003). Liebman (1989) reported that the taller cultivar grown in mixtures with barley and white mustard yielded 45% more grain than the shorter, however the yield potential of the two cultivars in the absence of weeds, and therefore their sensitivity to yield loss, is unknown. In cases where differences were observed, yield loss due to weeds in tall cultivars was on average 10 to 40% lower than in short cultivars (Wall and Townley-Smith 1996; McDonald 2003).

#### 2.1.3.2.2 Leaf Area Index

In addition to long vines, high leaf area index is demonstrated to improve weed suppression. Wall and Townley-Smith (1996) observed significant negative linear correlations ( $r = -0.41$  to  $r = -0.82$ ) between pea canopy leaf area index and wild mustard density or dry weight in seasons where cultivar differences were observed. Weed biomass declined at rates of -241 to -290 g m<sup>-2</sup> for each increase in leaf area index of 1. Organizing cultivars based on leaf area index generally explained weed suppression and tolerance similarly to vine length, although for some cultivars leaf area index was a better indicator of weed suppression than vine length. Differences in leaf area may therefore account for the strong weed suppression of a short compared with two

tall cultivars (Townley-Smith and Wright 1994), although this cannot be confirmed since leaf area index was not measured in the noted study.

#### 2.1.3.2.3 Biomass Production

While crop biomass production may be a response to, as well as a mechanism of competition, the ability of a pea cultivar to maintain high biomass in the presence of weeds provides a strong indicator of competitiveness. Spies et al. (2011) observed that cultivars that maintained greater biomass in the presence of weeds were strongly correlated ( $r = 0.90$ ) with greater weed suppression. In the same study, the cultivar that best maintained its biomass reduced weed growth by 73% compared with the cultivar that suffered the greatest biomass loss. This relationship between crop biomass loss and weed growth has been observed anecdotally as well: a cultivar that lost 10% of its biomass when grown in mixture reduced dry matter of competing cereal shoots, while a cultivar that suffered 29% biomass loss did not (Tofinga et al. 1993). This characteristic must be measured in the presence of weeds to distinguish between cultivars, since in the former study the 10 tested cultivars had similar biomass when grown weed-free (Spies et al. 2011).

#### 2.1.3.2.4 Early Crop Development

Characteristics such as vine length, leaf area index, and biomass accumulation are not static, but change over the life of the crop. Crop emergence, too, changes with time, albeit over a relatively short period at the beginning of crop growth. Very little work has been done on the temporal aspect of competition between field pea and weeds, however, significant effects of crop density or cultivar on weed emergence (Wall et al. 1991; Townley-Smith and Wright 1994; Wall and Townley-Smith 1996) suggest a role for strong early crop growth in competitive interactions. Significant negative correlations between leaf area index in the second week of crop growth, and final wild mustard biomass ( $r = -0.56$  to  $r = -0.70$ ; Wall and Townley-Smith 1996) give further support to the importance of early crop development.

The importance of rapid establishment of ground cover in competitive ability has been recognized in many crops, including rice, maize, sorghum, and potatoes (Wall 1983). In wheat, cultivars that had wider first leaves and higher crop dry matter at tillering were associated with greater weed suppression than those with narrower first leaves or lower early biomass (Lemerle

et al. 1996). In sugar beet, a cultivar with earlier canopy closure lowered survival of later emerging weeds, and reduced crop yield loss compared with two later closing cultivars (Lotz et al. 1991). An eco-physiological model that was developed to understand mechanisms of competition between crops and weeds affirmed these results, showing that relative growth of leaf area early in the season is the most important factor in determining competitive ability (Kropff et al. 1993). In terms of identifying more competitive field pea cultivars, this implies that important information may be missed if measures such as vine length, leaf area index, and biomass development are not taken multiple times during the season, beginning shortly after crop emergence. It also suggests that practices that promote rapid, uniform crop emergence may aid in weed suppression and tolerance.

#### 2.1.3.2.5 Leaf Type

Phenotypic variation in leaf type has been widely explored by pea breeders, and in addition to the wild (leafed) type, various “reduced haulm” types have been developed (Snoad 1974). Semi-leafless pea, the most common reduced haulm pea, expresses the recessive *afaf* (afila) gene, which converts all leaflets to tendrils. Reduced stipule pea expresses the recessive *stst* gene, which greatly reduces stipule size. Combinations of *afaf:stst* types (i.e. leafless pea) also exist.

The value of pea leaf type in competitive ability is not clearly demonstrated, despite considerable work in this area. In Saskatchewan, only semi-leafless cultivars are currently registered for seed production, although the leafed characteristic is present in some forage cultivars (Saskatchewan Ministry of Agriculture 2013). In other parts of the world, leafless and tare-leaf cultivars are also available (Heath and Hebblethwaite 1985; McDonald 2003). Several researchers have suggested that leafed pea should intercept more light, in turn improving their competitive ability compared with semi-leafless types (Wall et al. 1991; Tofinga et al. 1993; Harker et al. 2008). While greater light transmission through the canopy has been demonstrated with tare-leaf and leafless cultivars (Heath and Hebblethwaite 1985; McDonald 2003), differences in light transmission between semi-leafless and leafed cultivars have been inconsistent. One study found that a leafed cultivar had a significantly lower  $D_{50}$  value for light interception than the eight semi-leafless cultivars tested, indicating that it could intercept more light with fewer plants (Spies et al. 2010). However, a second leafed cultivar included in the

same study intercepted light similarly to most of the semi-leafless cultivars. Light interception differences observed between leafed and semi-leafless pea in other studies have either not been significant (McDonald 2003), or have been observed only after flowering (Heath and Hebblethwaite 1985). A reason for this inconsistency may be the fact that the foliage area among different semi-leafless cultivars can vary, and in fact can equal or exceed that of leafed cultivars (Kielinski and Blixt 1982).

In accordance with the failure to find consistent light transmission differences in the above studies, it has proven difficult to demonstrate that leafed cultivars are inherently more weed suppressive than semi-leafless cultivars. Greenhouse studies of pea competing with cereals or maize have found that leafed cultivars were able to suppress biomass or grain yield of the competing species, while semi-leafless cultivars were not (Tofinga et al. 1993; Semere and Froud-Williams 2001). In field-grown mixtures with oat, leafed cultivars had larger crowding coefficients than semi-leafless, indicating that they were stronger competitors in the mixtures (Rauber et al. 2001). In weed control studies, cultivars that were most suppressive of broadleaf weeds had the leafed characteristic (Townley-Smith and Wright 1994; Wall and Townley-Smith 1996; Harker et al. 2008; Spies et al. 2011), however two cultivars that were near isogenic for leaf type that were included in two of these studies had inconsistent effects on broadleaf weeds (Townley-Smith and Wright 1994; Wall and Townley-Smith 1996). Similarly, semi-leafless and tare-leaf cultivars had higher weed growth scores than leafed, but only in one experiment and with one weed type (McDonald 2003). Perhaps the best summation is that while leaf type may be a factor affecting weed suppression, other factors such as vine length (Wall and Townley-Smith 1996; Rauber et al. 2001; McDonald 2003) and measured leaf area index (Wall and Townley-Smith 1996) may be more important.

There is conflicting evidence that leafed cultivar yield tends to be more tolerant of competition. Three studies indicated that grain or biomass yield of leafed cultivars did not decrease to the same extent as semi-leafless cultivars when competing with weeds (Tofinga et al. 1993; Harker et al. 2008; Spies et al. 2011). Another study, however, found that two leafed and a single semi-leafless cultivar had similar yield responses to herbicide application, indicating that yield loss due to weeds was similar among cultivars (Townley-Smith and Wright 1994). Cases were also observed where tolerance was dependent on weed species or environmental conditions.

While weed-free yield was similar among cultivars, semi-leafless grain yield was significantly lower than leafed yield when competing with annual ryegrass, indicating greater yield loss (McDonald 2003). However, yield of all cultivars responded similarly to competition with wheat. Similarly, a semi-leafless cultivar grown at recommended seeding rates had higher yield loss in a year of high precipitation, but lower yield loss in years with low or intermediate precipitation (Wall et al. 1991). Studies on water economy of near-isogenic leafed and semi-leafless pea lines have shown that semi-leafless pea may require less water to accumulate higher leaf and pod dry matter than leafed or reduced-stipule cultivars (Alvino and Leone 1993), although another study concluded that normal leaf type and semi-leafless pea have similar performance under moisture stress (Martin et al. 1994).

Regardless of relative sensitivities to yield loss, semi-leafless pea may still offer yield advantages in the presence of weeds. Modern semi-leafless cultivars have been bred for high grain yield, which may lead to higher yield under competition, despite greater percentage loss (Harker et al. 2008; Spies et al. 2011).

#### 2.1.3.2.6 Determinacy, Time of Flowering and Relative Maturity

Relatively little is known about the effects of determinate versus indeterminate types, or relative times of flowering or maturity, on weed suppression or tolerance. A study of 21 Australian cultivars found that mid-season cultivars were more weed suppressive and higher yielding than early or late season cultivars. The yield differences were maintained regardless of weed presence or absence, indicating similar sensitivities to yield loss due to weeds (McDonald 2003).

#### 2.1.3.2.7 Flower Colour

Flower colour and seed pigmentation may indirectly affect competitive ability through crop emergence. In studies of pea lines isogenic for seed coat colour, the seed coats of unpigmented seeds cracked and separated from the cotyledons during imbibition, causing them to uptake water more rapidly than pigmented seeds (Powell 1989). This resulted in higher incidence of cotyledon damage, solute leakage, and greater susceptibility to fungal infection of the embryonic axis and cotyledons by *Pythium* spp. Similar results were reported with unpigmented versus pigmented faba bean lines (Kantar et al. 1996). While these reports have

not been advanced to produce a seeding rate recommendation, they imply that unpigmented cultivars should require higher seed numbers than pigmented lines to achieve the crop densities required to suppress weeds.

#### 2.1.3.2.8 Branching

Degree of branching is both a cultivar characteristic and a response to growing environment in field pea. The range in branching ability in commercial cultivars in Saskatchewan is relatively small and ranges from 0.85 to 1.99 branches plant<sup>-1</sup> for plants grown at very low densities (Spies et al. 2010), and from 0.19 to 1.21 branches plant<sup>-1</sup> at 50 plants m<sup>-2</sup> (Spies et al. 2011). Branching decreases on individual plants in response to increasing crop density. The rate of decrease may be as small as 0.0029 (Lawson 1982), or as high as 0.0097 (Spies et al. 2010) fewer branches for each additional plant per m<sup>2</sup>. At very low crop densities branching is also reduced by the presence of weeds (Lawson 1982), while at densities near 50 plants m<sup>-2</sup> or greater, more typical of a field pea crop, branching is unaffected by weeds (Lawson 1982; Spies et al. 2011).

Cultivar branching ability is not correlated with weed suppression or pea yield (Spies et al. 2011), and therefore is not a characteristic conferring competitiveness with weeds. However cultivars with greater branching ability are able to intercept more sunlight at low densities, and therefore may reach optimum yield at lower densities than cultivars that branch less (Spies et al. 2010). The range in optimum plant densities fell between 59 and 84 plants m<sup>-2</sup> for cultivars with branching potential of 1.66 and 0.85 branches plant<sup>-1</sup>, respectively.

#### ***2.1.3.3 Applications and Future Research***

Managing the pea canopy to enhance its competitive ability in the presence of weeds can increase yield by 40% or more, and reduce weed biomass by as much as 70%. Farmers coping with weeds are best served by seeding at rates at least 20% higher than recommended, and adjusting seeding rates for approximately 70% emergence, in addition to the tested seed germination levels. Selecting tall cultivars with high leaf area and biomass, which quickly establish ground cover through rapid emergence and early growth, will greatly aid in suppressing weeds and increasing yield. Cultivars with the leafed characteristic may also aid in weed suppression, although other factors such as vine length and measured leaf area may influence

their performance. Using isogenic pea lines to isolate individual morphological characteristics in competition studies will greatly enhance our understanding of their roles in weed suppression and tolerance.

## **2.2 Canopy Effects on Disease**

### **2.2.1 Symptoms and Crop Yield Loss due to Ascochyta Blight**

Ascochyta blight is the most prevalent disease of field pea in western Canada (Chang et al. 2007; Dokken-Bouchard et al. 2010; McLaren et al. 2010). Symptoms have been found in virtually all surveyed fields in Saskatchewan and Manitoba, at levels ranging from trace to severe. Symptoms of ascochyta blight are caused by a complex of three pathogens, *Mycosphaerella pinodes* (Berk. & Blox.) Vestergr., *Ascochyta pisi* Lib., and *Phoma medicaginis* var. *pinodella* (L. K. Jones) Boerema. *Mycosphaerella pinodes* is the dominant causal organism in Saskatchewan (Dokken-Bouchard et al. 2010), however, the other species of the complex are also frequently isolated from diseased pea crops in the Canadian prairies (Wang et al. 2000; Dokken-Bouchard et al. 2010; Morrall et al. 2010).

Symptoms of ascochyta blight begin at the lower nodes of the plant and progress upward (Roger and Tivoli 1996b; Béasse et al. 2000; Le May et al. 2005, 2009), resulting in higher disease levels at the base of the plant and lower levels toward the middle and top (Tivoli et al. 1996). Necrotic flecks merge over time to form large lesions on leaves, stems and pods. Severely diseased tissue senesces prematurely (Roger et al. 1999a; Béasse et al. 2000). Fruiting structures form on diseased tissue, and consist of pycnidia containing rain-dispersed conidia, and pseudothecia containing wind-borne ascospores. Pycnidia can form at any level of the plant after approximately 25% of the leaf area shows symptoms, whereas pseudothecia form only on senescent leaf tissue (Roger and Tivoli 1996b). Both pycnidia and pseudothecia may be present on the same organ, particularly at lower nodes.

Yield loss due to ascochyta blight may occur through loss of functional photosynthetic tissue, or through direct pod infection. Ascochyta blight severity on leaves is negatively correlated with pea growth rate and plant dry weight (Garry et al. 1998; Béasse et al. 2000). Both radiation interception efficiency (RIE) and radiation use efficiency (RUE) of the pea crop are reduced by ascochyta blight, with RUE reducing photosynthesis to the greatest extent

(Béasse et al. 2000; Le May et al. 2005). Both leaf and pod infection reduce yield by lowering seed number and seed weight (Tivoli et al. 1996; Garry et al. 1998; Beasse et al. 1999); however, pod infection primarily affects seed weight (Beasse et al. 1999). Seed yield loss in diseased plants may range from 6% to 68%, depending on factors such as plant growth stage at the time of infection, whether leaf or pod tissue is infected, and source inoculum concentration (Tivoli et al. 1996; Xue et al. 1997; Garry et al. 1998; Beasse et al. 1999).

### ***2.2.1.1 Factors Affecting Epidemic Development***

#### **2.2.1.1.1 Effects of Timing of Inoculation and Disease Onset**

Very early in the epidemic the youngest leaves may be more susceptible to infection than older leaves. Schoeny et al. (2008) demonstrated that lesions were significantly larger on leaves at the two youngest nodes two days after inoculation, but that differences in susceptibility had disappeared by five days post-inoculation. These differences disappeared more quickly on plants at the six leaf stage than at the 10 leaf stage.

Early disease onset reduces yield to a greater extent than later disease onset (Xue et al. 1997; Garry et al. 1998; Beasse et al. 1999). Disease onset prior to mid-flowering reduces yield more than onset at the beginning of seed filling (BSF), and the magnitude of yield decrease is strongly correlated with disease severity (Xue et al. 1997; Garry et al. 1998). Inoculating pods prior to mid-seed filling reduces yield more than inoculations after mid-seed filling (Beasse et al. 1999).

The mechanisms of yield decline differ for early versus late epidemics. While infections prior to pod formation reduce seed number (Garry et al. 1998) and increase incidence of seed infection (Xue et al. 1997), later infections lower individual seed weight (Garry et al. 1998). Pod infection does not affect seed water content, and therefore do not alter the timing of seed maturity (Beasse et al. 1999).

#### **2.2.1.1.2 Effects of Inoculum Density**

Disease severity increases with increasing source density of ascospores (Zhang et al. 2005) or conidia (Garry et al. 1998; Beasse et al. 1999; Roger et al. 1999a, 1999b; Béasse et al.

2000). However, environmental conditions were shown to be more important than inoculum availability in predicting onset of ascochyta blight epidemics in the field (Schoeny et al. 2007).

#### 2.2.1.1.3 Effects of Environment

##### *2.2.1.1.3.1 Light Intensity*

The complete absence of light results in production of sterile pycnidia and pseudothecia on artificial media (Roger and Tivoli 1996a), however, continuous darkness would not occur under field conditions. Similar disease levels can be reached in pea plants growing under a wide range of light intensities according to source inoculum concentration (Béasse et al. 2000). The decrease in photosynthesis for each disease score was shown to be similar for light intensities ranging from 100 to 2000  $\mu\text{mol m}^{-2}\text{s}^{-1}$ . At a low light intensity of 40  $\mu\text{mol m}^{-2}\text{s}^{-1}$ , the observed reduction in photosynthesis in diseased relative to healthy leaves was smaller than at higher light intensities, but this effect decreased as disease severity increased (Béasse et al. 2000). Therefore light intensity likely plays a very minor role in field epidemics.

##### *2.2.1.1.3.2 Temperature*

Temperature limits or encourages several stages of the infection process. At an optimum temperature of 20°C, incubation under continuous moisture for 4-5 h is required for lesions to form following exposure to ascospore inoculum (Carter 1963). Temperatures below 20°C lengthen the moisture duration required for symptoms to appear; moisture periods required for lesion development are 5-6 h at 15°C, 7-8 h at 10°C, and 46-47 h at 5°C. The dependence of pseudothecia formation, ascospore release from pseudothecia, and different stages of infection by ascospores on temperature has not been described.

Detailed studies of the relationships between temperature, moisture, and various stages of the infection processes have been conducted for *M. pinodes* conidia on pea seedlings in a controlled environment (Roger et al. 1999a, 1999b). Under continuous moisture regimes, conidial germination began after 2 h, appressoria were observed after 4 h, and hyphal penetration began after 8 h at 15 to 30°C. At optimal temperatures of 15 to 25°C an incubation period of one day was needed for symptoms to appear, and an intermediate disease score was reached after three to four days. Pycnidia were observed three to four days post inoculation at optimal

temperatures. Temperatures of 5 and 10°C delayed infection processes, and temperatures of 5, 10, and 30°C resulted in low disease scores and limited pycnidial formation.

#### *2.2.1.1.3.3 Continuous versus Interrupted Leaf Wetness*

Moisture is needed for a minimum of 2 h for conidia to germinate, and infection does not take place in its absence (Roger et al. 1999b). The viability of conidia is also limited, such that a germination rate of only 2% was observed if moisture was not made available until 12 days after inoculation. A study of the effects of dry periods during the infection process demonstrated that when moisture was removed less than 6 h after inoculation, disease development was severely limited. Disease reduction occurred when the dry period began before appressoria had formed; longer initial wetting periods of 12-72 h promoted appressorium formation and hyphal penetration, and resulted in higher disease severity. Regardless of the initial moisture levels, dry periods of 14 or 21 days slowed symptom development, particularly if inoculum levels were low and moisture conditions were not ideal.

#### *2.2.1.1.3.4 Type of Moisture*

The source of moisture is also important for ascochyta blight development. A relative humidity threshold of 70% was calculated to most accurately predict the onset of epidemics from airborne ascospore inoculum in the field (Schoeny et al. 2007). For indoor inoculations with conidial suspensions, leaf wetness shortened incubation period, increased disease progress, and decreased the time to pycnidial formation compared with high relative humidity moisture regimes (Roger et al. 1999a, 1999b). The moisture duration needed for conidial germination, appressorium formation, and hyphal penetration were not significantly influenced by the source of the moisture (leaf wetness versus high relative humidity).

### **2.2.2 Mechanisms of Canopy Effects on Disease Levels**

In addition to external factors such as pathogen inoculum availability and environmental conditions, characteristics of the pea canopy itself may influence symptom severity and yield loss. Spatial characteristics of pea canopies may moderate disease progress by altering microclimate, inoculum interception by plant tissue, and/or tissue receptivity to infection (Tivoli et al. 2013). Since canopy characteristics change over the life of the crop, the relative importance of each of these mechanisms within the same crop canopy may change over time.

### ***2.2.2.1 Effects on Temperature and Moisture in Pea Crop Canopies***

Although several reports have suggested that ascochyta blight development in pea canopies with different morphological characteristics is likely influenced by differences in canopy microclimates (Roger et al. 1999b; Le May et al. 2009; Schoeny et al. 2010), only one study (Schoeny et al. 2010) has directly measured the microclimate under different pea crop canopies in the field. In that study, the authors observed that a monocrop of one pea cultivar cooled the air temperature by up to 2.2°C, while a cereal-pea intercrop canopy showed less of a cooling effect. While temperature effects were small, the differences in moisture duration of the two canopies were more pronounced. After pea crop flowering, the daily duration of leaf wetness in the cereal-pea intercrop was consistently shorter, in some cases by as much as 15 h, than in the pea monocrop. As expected, under moderate and severe disease pressure, disease severity on pods and stems was significantly lower in the intercrop. Although the authors did not take quantitative measures of canopy density such as LAI, which may have offered insight into the relationships between canopy structure, microclimate, and ascochyta blight epidemic development, the study illustrates that altering canopy structure can have a substantial impact on crop microclimate.

### ***2.2.2.2 Effects on Spore Dispersal***

#### **2.2.2.2.1 Airborne Ascospores**

The dynamics of ascospore dispersal in the field are well-studied for *M. pinodes*. Peak release occurs during the second evening following a rainfall event (Zhang et al. 2005); however ascospores are also released on rainless days, particularly when there is dew or high relative humidity (Carter 1963; Roger and Tivoli 1996b; Zhang et al. 2005). Spatial progress of ascochyta blight epidemics is influenced by wind direction. Disease levels were found to decline by 50% within 45 m in directions downwind of ascospore inoculum, while the same decrease occurred within 16 m in upwind directions (Zhang et al. 2004).

Several studies have found that ascospore inoculum is available throughout the season, suggesting a role in not only initiating epidemics, but in secondary spread as well. In French winter plantings, counts of lesions on trap plants upwind of test plots, which were inferred to be caused by ascospores, reached two peaks, with the first peak occurring between mid-September

and mid-December, and a second, larger peak between mid-March and mid-May (Schoeny et al. 2007). In summer plantings, ascospores were found in traps throughout the season, from the end of May to the end of July (Roger and Tivoli 1996b). In studies in Australia, ascospores were found in traps from the beginning of May to the end of August, with peaks occurring in early June following the first appearance of pseudothecia on senescent leaves, and again between late July and early August (Carter 1963). In experiments in western Canada the majority of ascospores were trapped within 23 days of inoculation (Zhang et al. 2005), however, trap placement at 1 m above the crop canopy may account for the limited catches later in the season. Roger and Tivoli (1996b) found that before canopy closure, most ascospores were trapped 1 m above the soil surface, while after canopy closure the majority of catches occurred between 0 and 60 cm above the ground. After canopy closure, foliage may present a barrier to ascospore dispersal, since pseudothecia are formed close to the base of the plant (Roger and Tivoli 1996b). Canopy characteristics may therefore play a role in spatial disease progress by encouraging or limiting ascospore escape from crop foliage late in the season; however this aspect has not been examined in detail.

#### 2.2.2.2.2 Rain-Splashed Conidia

Similar to ascospores, peak releases of *M. pinodes* conidia occur in the evening during or following a rainfall event (Zhang et al. 2005). During rainfall, conidia are primarily splashed downward to lower nodes, and contribute to localized spread of the disease on the source and neighbouring plants (Schoeny et al. 2008). The largest numbers of conidia are trapped at the soil surface (Roger and Tivoli 1996b), and they very rarely are trapped at a height of 1 m (Zhang et al. 2005).

Detailed studies of the effects of different pea crop canopies on conidial splash dispersal have been conducted using a rainfall simulator (Schoeny et al. 2008, 2010). The authors compared the number of lesions on plants at specific distances from an inoculum source, either standing alone or within canopies. In an open canopy, comprised of plants at the six-leaf stage, conidia dispersal was enhanced, while in canopies at the eight- and ten-leaf stages dispersal was limited (Schoeny et al. 2008). In a second series of experiments, the effects of a reduced density (50%) pea monocrop and a 50:50 cereal-pea intercrop were compared with a high density pea monocrop (Schoeny et al. 2010). While lowering the planting density gave the greatest reduction

in dispersal, in canopies at the five- to seven-leaf stage the wheat plants added an additional barrier to splash relay. These studies show that the relative proximity of host tissue in pea canopies may enhance or subdue dispersal of *M. pinodes* conidia.

### ***2.2.2.3 Effects on Tissue Receptivity to Infection***

Tissue at different levels of the pea plant show different levels of susceptibility to ascochyta blight infection. First, the youngest tissue at the top of the pea plant may initially develop larger lesions than tissue on the rest of the plant, but the differences disappear within a few days of inoculation (Schoeny et al. 2008). Second, senescent pea tissue is more susceptible to ascochyta blight infection than green tissue. When whole plants were inoculated, disease severity increased with tissue age, until it reached a plateau that corresponded with tissue yellowing (Richard et al. 2012). This relationship implies that canopies with lower light availability at their base may have more severe ascochyta blight symptoms due to increased senescence of lower leaves.

## **2.2.3 Canopy Characteristics that Moderate Ascochyta Blight Development**

Although very few studies have been conducted linking canopy characteristics with ascochyta blight development, those available have identified several characteristics associated with reduced or elevated disease levels. These characteristics may be measured at the level of the canopy, or the level of individual plants or cultivars.

### ***2.2.3.1 Canopy Level***

#### **2.2.3.1.1 Lodging**

Ascochyta blight severity increases with the degree of lodging (Banniza et al. 2005; Wang et al. 2006). Reduced lodging treatments developed similarly low disease levels to fungicide-treated plots, with approximately 40 and 24% lower disease levels on stems and leaves than in untreated plots (Wang et al. 2006). Preventing lodging increased seed yield by 31%, and 1000 seed weight by 10% relative to controls (Wang et al. 2006). However, it is not clear what proportion of this yield increase was due to reduced ascochyta blight severity compared with reduced lodging in itself, since fungicidal control in reduced lodging treatments was incomplete, and since yield increases of up to 46% have previously been observed in reduced lodging

treatments without mention of whether ascochyta blight was present (Schouls and Langelaan 1994). Regardless it is clear that reducing lodging is desirable to lower disease and increase yield.

#### 2.2.3.1.2 Crop Density

The effects of sowing density on disease progress have been shown to be localized to particular times in crop development, and particular nodes of the plant. Densities of 99 plants m<sup>-2</sup> or higher may encourage disease development between the beginning of flowering (BF) and BSF (Béasse et al. 2000). Although yield data were not presented, it was previously shown that infections during this period can have a substantial impact on yield (see section 3.2.1).

The measured disease increase may also depend on the nodes examined; on stems between nodes 5 and 15, and leaves between nodes 8 and 18, disease severity increased as sowing density increased from 30 to 120 plants m<sup>-2</sup> (Tivoli et al. 1996). Because nodes located near the centre and top of the plant are responsible for the majority of the pea plant's photosynthetic activity (Béasse et al. 2000; Le May et al. 2005), this effect would also be expected to reduce yield. Indeed, the authors showed a yield reduction of 18 to 37% that was significantly correlated with the disease parameters at these nodes and increasing planting densities (Tivoli et al. 1996). In contrast, in the absence of disease, planting density had no adverse effects on yield.

#### 2.2.3.1.3 Mean Distance between Nodes

The Mean Distance between Nodes (MDN) describes the spatial relationship between the node assessed, the two nodes directly above and below, and the same three nodes on the eight surrounding plants. Large MDN resulted in higher disease severity on leaves (Le May et al. 2009). While this result is not intuitive, it is very likely that a complex and changing relationship exists among MDN, spore dispersal, and microclimate. The parameter is influenced by cultivar characteristics (branching ability, internode length, and vine length), and planting density (distance between plants and vine length).

### ***2.2.3.2 Cultivar Level***

#### 2.2.3.2.1 Leaf Area Index

Leaf Area Index (LAI) is a measure of canopy density that describes cumulative leaf area relative to ground area covered. LAI may be measured over the entire plant (Schoeny et al. 2008, 2010), or as a function of the different nodes of the plant (Béasse et al. 2000; Le May et al. 2005, 2009). High cumulative LAI above the node assessed was strongly associated with high disease severity at that node (Le May et al. 2009), suggesting that leafiness at the middle and top of the plant creates ideal conditions for disease development in the canopy below.

The LAI profile is important to both the RIE and the RUE of the canopy, which impacts total photosynthesis. The impact of ascochyta blight on growth is highest if disease is severe at the nodes at and above maximum LAI (Béasse et al. 2000). The location of the maximum LAI as a function of node position was shown to be similar across cultivars, located at nodes 8-15 (Le May et al. 2005, 2009), however different cultivars can show large differences in maximum LAI location as a function of distance up the stem (Le May et al. 2009). The value of the maximum LAI can also differ significantly among cultivars (Le May et al. 2009). Short, dense canopies, with high maximum LAI located low on the stem, are likely to develop more severe symptoms and show greater reductions in photosynthesis.

#### 2.2.3.2 Internode Length

Short internodes are associated with higher disease levels on leaves or reproductive structures at the two adjacent nodes (Le May et al. 2009). Internode length is determined by cultivar characteristics and planting density, through its effect on plant vine length (Tivoli et al. 1996).

#### ***2.2.3.3 Applications and Future Research***

Significant potential exists to moderate ascochyta blight severity through canopy or plant architectural traits. The strongest evidence indicates that minimizing lodging and lowering seeding rates reduces ascochyta blight severity, and increases yield in its presence. Further studies should be conducted to optimize seeding rates in inoculated plots, particularly under organic conditions where high seeding rates are recommended to control weeds. Very few studies have been conducted linking other canopy traits with ascochyta blight development. Those available indicate that traits such as mean distance between nodes, leaf area, and internode length are also important. However the relative importance of these traits in reducing disease

severity and increasing yield is not established. Furthermore, the extent to which these characteristics may differ among canopies and cultivars is unknown, since very few cultivars have been examined to date. Therefore, further research is needed before canopy traits can be confidently applied to manage ascochyta blight in the field.

## **3.0 YIELD AND AGRONOMIC ADVANTAGES OF LEAFED AND SEMI-LEAFLESS FIELD PEA MIXTURES UNDER ORGANIC MANAGEMENT**

### **3.1 Introduction**

Organic crop production in Canada occupies approximately 0.7 million hectares, 83% of which reside in the prairie provinces of Alberta, Saskatchewan, and Manitoba (Macey 2010). Field pea is an important organic crop in the Canadian prairies, and is grown both for grain and green manure. Field pea is known to increase soil reserves of nitrogen (Stevenson and van Kessel 1996; Maidl et al. 1996) and provide yield benefits in rotations (Stevenson and van Kessel 1996), which are of increased importance in the absence of fertilizers. However, growing field pea organically can be challenging, since the crop is relatively sensitive to weed competition compared with other crops such as barley and canola (Harker 2001). In central Alberta, 67% of conventional pea fields surveyed experienced yield loss due to weeds, with an average loss of 46% (Harker 2001).

Growing more competitive cultivars can improve weed control and mitigate yield loss due to weeds in field pea. Long vines (Wall and Townley-Smith 1996; McDonald 2003; Spies et al. 2011), high leaf area index (Wall and Townley-Smith 1996), and the ability to maintain biomass in the presence of weeds (Spies et al. 2011) are cultivar characteristics that are associated with improved weed suppression in field pea cultivars. The leaf type of field pea cultivars may also play a role in their competitive ability. Semi-leafless cultivars, the more common of the two leaf types grown on the Canadian prairies, express the recessive *afaf* (afila) gene, which modifies all leaflets to tendrils (Snoad and Gent 1976; Kielpinski and Blixt 1982). Semi-leafless cultivars are favoured for their high lodging resistance and seed yield (Snoad and Gent 1976; Kielpinski and Blixt 1982; McDonald 2003; Harker et al. 2008). Wild type, or “leafed” pea cultivars are typically grown in the Canadian prairies for biomass used as forage or green manure. While characteristics such as vine length or leaf area index may be better indicators of competitive ability than leaf type (Townley-Smith and Wright 1994; Wall and Townley-Smith 1996; Rauber et al. 2001; McDonald 2003), reports show a general tendency of leafed cultivars to be more weed suppressive (Townley-Smith and Wright 1994; Wall and

Townley-Smith 1996; Harker et al. 2008; Spies et al. 2011), and less sensitive to weed competition than semi-leafless types (Tofinga et al. 1993; Harker et al. 2008; Spies et al. 2011).

Intercropping experiments have shown that yield is improved if complementary crops are grown together rather than separately in monocultures. There are many examples of pea-cereal intercrops surpassing yields of pea and cereals grown alone (Semere and Froud-Williams 2001; Hauggaard-Nielsen and Jensen 2001; Rauber et al. 2001; Saucke and Ackermann 2006; Hauggaard-Nielsen et al. 2006; Neumann et al. 2009). Field pea roots are able to modify their rooting profile (Tofinga and Snaydon 1992) and fix greater quantities of nitrogen from the atmosphere when grown in mixtures with cereals (Tofinga et al. 1993; Soon et al. 2004), which allows the intercrop to use resources more efficiently than either crop alone. Additionally, other mechanisms such as improved weed control (Liebman and Robichaux 1990), and reduced ascochyta blight severity on pea in mixtures with cereals (Fernández-Aparicio et al. 2010; Schoeny et al. 2010) may contribute to yield improvements in intercrops.

While resource use is expected to be similar among cultivars of the same crop, mixtures of complementary cultivars have also been observed to improve yield (Schouls and Langelaan 1994; Cowger and Weisz 2008), or improve yield stability (Pridham et al. 2007) compared with single-cultivar crops. The mechanisms of yield improvement may be specific to the crop and cultivars used. In field pea, the poor standing ability of leafed pea limits yield in sole crops. Preventing lodging by building supports for the crop was shown to improve leafed pea yield by as much as 86%, resulting in similar seed yield to a semi-leafless cultivar (Schouls and Langelaan 1994). Combining a semi-leafless with a leafed cultivar in mixtures of 53 to 67% semi-leafless pea similarly improved its lodging resistance, and led to yield improvements of as much as 11% above either cultivar grown alone (Schouls and Langelaan 1994). Growing a competitive leafed with a semi-leafless cultivar under weedy conditions may bring additional yield increases, by reducing the yield limitation on semi-leafless pea imposed by weeds. However, the performance of leafed and semi-leafless pea mixtures competing with weeds has not been tested.

A four site-year study was conducted in central Saskatchewan to examine mixtures of leafed and semi-leafless field pea as a yield enhancement and weed management tool for organic production. The hypothesis was that the mixtures would improve yield compared with either

cultivar alone, by improving the weed suppression of the semi-leafless cultivar, and the lodging resistance of the leafed cultivar.

## **3.2 Materials and Methods**

### **3.2.1 Site Description and Growing Conditions**

The experiment was conducted on organically managed land in 2011 and 2012 at the University of Saskatchewan's Kernen Crop Research Farm near Saskatoon (latitude 52°09', longitude 106°32'), and a producer's farm near Vonda, central Saskatchewan (2011: latitude 52°19', longitude 106°4'; 2012: latitude 52°18', longitude 106°3'). Soil at the Kernen site belonged to the Sutherland soil association, and had a loam texture and pH of 7.2. The soil at the Vonda site belonged to the Oxbow soil association, and had a clay loam (2011) or loam texture (2012), with a pH of 8.0 to 8.2. The land at all sites was cultivated in the fall, and again in the spring, prior to planting. At all experimental sites pea was seeded onto wheat stubble.

### **3.2.2 Experimental Design and Management**

The experiment used a 2 x 5 factorial treatment design on a randomized block design. The two factors were target plant densities (88 and 176 plants m<sup>-2</sup> in 2010, or 88 and 132 plants m<sup>-2</sup> in 2011-12) and percentage of each of the two cultivars sown (0:100, 25:75, 50:50, 75:25, and 100:0% semi-leafless to leafed). Actual seeding rates were based on the germination rate of the seed, and an expected emergence of 75%. All treatment combinations were replicated four times per site, with the exception of the Vonda 2012 site, which had three replicates.

Pea was seeded into moisture in May (Table 3.1), with a cone seeder in 1.8 x 6 m plots that consisted of nine rows 20 cm apart. Seeds of the two cultivars were mixed prior to sowing. TagTeam® granular inoculant (*Penicillium bilaii* and *Rhizobium leguminosarum*, Novozymes North America Inc., Franklinton, North Carolina, U.S.A.) was applied to the seed row at the recommended rate of 4.6 kg ha<sup>-1</sup>. Weeds were mechanically controlled prior to canopy closure using harrows or a rotary hoe according to local practice for organic producers. A Canada thistle (*Cirsium arvense*) infestation was hand-weeded at the Kernen site in 2011 from prior to emergence until canopy closure, due to the patchy occurrence and extremely competitive nature of the weed. Aside from inoculant application, plots received no fertilizer, pesticide applications, or irrigation.

**Table 3.1:** Dates of planting, harvest, and plant measurements for 2011-2012 experiments in central Saskatchewan.

	<b>2011</b>		<b>2012</b>	
	Kernen	Vonda	Kernen	Vonda
Seeding	May 24	May 25	May 21	May 14
Crop and Weed Counts	June 30	June 30	June 21	June 7
Vine length Measurement 1	-	-	June 21	June 19
Vine length Measurement 2	-	-	August 21	August 8
Lodging Measurement	August 5	August 11	August 4	July 26
Biomass Sampling	August 15	August 6	August 13	August 10
Harvest	September 6	September 12	September 7	August 21

Cultivars used for the experiment were developed by the Crop Development Centre (CDC), University of Saskatchewan. CDC Sonata (leafed), and CDC Dakota (semi-leafless) were chosen based on two criteria: market class and vine length. First, the cultivars were chosen from two different market classes so that seeds could be separated by colour to determine relative yield. Second, they were chosen for their similar vine length (Table 3.2), to control for the effects of vine length on competitive ability (Wall and Townley-Smith 1996; McDonald 2003; Spies et al. 2011).

**Table 3.2:** Market type, morphological, and physiological characteristics of pea cultivars used in 2011-2012 field experiments in central Saskatchewan.

<b>Characteristic</b>	<b>CDC Sonata</b>	<b>CDC Dakota</b>
Market Type	Forage	Dun
Leaf Type	Leafed	Semi-leafless
Vine Length (cm)	85	85
Maturity	Late	Medium-late
Lodging Resistance	Fair	Good

2012 Variety Descriptions (Saskatchewan Pulse Growers 2012)

### 3.2.3 Data Collection

Pea and weed emergence was counted approximately three to four weeks after planting at each site. Pea plants of each cultivar were counted in two 1 m<sup>2</sup> quadrats per plot, and weeds were identified and counted by species in two 0.25 m<sup>2</sup> quadrats per plot. In 2012, the average vine length of each canopy was estimated prior to canopy closure, and again prior to harvest, by measuring the length of the main stem of five consecutive plants at two locations per plot.

Canopy lodging was measured during pod filling (approx. BBCH 75 to 79), 10 to 11 weeks after planting. A lodging index was used that represented a ratio of canopy height to vine

length of one plant of each cultivar at two locations per plot. The two cultivars were weighted equally in the calculation.

Crop and weed aerial biomass was sampled from two 0.25 m<sup>2</sup> quadrats per plot prior to natural crop desiccation by removing the aerial plant parts at the soil line. Biomass samples were oven-dried in paper bags at 70°C for 48 h prior to weighing. At harvest seven rows were harvested from the middle of each plot using a small plot combine (harvested area = 8.4 m<sup>2</sup>). After removing dockage, seeds of the two cultivars were separated using a colour sorting machine (Satake Scan Master II) and weighed separately. For each target crop density, relative yield of the leafed cultivar in mixture relative to monoculture were calculated as

$$RY_L = Y_{LS} / (p_L \times Y_L) \quad (3.1)$$

and relative yield of the semi-leafless cultivar in mixture relative to monoculture were calculated as

$$RY_S = Y_{SL} / (p_S \times Y_S) \quad (3.2)$$

where  $Y_{LS}$  or  $Y_{SL}$  is the yield of leafed or semi-leafless pea in mixture with semi-leafless or leafed pea, respectively,  $Y_L$  or  $Y_S$  is the yield of leafed or semi-leafless pea in a pure stand at the corresponding total density, and  $p_L$  or  $p_S$  is the proportion of leafed or semi-leafless pea in the mixture (adapted by Fowler (1982) from de Wit (1960)).

### 3.2.4 Statistical Analyses

Data were analyzed in SAS version 9.2 using the MIXED procedure (Littell et al. 2006). Site-year, replicate, and interactions of treatments with site-year were assigned as random effects, and percentage of semi-leafless in mixture was assigned as a fixed effect. The variable vine length was analyzed as a repeated measure using sampling date as the repeated factor, and plot within site-year as the subject. Treatment effects were declared significant at  $P < 0.05$ .

Exploratory analysis indicated that crop emergence varied depending on the percentage of the semi-leafless cultivar in the mixture ( $P < 0.05$ ). Actual crop emergence was tested as a possible covariate to account for these differences, and was determined significant in the case of weed and crop biomass, and crop yield. Target seeding rate was excluded from models to simplify the analysis. For covariate analyses the percentage of semi-leafless pea was considered

a class variable (Littell et al. 2006), and Fisher’s protected least significant difference (LSD) test was used to detect significant differences among the regression lines of each percentage semi-leafless pea against crop emergence. Orthogonal contrasts were used to test for significant linear, quadratic, or cubic relationships (Littell et al. 2006). Several models were tested that included different combinations of covariate with treatment, and final models were chosen based on the lowest AIC values for each response variable. In all cases where crop emergence was a significant covariate, a common slope model gave the best fit. For variables where crop emergence was not a significant covariate it was excluded from final models, and percentage semi-leafless pea was treated as a continuous (regression) variable.

Data were tested for homogeneity of variances prior to analysis, and heterogeneous variances were corrected if possible using transformations (Table 3.3). Where data were transformed for analysis, means were back-transformed for presentation. If assumptions of homogeneity could not be met for all factors (site-year, percentage semi-leafless, and seeding rate), variances were modeled for the remaining factor using a repeated/group statement (Littell et al. 2006). The best fit covariance structure to model variance was chosen using a combination of lowest AIC values and lowest number of parameters.

**Table 3.3:** Transformations used to meet assumption of homogeneity of variances, and whether and for which factors variances were modeled using repeated/group statement for PROC MIXED in SAS.

<b>Variable</b>	<b>Transformation Used</b>	<b>Modeled variance for</b>
Crop Emergence	None	Seeding Rate
Canopy Vine Length	None	None
Weed Density	None	Site-year
Lodging	None	Site-year
Weed Biomass	Ln	Site-year
Total Crop Biomass	Ln	Site-year
Relative Yield of Leafed Pea	1/y	Site-year
Relative Yield of Semi-leafless Pea	1/y	None
Total Crop Yield	√	None

### 3.3 Results and Discussion

#### 3.3.1 Environmental Conditions

In both seasons growing conditions were cooler in May, and warmer and drier in September, than the thirty year historical average (Table 3.4). The 2012 growing season was wetter than the thirty year average, particularly at the beginning of the season.

**Table 3.4:** Observed monthly weather conditions in 2011-2012 and 30-year climate averages for Saskatoon, central Saskatchewan.

	<u>Mean Temperature (°C)</u>			<u>Total Precipitation (mm)</u>		
	2011	2012	Historical average	2011	2012	Historical average
May	10.4	9.9	11.8	27.0	142.6	43.5
June	15.2	15.8	16.0	105.2	97.0	60.5
July	18.4	19.7	18.3	61.6	82.8	57.3
August	17.8	17.7	17.6	25.0	65.8	35.4
September	14.3	13.2	11.5	10.4	0.8	30.6
AVERAGE	15.2	15.3	15.0			
TOTAL				229.2	389.0	227.3

Annual values from permanent weather station at Kernen Crop Research Farm  
 Historical values from Saskatoon SRC Weather Station (52°09'00.000"N, 106°36'00.000"W), National Climate Data and Information Archive, Environment Canada, 1971-2000.

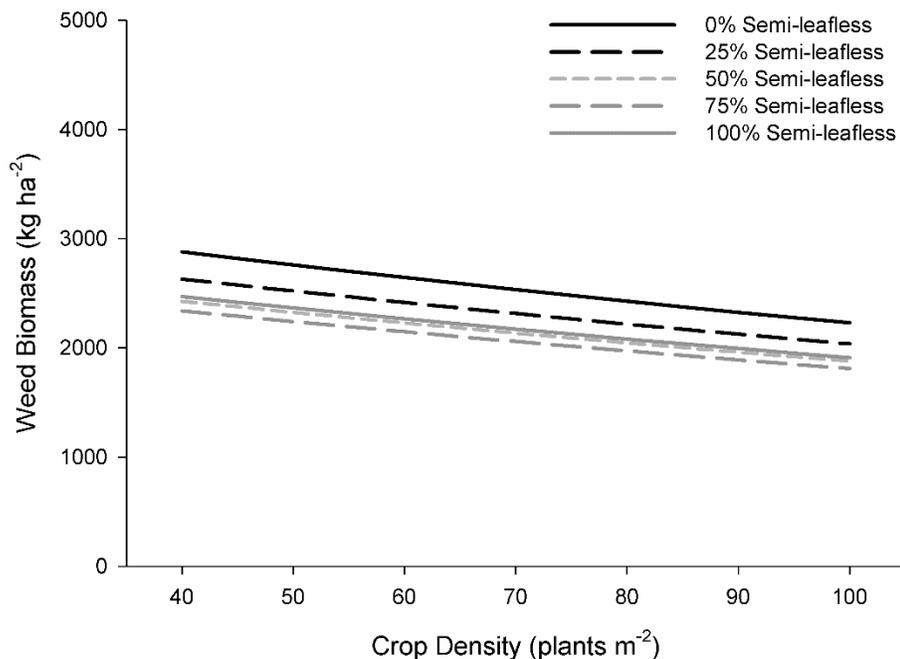
### 3.3.2 Weed Population and Effects of Mixtures on Weeds

An abundant weed community was present at all sites, with weed densities in plots averaging 870 weeds m<sup>-2</sup>, and end of season weed biomass averaging 2560 kg ha<sup>-1</sup>. Weed densities did not differ among plots with different mixture compositions ( $P = 0.9378$ ). The weed community was primarily composed of broadleaf weeds at Kernen, and grassy weeds at Vonda (Table 3.5). At each site, wild mustard (*Sinapis arvensis*), common lambsquarters (*Chenopodium album*), redroot pigweed (*Amaranthus retroflexus*), green foxtail (*Setaria viridis*), and wild oat (*Avena fatua*) accounted for 95% or greater of the weed population (Table 3.5).

**Table 3.5:** Common weeds at Kernan and Vonda experimental sites in 2011-2012.

Weed (common name)	<u>Weed</u> (botanical name)	<u>Percentage of Weeds (%)</u>			
		<u>2011</u>		<u>2012</u>	
		Kernan	Vonda	Kernan	Vonda
Wild Mustard	<i>Sinapis arvensis</i>	25	39	57	19
Common Lambsquarters	<i>Chenopodium album</i>	16	6	9	<1
Redroot Pigweed	<i>Amaranthus retroflexus</i>	27	<1	16	<1
Green Foxtail	<i>Setaria viridis</i>	26	14	13	30
Wild Oat	<i>Avena fatua</i>	1	40	2	49
ALL BROADLEAF		72	46	85	21
ALL MONOCOT		28	54	15	79

Weed biomass decreased with crop density following a near-significant trend ( $P = 0.07$ ), and model fit was improved by including crop density as a covariate. Canopies of each composition shared a similar rate of weed biomass decrease with increasing crop density. For all cultivar combinations, increasing crop density by between two and three plants per metre squared resulted in a one percent weed biomass reduction. Mixture and monoculture canopies differed in their intercepts, indicating that canopies of different cultivar compositions had different weed suppressive abilities ( $P < 0.0001$ ; Fig. 3.1). Incorporating semi-leafless pea into mixtures with leafed pea generally improved weed suppression compared with the leafed cultivar grown alone. Mixtures of 50% and 75% semi-leafless pea were significantly more weed suppressive than leafed monocultures. At the average crop density of 69 plants  $m^{-2}$ , growing 50% and 75% semi-leafless mixtures reduced weed biomass by 16 and 19% compared with the leafed monoculture, respectively (Fig. 3.1). Semi-leafless monocultures also trended towards greater weed suppression than leafed ( $P = 0.09$ ) and were similarly weed suppressive to all mixtures. The present results indicate that the semi-leafless cultivar, CDC Dakota, was a relatively strong competitor, and its weed suppression did not improve through mixture with leafed pea. In fact the opposite was true: weed suppression of the leafed cultivar improved through mixture with the more competitive semi-leafless cultivar.



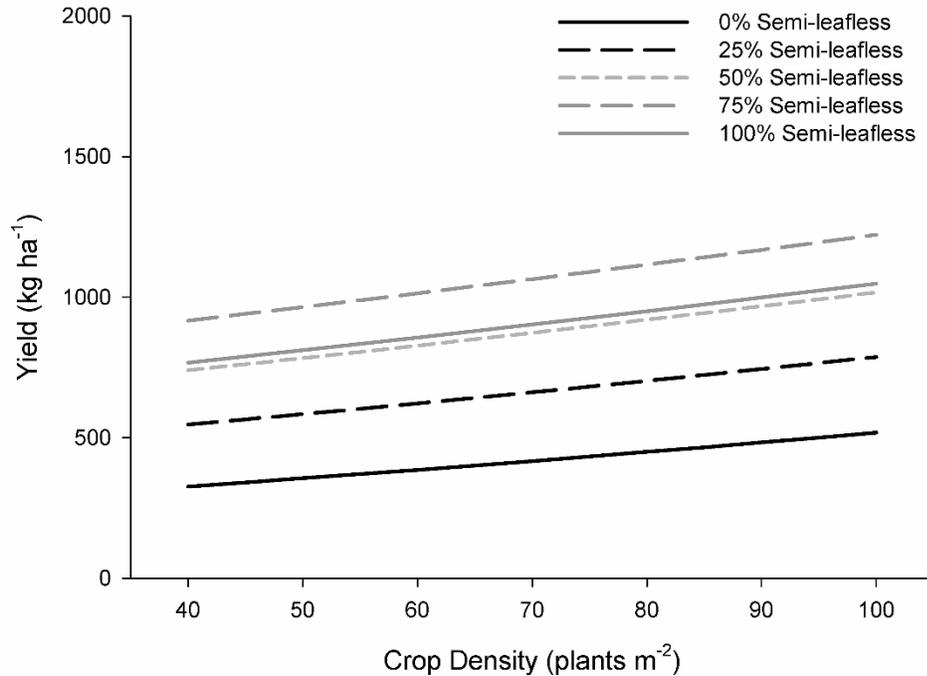
**Figure 3.1:** Predicted weed biomass response to crop density and mixing proportion of leafed with semi-leafless field pea over four site-years in central Saskatchewan.

### 3.3.3 Grain and Biomass Yield of Mixtures under Competition from Weeds

Crop yield varied by site-year, and was considerably lower at Vonda than Kernen. At Kernen, yield reached 57-60% of the provincial 10-year average for conventional production of 1947 kg ha<sup>-1</sup> (Saskatchewan Ministry of Agriculture, 2011). At Vonda, attained yield was 23-34% of the provincial average. Site differences, however, did not change the overall response of crop yield to monoculture and mixture treatments.

Yield tended to increase as crop density increased ( $P = 0.06$ ), and monoculture and mixture yield was modeled using crop density as a covariate to account for this effect. Grain yield was strongly influenced by cultivar composition of monocultures and mixtures ( $P < 0.0001$ ; Fig. 3.2). The 75% semi-leafless mixture showed a significant yield advantage compared with monocultures of either component cultivar ( $P < 0.05$ ). At the average crop density of 69 plants m<sup>-2</sup>, the yield difference amounted to a 22% increase compared with the semi-leafless monoculture, and a 230% increase compared with the leafed monoculture. All remaining mixtures out-yielded leafed, but did not surpass the yield of semi-leafless

monocultures. These results confirm the hypothesis that mixtures increase seed yield under competition from weeds, a major production constraint for organic producers.



**Figure 3.2:** Predicted crop yield response to crop density and mixing proportion of leafed with semi-leafless field pea over four site-years in central Saskatchewan.

Crop biomass, like grain yield, increased significantly with crop density ( $P = 0.0008$ ), and addition of semi-leafless pea ( $P < 0.0001$ ; Table 3.6). After treatment means were adjusted for unequal densities, the semi-leafless monoculture and all mixtures improved crop biomass compared with the leafed monoculture ( $P < 0.0005$ ). Although mixture biomasses did not differ significantly from the semi-leafless monoculture ( $P > 0.2794$ ), biomass yield showed a similar peak to grain yield in mixtures with 75% semi-leafless pea, which yielded 12% more biomass than the semi-leafless monoculture (Table 3.6). Biomass yield showed a highly significant quadratic response to mixture ( $P = 0.0002$ ), confirming that yield peaked before declining at the highest percentage of semi-leafless pea.

**Table 3.6:** Above-ground crop biomass as affected by mixture of leafed and semi-leafless field pea in 2011-2012 growing seasons.

<b>Cultivar Composition</b>		Crop Biomass (kg ha <sup>-1</sup> )
% Semi-leafless in Mixture	% Leafed in Mixture	
0	100	1670 (221)†
25	75	2450 (322)
50	50	2830 (370)
75	25	2980 (391)
100	0	2650 (357)

† Means followed by standard errors of means in parentheses

When grain yield of each cultivar in mixture was examined relative to its respective monoculture, yield of the leafed cultivar responded positively to mixture with semi-leafless pea ( $P < 0.0001$ ). The degree of yield improvement in the leafed cultivar was enhanced as the percentage of semi-leafless pea in the mixture increased (Table 3.7). In mixtures of 25% leafed and 75% semi-leafless pea, the combination which showed the highest yield, the leafed cultivar yielded 176% of the expected yield based on the proportion of the cultivar in the mixture. In contrast, the semi-leafless cultivar yielded similarly whether grown in mixtures or monocultures ( $P = 0.4659$ ; Table 3.7). Relative yields of the two cultivars strongly suggest that the yield potential of leafed pea was improved by combining it in mixture with semi-leafless pea. The fact that semi-leafless pea relative yield remained constant is consistent with the fact that weed suppression was similar between mixtures and the semi-leafless cultivar grown alone.

**Table 3.7:** Effect of leafed and semi-leafless pea mixing proportion on yield of each component cultivar relative to monoculture yield. Projected monoculture yield is adjusted for the proportion of the cultivar in mixture.

<b>Cultivar Composition</b>		<b>Yield in Mixture Relative to Monoculture</b>	
% Semi-leafless in Mixture	% Leafed in Mixture	Leafed	Semi-leafless
0	100	1.00 (0.12)†	-
25	75	0.85 (0.17)	0.92 (0.08)
50	50	1.25 (0.19)	1.08 (0.12)
75	25	1.76 (0.38)	1.07 (0.12)
100	0	-	1.00 (0.10)

† Means followed by standard errors of means in parentheses

Several factors may have contributed to the yield increase of the leafed cultivar in mixture with semi-leafless pea. Conventional interpretation suggests that less complete overlap of resource requirements between different species compared with the same species accounts for the yield benefits observed in some mixtures (de Wit 1960). The declining relative yield of the leafed cultivar as the mixtures shifted towards leafed monocultures is consistent with the

interpretation that the leafed cultivar is more sensitive to its own density compared with another cultivar (Joliffe et al. 1984). However, since each cultivar was not grown in monocultures of different densities to compare with its density in each mixture, the design of the experiment does not allow separation of response of each cultivar to monoculture density compared with mixture (Joliffe et al. 1984). The presence of competing weeds in the experiments further complicates this interpretation.

The agronomic benefits of mixture canopies compared with leafed monoculture canopies are consistent with the leafed yield response to mixture. In addition to improving weed suppression, adding increasing percentages of semi-leafless pea to leafed pea decreased lodging linearly ( $P = 0.0245$ ; Table 3.8). Previously, Schouls and Langelaan (1994) reported on the ability of semi-leafless pea to improve lodging resistance and yield of leafed pea in mixtures under weed-free conditions. The present experiment shows that this effect also occurs when weeds are interfering with the crop. The degree of yield increase, 22 and 230% compared with the semi-leafless and leafed monocultures, respectively, is greater than the 5 to 11% yield increases reported when lodging was evaluated alone (Schouls and Langelaan 1994). The combined effects of improved weed control and lodging resistance on leafed yield presents a possible mechanism for the greater magnitude of yield increase in mixture than previously reported. The use of mixtures to create more favourable canopy characteristics compared with individual cultivars may be particularly useful under organic conditions, where yield is often restricted by lack of adequate crop management tools.

**Table 3.8:** Response of canopy lodging to mixture of leafed and semi-leafless field pea in 2011-2012 growing seasons. A lodging index of 1 indicates a fully upright canopy.

<b>Cultivar Composition</b>		Lodging Index (/1)
% Semi- leafless in Mixture	% Leafed in Mixture	
0	100	0.87
25	75	0.90
50	50	0.91
75	25	0.92
100	0	0.92
SE†		0.020

† Standard error of means

### 3.3.4 Leafed versus Semi-leafless Pea for Organic Production

In addition to comparison with mixtures, growing each component cultivar in monoculture also allowed comparisons of a leafed cultivar relative to a semi-leafless cultivar. It was noted previously that leafed cultivars may be more weed-suppressive than semi-leafless (Harker et al. 2008; Spies et al. 2011). The results of the present study were consistent with other studies, however, in finding that leaf type alone did not predict competitive ability (Townley-Smith and Wright 1994; Wall and Townley-Smith 1996; McDonald 2003).

The two cultivars used differed in respects other than leaf type which may affect competitiveness with weeds. Although efforts were made to match the two cultivars based on vine length (Saskatchewan Pulse Growers 2012), CDC Dakota and CDC Sonata did differ in vine length during the growing season. During early crop growth, CDC Dakota (semi-leafless) plants had significantly longer vines than leafed CDC Sonata plants ( $P < 0.0001$ ; Table 3.9). By the end of the season, the trend had reversed and CDC Sonata vines were longer than CDC Dakota ( $P = 0.053$ ). Although leaf area index of the different canopies was not measured in this study, light interception data from a companion study under weed-free conditions showed that differences in early vine length may be associated with differences in light availability at the base of the canopy (Chapter 4). Under weed-free conditions, CDC Dakota developed and maintained a fuller canopy than CDC Sonata until crop flowering, while after flowering, both cultivars intercepted light similarly. Greater leaf area during early crop growth has been correlated with weed suppressive ability of field pea competing with wild mustard (Wall and Townley-Smith 1996), and high early biomass accumulation is associated with weed suppression in wheat (Lemerle et al. 1996).

**Table 3.9:** Effect of leafed and semi-leafless field pea mixtures on mean vine length in 2012. Data represent means for Kernen and Vonda field sites.

<b>Cultivar Composition</b>		<b>Mean Vine Length (cm)</b>	
% Semi-leafless in Mixture	% Leafed in Mixture	June	August
0	100	11.0	67.2
25	75	13.3	64.3
50	50	13.9	59.8
75	25	14.6	59.5
100	0	15.2	56.4
SE†		0.572	3.89

† Standard error of means

Differences in rates of emergence may also have affected establishment of leafed and semi-leafless canopies. Although it was possible to adjust for unequal final stand densities using analysis of covariance, CDC Dakota appeared to emerge more rapidly and uniformly than CDC Sonata (personal observation) and this may also have been an advantage in competing with weeds due to the relative time of emergence (O'Donovan et al. 1985; O'Donovan 1992). The higher average seed weight of the grain cultivar CDC Dakota (216 g /1000 seeds) compared with forage cultivar CDC Sonata (200 g /1000 seeds) may account for the differences in plant establishment. Seedling vigour was significantly reduced when small versus medium or large seed of Austrian winter pea was planted under cool, wet conditions (Murray et al. 1984). Polyphenolic compounds in the seed coat of pigmented cultivars such as CDC Dakota may also have the effect of improving germination and emergence. When pea lines isogenic for seed coat colour are used, pigmented lines suffer lower levels of seed imbibition damage and soil-borne disease compared with unpigmented lines (Powell 1989). Studies on wheat, barley, and canola show that crop seed yield decreases, and weed seed production increases, the earlier the weed emerges relative to the crop (O'Donovan et al. 1985; O'Donovan 1992). The relatively rapid emergence of larger seeded, pigmented lines such as CDC Dakota may therefore reduce the impact of weeds by promoting crop establishment ahead of weeds.

### **3.3.5 Applications of Leafed and Semi-leafless Pea Mixtures**

The potential to adopt leafed and semi-leafless field pea mixtures as an organic production tool in western Canada must be discussed within the context of market class. Because of their poor lodging resistance, leafed cultivars have received minimal attention from plant breeders, particularly for grain production. In Saskatchewan, of the 43 dry pea cultivars available, only two have the leafed growth habit (Saskatchewan Ministry of Agriculture 2013). These two varieties, 40-10 and Trapper, as well as CDC Sonata, were developed for forage production rather than grain. Forage pea cultivars are bred to produce large amounts of biomass, and small seeds. In contrast, yellow, green, and specialty grain pea cultivars such as CDC Dakota are bred to produce high grain yield and larger seeds for human or animal consumption. The pairing of a forage with a specialty grain pea cultivar in this experiment allowed seeds to be separated by colour to study their yield responses in detail. However, as the available leafed pea

cultivars are not suitable for commercial grain production, the use of this technique to improve grain yield is currently limited.

Intercropping leafed with semi-leafless pea presents a novel approach to solving the agronomic problems of leafed pea. The increased seed yield potential, and reduced lodging of leafed pea in mixture suggest that breeding larger-seeded leafed varieties specifically for grain production in mixtures with semi-leafless pea may be warranted. Leafed grain cultivars for mixture with semi-leafless pea may be particularly useful under organic conditions, where the use of crop inputs to increase yield is restricted. Since leafed cultivars have not been the recent focus of breeding programs, the lower disease resistance, later maturity, and longer vines typical of leafed cultivars (Saskatchewan Ministry of Agriculture 2013) should also be addressed in breeding efforts.

Improved biomass production for forage or green manure presents perhaps the most immediately accessible use for this technique. In our study we observed that in addition to higher grain yield, crop biomass production was improved in mixture compared with monocultures (Table 3.6). While the high biomass yield of semi-leafless cultivar CDC Dakota would not appear typical of semi-leafless grain pea, forage yield improvements have previously been reported in 50:50 mixtures of lodging-resistant semi-leafless, and lodging-susceptible leafed cultivars in Serbia (Ćupina et al. 2010).

Whether further work is needed to adopt mixtures for biomass in western Canada will depend whether the crop is intended for animal consumption. For green manure, the present as well as previous reports suggest that mixtures comprised of at least 50% semi-leafless pea could be immediately used by organic producers to increase biomass yield (Ćupina et al. 2010). For use as animal feed, however, the crude protein content of mixtures that include semi-leafless cultivars bred for grain would need to be measured at early flowering to confirm that they are appropriate for animal consumption. In the latter case it is an advantage that semi-leafless cultivars that meet the nutritional and digestibility criteria for forage production have already been developed, and these cultivars could immediately be grown in mixtures with leafed cultivars.

The potential of pea cultivar mixtures as an organic production tool merits further exploration. Because CDC Dakota is a relatively competitive cultivar, it is unknown whether

combining semi-leafless pea with a more competitive leafed cultivar will improve its yield in mixture relative to monoculture. However, the yield increase observed in a leafed cultivar when grown with a more weed suppressive and lodging resistant semi-leafless cultivar is consistent with other studies in showing that characteristics that alter the entire plant canopy may improve the productivity of mixtures compared with monocultures. Thus, pairing cultivars of field pea that each possess features beneficial to the canopy environment, such as weed and disease suppressive abilities, is a basis for further study.

## **4.0 EFFECT AND UNDERLYING MECHANISMS OF LEAFED AND SEMI-LEAFLESS PEA CULTIVAR MIXTURES ON DEVELOPMENT OF ASCOCHYTA BLIGHT EPIDEMICS**

### **4.1 Introduction**

Ascochyta blight, caused primarily by *Mycosphaerella pinodes* (Berk. & Blox.) Vesterg., limits field pea production in the Canadian prairie provinces (Chang et al. 2007; Dokken-Bouchard et al. 2010; McLaren et al. 2010). Of pea crops surveyed in Saskatchewan and Manitoba in 2009, 95-100% of them showed symptoms of the disease (Dokken-Bouchard et al. 2010; McLaren et al. 2010). Canadian cultivars currently do not have higher than “Fair” resistance to the disease (Saskatchewan Ministry of Agriculture 2013), and although several fungicides are registered for use in pea, fungicide application for ascochyta blight control is often not cost-effective due to its variable effect on yield (Gossen et al. 2011). Modifying the spatial characteristics of pea canopies may reduce the impact of ascochyta blight epidemics in the absence of fungicides.

Plant and canopy architectural features have the potential to modify the climatic conditions experienced by the pathogen. As for many pathogens, temperature and moisture conditions impact spore germination and penetration, lesion expansion, and fruiting structure development of *M. pinodes* (Roger et al. 1999a, 1999b). As air temperatures deviate from the optimum of 20°C, longer moisture durations are required for fungal development (Roger et al. 1999a, 1999b). Therefore shifting canopy temperatures from their optimum, shortening the moisture duration on the leaf surface, or both, may slow epidemic progress. Schoeny et al. (2010) demonstrated shorter moisture durations after flowering in pea intercropped with wheat compared with pea monocrops. Disease severity on pods and stems was lowered in the same intercrops by 32 to 49% in moderate and severe epidemics.

Canopy features may be manipulated by several means. The practice of intercropping pea with cereals has not been widely adopted in western Canada despite demonstrated benefits to yield, weed control, and disease control (Hauggaard-Nielsen and Jensen 2001; Rauber et al. 2001; Hauggaard-Nielsen et al. 2006; Neumann et al. 2009; Fernández-Aparicio et al. 2010; Schoeny et al. 2010). However, while available pea cultivars do not differ in ascochyta blight

susceptibility, those available exhibit a range of characteristics including leaf type, vine length, and lodging resistance (Saskatchewan Ministry of Agriculture 2013). Leaf type in particular may alter disease progress in field pea. Semi-leafless types express the recessive *afaf* (afila) gene, which converts all leaflets to tendrils (Snoad and Gent 1976; Kielpinski and Blixt 1982). The larger tendrils help support the crop, increasing resistance to lodging. Since more severely lodged plants develop more severe ascochyta blight symptoms (Banniza et al. 2005; Wang et al. 2006), combining lodging-susceptible (wild type) leafed pea with semi-leafless pea may create a canopy less conducive to ascochyta blight. Even in the absence of lodging, the reduced leaf area of semi-leafless pea may enhance canopy air flow and light penetration, increasing temperature and limiting moisture available for fungal processes. Growing pea cultivars of different leaf types alone or in mixtures may therefore produce epidemics of different severities and rates of development.

The objective of this study was to identify relationships between pea canopy architectural features and ascochyta blight epidemic development. A leafed and semi-leafless pea cultivar were sown alone and in mixtures of different proportions to achieve a range of architectural features for comparison. The hypothesis was that intercropping semi-leafless with leafed pea, through its effects on canopy architecture, would create a microclimate less conducive to disease and reduce disease severity compared with growing leafed pea alone.

## 4.2 Materials and Methods

### 4.2.1 Site Description and Growing Conditions

The experiment was conducted in Saskatoon, SK, at a conventionally managed site owned by the University of Saskatchewan in 2011 and 2012 (Table 4.1). The land was fallowed the previous season, cultivated in the fall, and again in the spring prior to planting.

**Table 4.1:** Locations and soil properties in the upper 15 cm of 2011-2012 field experiments to evaluate the effect of leafed and semi-leafless pea cultivar mixtures on ascochyta blight suppression.

	2011	2012
Location	52°7'26"N, 106°37'28"W	52°7'22"N, 106°37'32"W
Soil association	Bradwell	Bradwell
Soil zone	Dark Brown	Dark Brown
Soil texture	Loam	Loam
pH	7.5	7.7
E.C. (mS cm <sup>-1</sup> )	0.5	0.2
Soil test N (µg g <sup>-1</sup> )	72	22

#### 4.2.2 Experimental Design and Management

The experiment tested the effect of five ratios of semi-leafless to leafed pea (0:100, 25:75, 50:50, 75:25, and 100:0%) using a randomized complete block design with four replications. Plants were seeded at a target seeding rate of 88 plants  $\text{m}^{-2}$ , the recommended density for field pea production in Saskatchewan (Saskatchewan Pulse Growers 2000). Actual seeding rates were based on the germination rates of the seed, and an expected emergence of 75%.

The experiment used cultivars CDC Dakota (semi-leafless) and CDC Sonata (leafed), both bred by the Crop Development Centre (CDC) at the University of Saskatchewan. The cultivars were matched based on their similar vine length and maturity (Saskatchewan Pulse Growers 2012), to separate these effects from leaf type. Both had “fair” resistance to ascochyta blight (Saskatchewan Ministry of Agriculture 2013), and developed similar levels of symptom severity when whole plants were inoculated with *M. pinodes* in preliminary greenhouse tests (Appendix).

Pea was seeded into moisture in mid- to late-May (Table 4.2), with a cone seeder in 3.6 x 6 m plots that consisted of 18 rows 20 cm apart. Seeds of the two cultivars were mixed prior to sowing. TagTeam® granular inoculant (*Penicillium bilaii* and *Rhizobium leguminosarum*, Novozymes North America Inc., Franklinton, North Carolina, U.S.A.) was applied to the seed row at the recommended rate of 4.6 kg  $\text{ha}^{-1}$ .

The site was managed to encourage disease development, and minimize the impact of other pests. Plots were artificially inoculated by spreading approximately 175  $\text{cm}^3$  of ascochyta blight-infested pea residue in each plot six and eight weeks after planting in 2011 and 2012, respectively (Table 4.2). The trial received overhead irrigation during dry periods, five times in 2011, and once in 2012, to encourage disease development (Table 4.3). Plots were treated with Odyssey® herbicide (Imazamox 35% a.e. + Imazethapyr 35% a.e., BASF Canada Inc., Mississauga, Ontario, Canada) after planting for weed control. Matador® 120EC insecticide (Lambda-cyhalothrin 120g/L, Syngenta Canada Inc., Guelph, Ontario, Canada) was applied to control a pea aphid infestation during pod filling in 2011. The crop was treated at the end of the

season in 2011 with Reglone® Desiccant (Dibromide 240g/L, Syngenta Canada Inc., Guelph, Ontario, Canada) to facilitate seed drying. No fungicide applications were made.

**Table 4.2:** Seeding, harvest, crop management, and data collection dates in field experiments to evaluate the effect of leafed and semi-leafless pea cultivar mixtures on ascochyta blight suppression in 2011 and 2012.

	<b>2011</b>	<b>2012</b>
Seeding	May 24	May 12
Herbicide Application	May 24	May 12
Plant Emergence Assessment	June 27	June 7
First Weekly Plant Growth Assessments	June 27	June 21
Microclimate Sensor Setup	June 30	June 21
Plot Inoculation	July 5	July 5
First Weekly Disease Assessment	July 21	July 12
Insecticide Application	July 29	-
First Weekly Lodging Assessment	August 6	July 20
Desiccant Application	August 17	†
Harvest	†	†

†Harvest data were not collected due to animal damage

**Table 4.3:** Irrigation dates and volumes applied in 2011 and 2012.

<b>2011</b>		<b>2012</b>	
Application Date	Irrigation Volume (mm)	Application Date	Irrigation Volume (mm)
July 18	3.0	July 26	6.0
August 2	12.5		
August 3	25.0		
August 10	19.0		
August 15	12.5		

### 4.2.3 Data Collection

Data were collected on disease, canopy development, and microclimate. Yield data were not collected due to extensive damage by geese in plots just prior to seed harvest in both seasons.

#### 4.2.3.1 *Ascochyta Blight Epidemic Development*

Disease development in plots was measured weekly for four weeks, from disease onset until termination of experiments, in both years. Ten plants were randomly selected from a different plot sub-section each week for destructive sampling. Stratified sampling was used to avoid interference of plant removal with canopy characteristics and microclimate. Plants were clipped at the soil line using hand pruners. Disease severity was estimated using percentage necrosis rather than a rating scale to allow more accurate modeling of symptom development over time. The percentage necrosis on the stem, stipule, tendril, and leaflet (if applicable) tissue

of the main stem of each of the 10 plants was estimated visually in a systematic manner. The proportion of necrosis at each node was summed, the sum was divided by the total number of nodes on the same stem, and the quotient was multiplied by 100. For example, a main stem with five nodes with 100% necrosis, three nodes with 50% necrosis, and a total of 20 nodes, would have 33% necrosis. After rating each plant for percentage necrosis, progress of disease symptoms up the plant and degree of senescence were measured on the same main stems. Symptom progress up plants was measured by counting the number of nodes from the ground upward at which ascochyta blight symptoms were observed. Senescence was measured by counting the number of nodes at which leaf yellowing or browning was observed.

#### ***4.2.3.2 Canopy Development***

Plant emergence was measured three to four weeks after planting (Table 4.2). All emerged pea plants of each cultivar were counted in two 1 m<sup>2</sup> quadrats per plot. Crop growth was measured weekly throughout the season until final disease measurements were taken. Five adjacent plants in two locations per plot were tagged for weekly vine length and node measurements. Vine length was measured as the distance from the base to the top of the main stem of each plant. The number of nodes was counted on the same stem. Both vine length and number of nodes were averaged weekly for the 10 plants assessed.

Light interception was used as an estimate of leaf area of the different canopies. A ceptometer (AccuPAR LP-80, Decagon Devices, Pullman, Washington, U.S.A.) was used to sample light levels above and at the base of the canopy at four locations in each plot. The proportion of light intercepted was calculated based on photosynthetically active radiation (PAR) using the equation:

$$\text{Intercepted PAR} = 1 - (\text{PAR below canopy} / \text{PAR above canopy}) \quad (4.1)$$

Light interception was measured weekly, beginning prior to canopy closure. Disease onset and the first disease assessment coincided with the fourth week of PAR measurements in 2011, and the fifth week in 2012. Weekly PAR measurements continued into the third week of the epidemic in 2011, and the second in 2012, but in both seasons measurements were terminated prior to the final disease assessment due to equipment malfunctions. An additional measurement

was taken in a single plot of each treatment with a quantum photometer (LI-189, LI-COR Inc., Lincoln, Nebraska, U.S.A.) the week following ceptometer failure in 2012.

Lodging was measured three times following the onset of disease in each year. A lodging index was calculated using the ratio of canopy height to vine length for one plant of each cultivar at two locations in each plot. When both cultivars were grown together in mixture, the index was weighted equally between the two cultivars.

#### **4.2.3.3 Microclimate**

Canopy microclimate was measured in each plot of two replicates in each year. Data loggers (HOBO® Pro v2, Onset Computer Corporation, Bourne, Massachusetts, U.S.A.) containing internal temperature and humidity sensors were installed at the base of the crop canopy in each plot. Temperature and relative humidity were logged every half hour, from 4-5 weeks after planting (Table 4.2) until the conclusion of the experiment. Daily maximum and minimum temperatures were calculated based on logged temperatures, and daily moisture durations were calculated by counting the number of consecutive hours where canopy relative humidity exceeded 95%. Rainfall data were collected using a tipping bucket rain gauge at a permanent weather station at the Kernen Crop Research Farm, Saskatoon, SK, and irrigation data were provided by staff at the University of Saskatchewan Crop Science Field Lab.

#### **4.2.4 Statistical Analyses**

Data were analyzed using the MIXED procedure in SAS. The two years were analyzed separately to facilitate comparisons of epidemic development with canopy characteristics. Plant emergence and disease severity were analyzed as regressions on percentage of semi-leafless pea in the mixture, with replicate as a random effect. Regressions of disease severity on percentage of semi-leafless pea were performed for each week after disease onset. With the exception of moisture duration data, all remaining variables were analyzed as repeated measures data (Littell et al. 2006). Percentage of semi-leafless pea in the mixture, time, and the interaction of percentage of semi-leafless pea with time, were treated as fixed effects, and block as a random effect. Percentage of semi-leafless pea in the mixture was treated as a class variable for repeated measures analysis (Littell et al. 2006), and treatment means were separated using Fisher's

protected least significant difference (LSD) test. Treatment effects were declared significant at  $P < 0.05$ .

For moisture duration data, the number of days where moisture duration exceeded 4, 8, or 12 h in the periods prior to and after-flowering were analyzed. At the optimum temperature of 20°C, 4 h is the minimum required duration of high relative humidity or leaf wetness for appressorium formation, and 8 h the minimum for hyphal penetration (Roger et al. 1999a, 1999b). Since infection is unsuccessful if moisture is interrupted prior to appressorium formation (Roger et al. 1999b), 4 h represents the absolute minimum moisture requirement for successful infection. At temperatures above or below the optimum of 20°C, required moisture durations increase for all infection processes, therefore longer moisture durations indicate a higher likelihood of infection success. Moisture duration data were analyzed with ANOVA, and means for each monoculture or mixture were separated using Fisher's protected LSD.

Data were tested for homogeneity of variances and normality of residuals prior to analysis, and transformations were used to meet statistical assumptions if possible (Table 4.4). Data were back-transformed for presentation. Since back-transformation results in asymmetric standard errors above and below the mean, the larger value is presented. The covariance structure to model response of treatment variances to time for each variable was chosen using a combination of lowest values of fit statistics and lowest number of parameters. Canopy characteristics were tested for correlation with disease severity using Pearson correlation analysis. Correlations were performed on untransformed data.

**Table 4.4:** Transformations used to meet assumption of homogeneity of variances, and covariance structures used in repeated measures analysis using PROC MIXED in SAS.

Variable	<b>2011</b>		<b>2012</b>	
	Transformation Used	Covariance Structure used	Transformation Used	Covariance Structure used
Emergence	None	N/A	1/y	N/A
% Necrosis	Arcsine( $\sqrt{y}$ )	Simple	$y^{0.41993\ddagger}$	Simple
Proportion of infected plant nodes	Arcsine( $\sqrt{y}$ )	Simple	None	ANTE(1)
Vine length	Ln(y + 1)	Simple	$y^{-0.26364\ddagger}$	CSH
Nodes	None	Simple	Ln(y + 1)	Simple
Leaf Area Index	$\sqrt{y}$	Simple	Ln(y + 1)	CSH
Intercepted PAR	$y^{2.37435\ddagger}$	Simple	None	ANTE(1)
Lodging index	None	CSH	$y^{3.47016\ddagger}$	CSH
Proportion of senesced stipules	-	-	$y^{-0.67875\ddagger}$	Simple

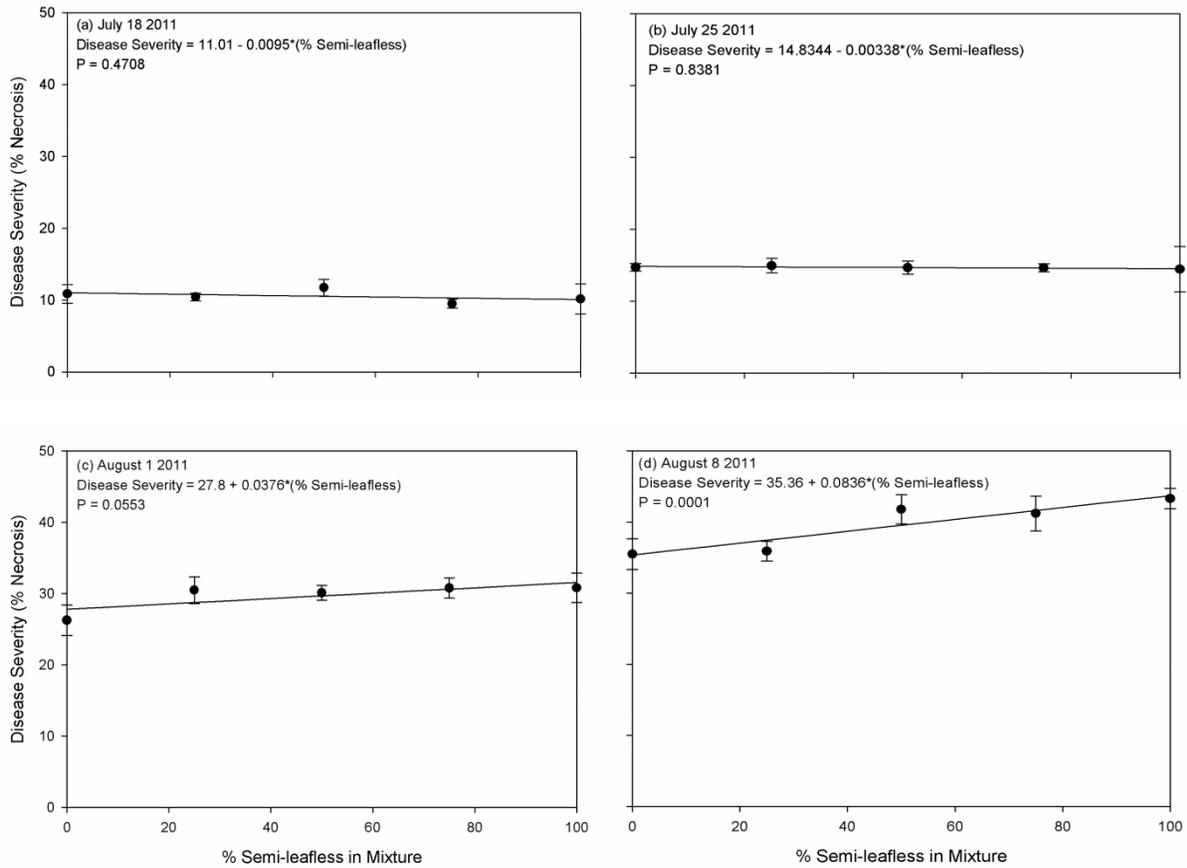
‡Exponent for exponent transformations = 1-slope of regression of standard deviations against means

## 4.3 Results and Discussion

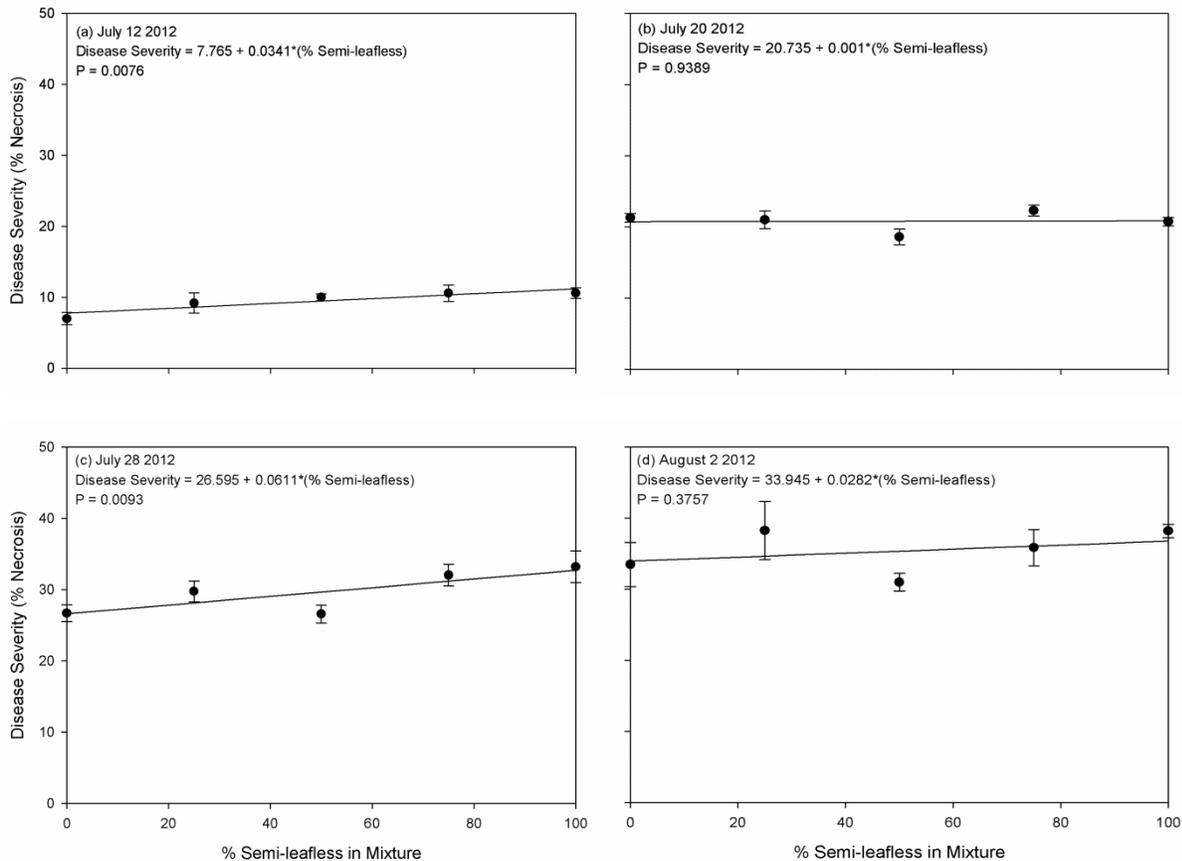
### 4.3.1 Effect of Monocultures and Mixtures on *Ascochyta* Blight Epidemic Development

*Ascochyta* blight symptoms were first observed in plots eight weeks after planting in 2011, and nine weeks after planting in 2012. In 2011 disease onset corresponded with the first week of flowering, and in 2012 symptoms were observed one week after flowering began. Disease epidemics were of moderate severity in both seasons, reaching an average of 40% plant tissue necrosis in 2011, and 35% in 2012.

Disease severity was regressed against percentage of semi-leafless pea to determine the role of mixture composition in predicting disease progress during the different weeks of the epidemics. No quadratic effects were observed ( $P > 0.1778$ ), indicating that the disease severities of mixtures fell between those of the two component cultivars. Linear regressions were significant or close to significant during the last two weeks of the epidemic in 2011 (Fig. 4.1), and the first and third weeks in 2012 (Fig. 4.2). During all weeks where percentage of semi-leafless pea in the mixture was a significant regression variable, disease severity increased with percentage of semi-leafless pea in the mixture. The greatest rates of increase were 0.08 in the fourth week of the epidemic in 2011 (Fig. 4.1d), and 0.06 in the third week of the epidemic in 2012 (Fig. 4.2c), indicating that during those weeks increasing the percentage of semi-leafless pea in mixture by 12 to 17% increased the percentage of necrotic tissue in the canopy by 1%. Since preliminary studies had indicated that both cultivars had similar levels of susceptibility to *ascochyta* blight when whole plants were inoculated with *M. pinodes* under greenhouse conditions (Appendix), disease differences may be attributed to canopy or plant characteristics other than physiological disease resistance. However, higher disease severity in the semi-leafless cultivar was unexpected because canopies comprised of mainly the leafed cultivar were expected to have greater leaf area, and therefore cooler and wetter microclimate conditions more conducive to *ascochyta* blight development. In addition to their effects on microclimate, plant or canopy characteristics may also act on epidemic development through inoculum interception and tissue receptivity to infection (Tivoli et al. 2013). Canopy and plant growth data were therefore examined in relation to these three mechanisms to better understand potential causes of the differences observed.



**Figure 4.1:** Rates of change in ascochyta blight severity with increasing percentage of semi-leafless pea in cultivar mixtures with leafed pea during the first (a), second (b), third (c), and fourth (d) weeks of epidemic development in 2011.



**Figure 4.2:** Rates of change in ascochyta blight severity with increasing percentage of semi-leafless pea in cultivar mixtures with leafed pea during the first (a), second (b), third (c), and fourth (d) weeks of epidemic development in 2012.

### 4.3.2 Relationships among Canopy Density, Microclimate and Disease Severity

Plant density, vine length, and estimated canopy leaf area may influence the duration of canopy moisture through their effects on air flow and penetration of solar radiation through the canopy. Canopies of different compositions differed in these three aspects during some periods in the growing season. Average plant density differed among canopies throughout the growing season due to lower plant emergence in the leafed cultivar ( $P < 0.005$ ). Plant density increased linearly as canopy composition shifted towards greater percentages of semi-leafless pea, ranging from 66 to 82 plants  $m^{-2}$  in 2011, and 49 to 76 plants  $m^{-2}$  in 2012 (Table 4.5).

In addition to having a denser stand, the semi-leafless cultivar grew more vigorously at the beginning of the season than the leafed; prior to flowering, semi-leafless pea plants had longer vines in both years ( $P < 0.0006$ ). After flowering the trend reversed; vine length of the leafed cultivar continued to increase, and semi-leafless vine growth slowed (Table 4.6). The

leafed cultivar had approximately 15 cm longer vines than the semi-leafless by the end of both seasons.

**Table 4.5:** Mean plant densities in monocultures and mixtures of leafed with semi-leafless pea in 2011 and 2012. Intercept and slope coefficients are for linear regressions where predicted plant density = intercept + slope\*% semi-leafless in mixture.

Mixture	Plant Density (plants m <sup>-2</sup> )	
	2011	2012
100% Leafed:0%Semi-leafless	66 (6)	49 (6)
75%Leafed:25%Semi-leafless	69 (3)	57 (8)
50%Leafed:50%Semi-leafless	76 (3)	49 (3)
25%Leafed:75%Semi-leafless	75 (3)	65 (2)
0%Leafed:100%Semi-leafless	82 (4)	76 (2)
<i>Intercept</i>	66.175	48.170
<i>Slope</i>	0.152	0.245

Means are followed by standard errors of means

**Table 4.6:** Mean vine length of main stems for leafed and semi-leafless pea monocultures and mixtures during 2011 and 2012 growing seasons. The last four weeks measured correspond with the first, second, third and fourth weeks of epidemic development.

Year	Mixture	Mean Vine Length (cm)						
		June 27	July 4	July 11	July 18	July 25	August 1	August 8
2011	100% Leafed:0%Semi-leafless	17.2 (1.0)	27.3 (1.2)	36.0 (1.0)	53.4 (1.9)	67.6 (3.2)	68.2 (1.1)	73.4 (2.4)
	75%Leafed:25%Semi-leafless	18.9 (0.8)	30.1 (0.8)	38.3 (0.8)	54.5 (1.1)	63.2 (1.9)	65.2 (2.2)	65.1 (2.3)
	50%Leafed:50%Semi-leafless	19.7 (0.9)	29.4 (0.7)	38.5 (1.7)	54.3 (3.2)	61.3 (3.8)	64.0 (3.4)	64.6 (3.7)
	25%Leafed:75%Semi-leafless	19.9 (1.3)	30.2 (1.5)	38.5 (1.8)	52.6 (4.1)	59.9 (2.6)	60.2 (2.5)	58.4 (1.4)
	0%Leafed:100%Semi-leafless	20.2 (1.5)	30.8 (1.0)	39.5 (1.0)	53.4 (1.2)	55.7 (1.4)	57.3 (0.3)	57.1 (1.4)
			June 21	June 28	July 6	July 12	July 20	July 28
2012	100% Leafed:0%Semi-leafless	16.0 (0.8)	22.7 (0.6)	38.5 (1.9)	47.5 (2.8)	68.8 (6.6)	73.8 (6.4)	79.3 (7.0)
	75%Leafed:25%Semi-leafless	18.0 (1.0)	23.9 (1.1)	41.0 (3.6)	50.5 (3.1)	65.5 (2.4)	67.8 (2.8)	70.0 (2.0)
	50%Leafed:50%Semi-leafless	16.2 (0.5)	24.3 (0.7)	41.5 (0.8)	46.2 (2.1)	60.4 (3.3)	62.7 (3.9)	65.8 (5.7)
	25%Leafed:75%Semi-leafless	19.3 (1.4)	27.1 (0.4)	43.3 (3.0)	51.2 (2.2)	57.6 (2.0)	60.5 (2.4)	65.5 (4.1)
	0%Leafed:100%Semi-leafless	19.7 (0.7)	28.2 (2.2)	48.2 (1.2)	51.4 (3.7)	59.5 (4.6)	60.8 (2.9)	63.9 (3.1)

Means are followed by standard errors of means

Interception of light by the different canopies reflected the differences in early canopy development in 2012, but not in 2011. In 2012, semi-leafless pea and mixtures intercepted more light than leafed canopies prior to flowering ( $P = 0.0014$ ), while after flowering no differences were observed. Light interception was similar among canopies in 2011 (Table 4.7).

**Table 4.7:** Effect of proportions of leafed and semi-leafless pea in monocultures or mixtures on light intercepted by plant canopies during the 2011 and 2012 growing seasons.

Year	Mixture	PAR Intercepted by Canopy (proportion intercepted)					
		June 27	July 4	July 11	July 18	July 25	August 1
2011	100% Leafed: 0%Semi-leafless	0.26 (0.03)	0.62 (0.03)	0.88 (0.02)	0.92 (0.01)	0.97 (0.01)	0.96 (0.01)
	75%Leafed: 25%Semi-leafless	0.31 (0.04)	0.67 (0.01)	0.89 (0.02)	0.92 (0.01)	0.96 (0.01)	0.94 (0.01)
	50%Leafed: 50%Semi-leafless	0.34 (0.04)	0.70 (0.04)	0.88 (0.01)	0.91 (0.01)	0.95 (0.01)	0.93 (0.01)
	25%Leafed: 75%Semi-leafless	0.38 (0.04)	0.67 (0.02)	0.88 (0.01)	0.93 (0.01)	0.96 (0.004)	0.95 (0.003)
	0%Leafed: 100%Semi-leafless	0.36 (0.03)	0.64 (0.03)	0.86 (0.01)	0.89 (0.02)	0.95 (0.01)	0.95 (0.01)
		June 21	June 28	July 6	July 12	July 20†	July 28†
2012	100% Leafed: 0%Semi-leafless	0.32 (0.04)	0.68 (0.06)	0.93 (0.02)	0.97 (0.003)	0.97	0.96
	75%Leafed: 25%Semi-leafless	0.45 (0.01)	0.76 (0.01)	0.94 (0.01)	0.97 (0.004)	0.97	0.96
	50%Leafed: 50%Semi-leafless	0.51 (0.04)	0.77 (0.03)	0.94 (0.01)	0.97 (0.01)	0.97	0.97
	25%Leafed: 75%Semi-leafless	0.52 (0.03)	0.76 (0.01)	0.95 (0.001)	0.97 (0.004)	0.97	0.97
	0%Leafed: 100%Semi-leafless	0.59 (0.01)	0.81 (0.03)	0.95 (0.003)	0.97 (0.001)	0.96	0.97

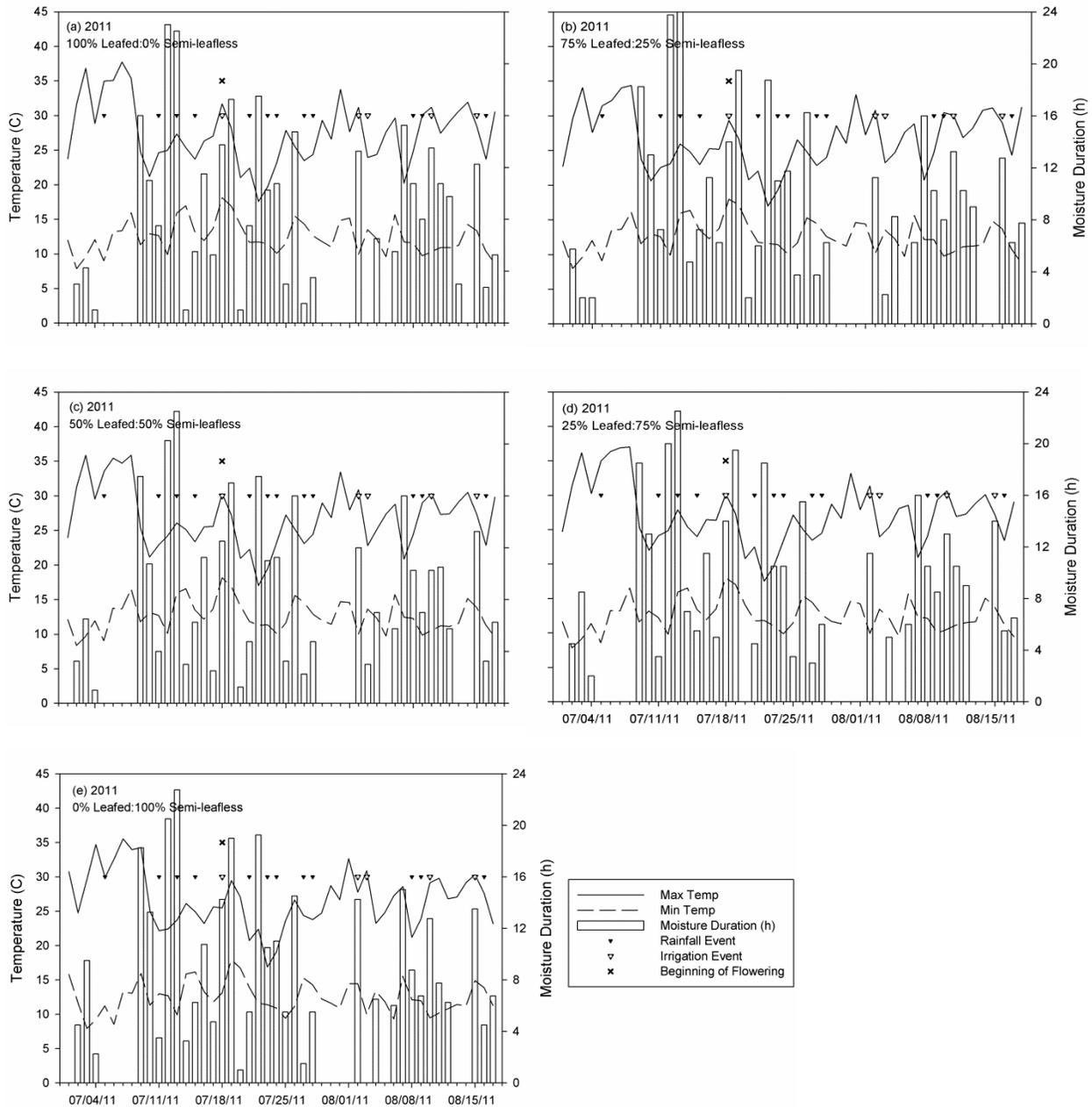
†Observations were made in a single plot of each treatment on the indicated sampling dates due to equipment malfunction

Means are followed by standard errors of means

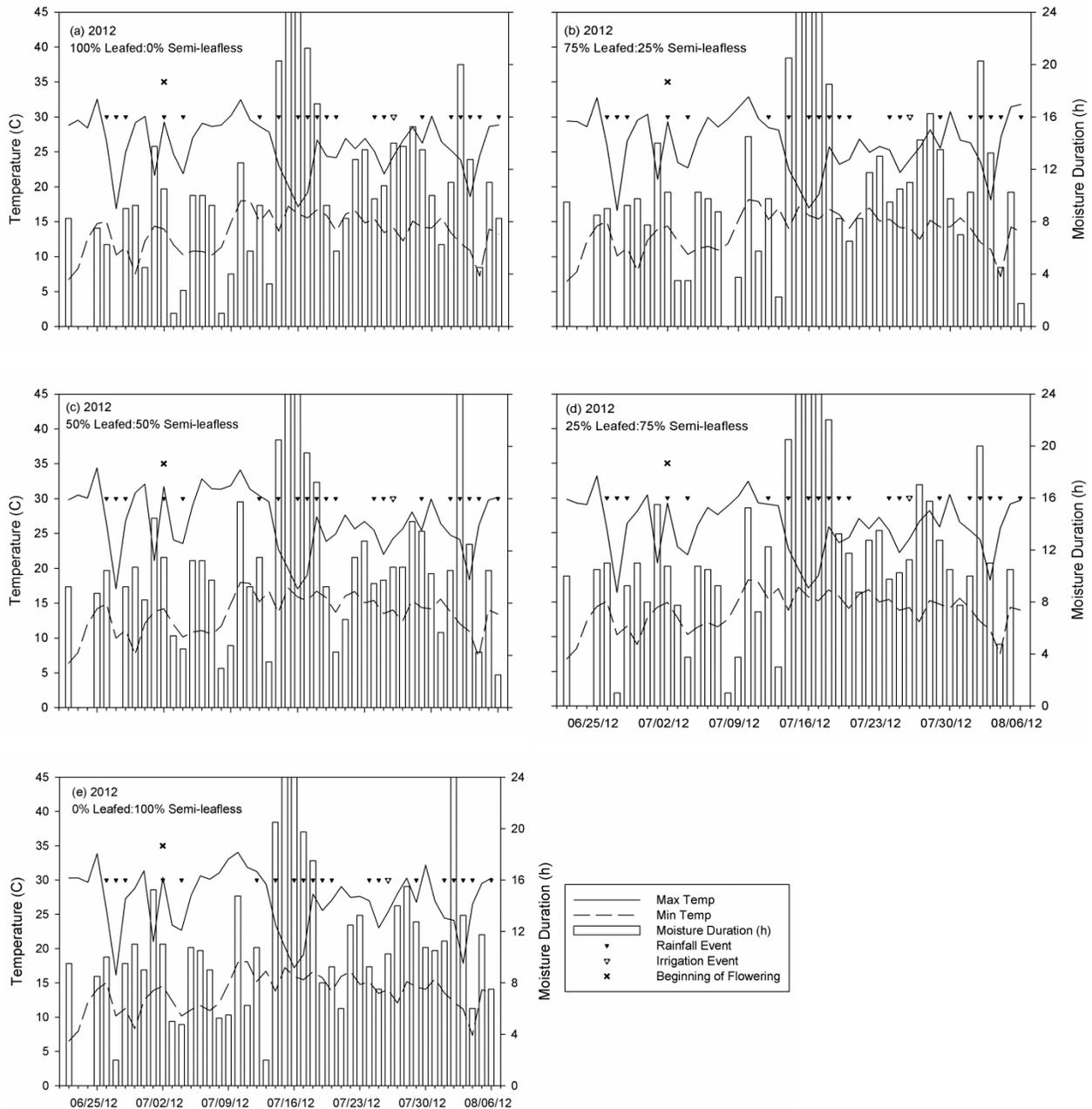
Canopy moisture followed two distinct patterns. First, all canopies shared a diurnal moisture pattern, frequently experiencing relative humidities greater than 95% during the evenings, and low humidities during the day. Second, monoculture and mixture treatments affected the durations of canopy moisture in the same manner as they affected light interception. In 2011, moisture durations were similar among monocultures and mixtures both before and after flowering ( $P > 0.2082$ ; Fig. 4.3), consistent with canopy light interception measurements. In the period prior to flowering in 2012, the number of hours where canopy relative humidity exceeded 95% was frequently lower in leafed canopies than semi-leafless and mixture canopies. In the 11 days before flowering where microclimate was monitored, the moisture duration exceeded 8 h on four occasions in the leafed, and six or seven occasions in remaining canopies ( $P = 0.0148$ ; Fig. 4.4a-e). After flowering, and disease onset, all canopies experienced similar moisture durations ( $P > 0.33$ ).

Leaf area index, another measure of canopy leaf area, has been positively correlated with disease severity in previous studies (Le May et al. 2009), and microclimatic differences were suggested as a possible mechanism. Our study confirms that differences in canopy leaf area can indeed correspond with differences in microclimate, specifically the length of time that canopy relative humidity is favourable to disease development. The greater disease severity observed in semi-leafless and mixture canopies in early 2012 affirms that ascochyta blight severity increases with the duration of leaf moisture during wet periods (Roger et al. 1999b).

While differences in canopy moisture duration prior to flowering are consistent with the lower disease levels observed in leafed canopies during the early phase of the 2012 epidemic, they did not correspond with the later phase of the 2012 epidemic. Since moisture duration did not differ among treatments in 2011, it is also not a plausible explanation for disease differences observed that year. It would be possible, however, for such differences as occurred in early 2012 to have more enduring impacts on disease development in other growing seasons, as the timing of disease onset in a natural setting will vary with weather conditions. The presence of ascospores for disease initiation has been shown to be associated with cumulative degree-days (Schoeny et al. 2007) and the amount or frequency of rainfall (Carter 1963; Bretag 1991; Zhang et al. 2005; Schoeny et al. 2007).



**Figure 4.3:** Daily maximum and minimum temperatures, durations of canopy moisture, occurrences of rainfall or irrigation, and the beginning of flowering in monocultures and mixtures of leafed and semi-leafless pea in 2011. Moisture duration data for 25% Leafed: 75% Semi-leafless treatment (d) represent a single plot due to humidity sensor failure.



**Figure 4.4:** Daily maximum and minimum temperatures, durations of canopy moisture, occurrences of rainfall or irrigation, and the beginning of flowering in monocultures and mixtures of leafed and semi-leafless pea in 2012.

### 4.3.3 Evidence for Other Relationships among Canopy Characteristics and *Ascochyta* Blight Development

Two other mechanisms, spore dispersal and host tissue receptivity to infection, may explain relationships between canopy characteristics and disease in weeks where microclimate

differences were absent. Canopy structural features such as node position and proximity of neighbouring plants have been shown to affect natural patterns of *M. pinodes* inoculum spread (Schoeny et al. 2008, 2010). Plant density, vine length, number of nodes, leaf area, and the degree of lodging are examples of features in the current experiment that may affect the likelihood of spore interception by host tissue.

The proximity of pea plants to each other may affect the interception of conidia, which may explain why plant density was positively correlated with disease severity during both the first and third weeks of the epidemic in 2012 (Table 4.8), despite a lack of microclimate differences at the latter date. Experiments with a rain simulator have shown that host “dilution” by spacing plants farther apart resulted in fewer infections at similar distances from a point inoculum source compared with plants grown closer together (Schoeny et al. 2008, 2010). The greater plant density in semi-leafless than leafed canopies is consistent with a greater likelihood of interception of *M. pinodes* conidia by plant tissue during rain splash.

**Table 4.8:** Pearson correlation coefficients for relationship between canopy architectural features and ascochyta blight severity in 2011 and 2012.

Year	Canopy Feature	<u>Correlation with Disease Severity</u>			
		July 18	July 25	August 1	August 8
2011	Plant Density	-0.30	-0.27	0.21	0.29
	Vine Length	0.10	-0.06	-0.09	-0.55*
	Number of Nodes	-0.08	0.12	0.50*	-0.25
	Intercepted PAR	0.49*	0.03	-0.15	-
	Lodging Index†	-	-	0.38	0.48*
		July 12	July 20	July 28	August 2
2012	Plant Density	0.53*	0.03	0.59**	0.30
	Vine Length	0.02	0.01	-0.32	0.05
	Number of Nodes	0.47*	-0.07	0.17	-0.01
	Intercepted PAR	0.13	-	-	-
	Lodging Index†	-	-0.08	0.33	0.11

Associations marked by ‘\*’ are significant at P=0.05, ‘\*\*’ at P=0.01, and ‘\*\*\*’ at P<0.0001 on the given sampling date

†Lodging index values fell between 0 and 1, with 1 indicating the canopy was completely upright

Spore dispersal effects may also be responsible for the significant correlations between vine length or number of nodes and disease severity on dates when canopy composition was a significant factor in disease development. During epidemic development the leafed cultivar had longer vines than the semi-leafless (Table 4.6), and had fewer nodes overall in 2011 ( $P < 0.0001$ ) and until the third week of the epidemic in 2012 ( $P = 0.0321$ ; Table 4.9). Vine length was negatively correlated with disease severity, while number of nodes correlated positively with

disease severity (Table 4.8). The combination of longer vines with fewer or a similar number of nodes indicates that on average, the leafed cultivar had longer internodes than the semi-leafless. Shorter internode length was previously shown to be correlated with higher levels of disease (Le May et al. 2009), and it was proposed that longer internodes reduce the success of rain-splashed spores in producing new infections. This explanation is consistent with the disease severity differences observed in the current study. In addition, for the two cultivars used, internode length differences had a temporal element. Due to the more indeterminate growth habit of the leafed cultivar, its internodes continued to lengthen late in the season, while semi-leafless internode growth slowed early in the epidemic in both seasons (Tables 4.6 and 4.9). Determinacy through its effects on internode development may therefore also impact ascochyta blight severity.

Leaf area differences among canopies may also interfere with the spore dispersal of *M. pinodes*. Pea canopies may have the effect of either restricting the relay of the pathogen's spores to neighbouring plants ("barrier" effect), or enhancing it ("relay" effect). The relay effect is present in canopies with relatively low leaf areas, while the barrier effect increases with increasing leaf area (Schoeny et al. 2008). Since all canopies had similar leaf areas during epidemic development in both 2011 and 2012, differences in spore relay due to canopy density do not appear to have played a major role in the current study. Further, the higher leaf area of semi-leafless monocultures prior to epidemic onset in 2012 does not support the notion that differences in spore relay played a major role in early disease levels.

**Table 4.9:** Node development in mixtures of different proportions of leafed and semi-leafless pea during epidemic development in 2012.

Year	Mixture	<u>Number of Nodes</u>			
		July 18	July 25	August 1	August 8
2011	100% Leafed:0%Semi-leafless	17.9 (0.7)	20.3 (0.2)	20.4 (0.6)	21.7 (0.7)
	75%Leafed:25%Semi-leafless	19.1 (0.2)	21.1 (0.4)	21.1 (0.8)	21.3 (0.9)
	50%Leafed:50%Semi-leafless	19.4 (0.6)	21.3 (0.4)	21.5 (0.6)	22.5 (0.5)
	25%Leafed:75%Semi-leafless	20.7 (0.2)	22.0 (0.4)	21.5 (0.7)	21.1 (0.7)
	0%Leafed:100%Semi-leafless	20.9 (0.7)	21.6 (0.4)	21.4 (0.6)	21.7 (0.4)
		July 12	July 20	July 28	August 2
2012	100% Leafed:0%Semi-leafless	16.2 (2.8)	18.4 (6.6)	21.9 (6.4)	21.8 (7.0)
	75%Leafed:25%Semi-leafless	16.9 (3.1)	17.2 (2.4)	20.9 (2.8)	21.1 (2.0)
	50%Leafed:50%Semi-leafless	17.6 (2.1)	18.4 (3.3)	22.0 (3.9)	21.1 (5.7)
	25%Leafed:75%Semi-leafless	19.2 (2.2)	17.3 (2.0)	21.6 (2.4)	20.2 (4.1)
	0%Leafed:100%Semi-leafless	18.9 (3.7)	19.1 (4.6)	22.1 (4.6)	20.7 (3.1)

Means are followed by standard errors of means

The relationships between disease progress and lodging in this experiment were not consistent with expectations based on the literature. While the semi-leafless cultivar and all mixtures remained significantly more upright than the leafed in both seasons ( $P < 0.0001$ ; Table 4.10), lodging was either not correlated with disease, or positively correlated with more upright canopies rather than lodged canopies on the last scoring date in 2011 (Table 4.8). Others have observed that severely lodged plants typically develop more severe symptoms of ascochyta blight (Banniza et al. 2005; Wang et al. 2006). This may be caused by multiple mechanisms, including development of a more humid microclimate through reduced air flow, and allowing greater infection success through more direct contact of spores with host tissue. Since severe symptoms were not associated with more collapsed canopies, lodging did not appear to be a major factor in 2011 and 2012 epidemics.

**Table 4.10:** Effect of proportion of leafed and semi-leafless pea in mixture on canopy lodging index during the second, third and fourth weeks of epidemic development in 2011 and 2012. A lodging index of 1 indicates that plant stems were completely upright.

Year	Mixture	<u>Lodging Index (/1)</u>		
		July 25	August 1	August 8
2011	100% Leafed:0%Semi-leafless	0.83 (0.04)	0.58 (0.04)	0.42 (0.02)
	75%Leafed:25%Semi-leafless	0.93 (0.01)	0.80 (0.02)	0.62 (0.05)
	50%Leafed:50%Semi-leafless	0.96 (0.01)	0.88 (0.04)	0.85 (0.07)
	25%Leafed:75%Semi-leafless	0.96 (0.01)	0.95 (0.01)	0.91 (0.01)
	0%Leafed:100%Semi-leafless	0.95 (0.01)	0.96 (0.01)	0.97 (0.01)
		July 20	July 28	August 2
2012	100% Leafed:0%Semi-leafless	0.84 (0.03)	0.80 (0.02)	0.47 (0.02)
	75%Leafed:25%Semi-leafless	0.94 (0.01)	0.90 (0.02)	0.46 (0.05)
	50%Leafed:50%Semi-leafless	0.94 (0.01)	0.95 (0.01)	0.63 (0.15)
	25%Leafed:75%Semi-leafless	0.96 (0.002)	0.96 (0.01)	0.74 (0.12)
	0%Leafed:100%Semi-leafless	0.97 (0.01)	0.96 (0.01)	0.91 (0.06)

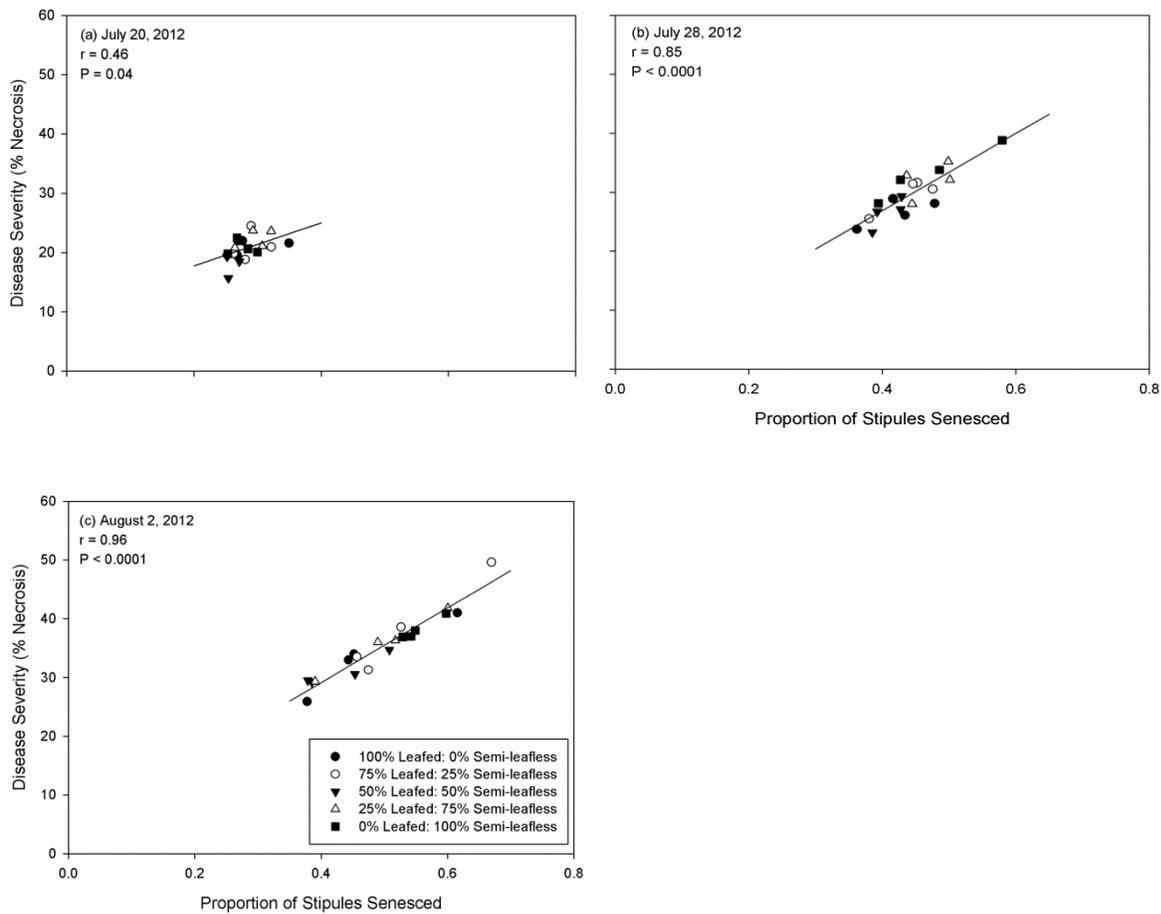
Means are followed by standard errors of means

Apart from microclimate and spore dispersal, differences in tissue susceptibility represent a third possible mechanism for differential disease development among mixture and monoculture canopies. Older, and particularly senescent plant tissue has been shown to be more receptive to ascochyta blight infection than green plant tissue (Richard et al. 2012). Therefore differences in relative maturities of the two cultivars used, or differences in tissue senescence due to plant or canopy density, may be expected to play a role in epidemic development. In the current study, however, the level of tissue senescence in monoculture and mixture canopies was not associated with the percentage of semi-leafless pea in the mixture (Table 4.11). Regressions of tissue senescence on percentage of semi-leafless pea were not significant overall ( $P = 0.5782$ ), nor on

any individual scoring dates ( $P > 0.1265$ ). Levels of senescence in leafed and semi-leafless monoculture canopies did not differ significantly from each other overall ( $P = 0.1483$ ), although the 50% semi-leafless treatment had significantly lower senescence than the semi-leafless monoculture and remaining mixtures ( $P < 0.0112$ ; Table 4.11). Patterns of tissue senescence caused by genetic differences among cultivars, or environmental differences caused by a gradient of canopy densities, therefore, do not appear to account for the significant regressions of disease severity on percentage of semi-leafless pea. However, the level of senescence observed was significantly and positively correlated with disease severity on all dates where senescence was measured ( $r = 0.46$  to  $0.96$ ). Correlation strength and significance increased with each sampling date (Figs. 4.5a-c). Tissue senescence therefore does appear to be linked with 2012 ascochyta epidemic development, despite lacking a clear relationship with either cultivar.

**Table 4.11:** Effect of proportion of leafed and semi-leafless pea in mixture on progress of tissue yellowing or browning from lower plant nodes upward during 2012 epidemic development.

Mixture	<b>Proportion of Plant Stipules Senesced</b>			
	July 12	July 20	July 28	August 2
100% Leafed:0%Semi-leafless	-	0.29 (0.02)	0.42 (0.02)	0.46 (0.05)
75%Leafed:25%Semi-leafless	-	0.29 (0.01)	0.44 (0.02)	0.52 (0.05)
50%Leafed:50%Semi-leafless	-	0.26 (0.01)	0.41 (0.01)	0.43 (0.03)
25%Leafed:75%Semi-leafless	-	0.21 (0.01)	0.47 (0.02)	0.49 (0.05)
0%Leafed:100%Semi-leafless	-	0.28 (0.01)	0.46 (0.04)	0.55 (0.01)



**Figure 4.5:** Pearson correlations between degree of tissue senescence and disease severity during the second (a), third (b), and fourth (c) weeks of epidemic development in 2012.

The causality of the positive relationship between tissue senescence and ascochyta blight severity in the current study is unclear. Others have found that senescence may be both caused by disease, and the cause of increased plant susceptibility to disease. Ascochyta blight infection causes premature tissue senescence (Roger and Tivoli 1996b; Béasse et al. 2000; Richard et al. 2012). Conversely, older pea tissue, and particularly tissue that is yellowing, is more susceptible to ascochyta blight infection (Richard et al. 2012). Under field conditions, symptoms follow patterns of natural senescence, appearing first and most severely at the oldest leaves and nodes at the bottom of the plant (Roger and Tivoli 1996b; Le May et al. 2009; Fernández-Aparicio et al. 2010). Further, ascochyta blight symptoms and reproductive structures of *M. pinodes* form more rapidly on pea tissue that is inoculated at later physiological stages (Heath and Wood 1969; Zimmer and Sabourin 1986; Roger and Tivoli 1996b; Garry et al. 1998).

The vertical distribution of disease symptoms suggests that tissue senescence at least partially moderated symptom progress. Although disease symptoms were present at 86 to 100% of plant nodes in all treatments during the three latter weeks of the epidemic (data not shown), senescence was observed at only 43 to 55% of plant nodes by the last scoring date (Table 4.11). The correlation between senescence and disease progress up plants on the last assessment date was not significant ( $r = -0.12$ ,  $P = 0.6008$ ), despite a strong and highly significant positive correlation with disease severity on that date. In other words, while symptom severity was related to senescence, the upward development of symptoms on plants was not. Lesions on younger tissue at the top of plants appeared as isolated small flecks, while lesions at the bottom of plants were typically larger. These observations are consistent with spores being dispersed to green tissue in the upper canopy, but lesion expansion on younger leaves near the top of the plant being limited compared with older leaves. This interpretation agrees with the finding of Richard et al. (2012) that disease severity increases gradually with tissue age, and plateaus once yellowing has occurred. An alternative explanation, however, is that since conidia are more abundant in the lower canopy (Roger and Tivoli 1996b; Zhang et al. 2005; Schoeny et al. 2008), the more numerous lesions on lower leaves resulted in more severe tissue chlorosis and necrosis. Under field conditions it is likely that both of these scenarios occur: lesion size is limited on green tissue at the top of the plant, and senescence is accelerated at the bottom of the plant as older leaves endure repeated cycles of infection.

In conclusion, the results suggest that within cultivars that possess similar levels of susceptibility to ascochyta blight, a range in other characteristics exists that may moderate disease development. Through growing monocultures or mixtures of two different cultivars it was possible to change properties at the canopy level that are known to affect ascochyta blight development - leaf area and microclimate. Other features that may affect disease development were also observed at the level of individual plants or cultivars - tissue senescence, vine length, node development, and more broadly growth habit (determinate or indeterminate). To truly test the effect of leaf type on microclimate and disease as was intended in this study, isogenic pea lines that differ only in leaf type are needed to isolate canopy effects from cultivar differences.

## 5.0 GENERAL DISCUSSION

The current study was undertaken to test the hypothesis that mixtures of leafed and semi-leafless pea cultivars would have higher yields, improved lodging resistance, weed and disease suppression, and a microclimate less conducive to disease than monocultures of each cultivar. The hypothesis was addressed through two experiments, each with its own objectives. The first evaluated the effect of leafed and semi-leafless cultivar mixtures on weed suppression, lodging resistance, and yield. The objective was to identify a ratio of leafed to semi-leafless pea that optimized yield and agronomic benefits for organic production. The second experiment addressed the effects of leafed and semi-leafless cultivar mixtures on microclimate, lodging, and disease. The objective was to identify canopy and cultivar traits that suppressed disease.

The first experiment affirmed the first part of the hypothesis: yield was in fact enhanced by growing mixtures of leafed with semi-leafless pea. The enhancement occurred both in grain and biomass yield. In both cases, mixtures of 75% semi-leafless pea out-yielded monocultures of both leafed and semi-leafless components. Yield enhancement has been previously reported for mixtures of leafed with semi-leafless pea, but only under weed-free conditions (Schouls and Langelaan 1994; Čupina et al. 2010). This study confirms the applicability of this technique to organic conditions, where the crop must compete with weeds throughout the season.

Based on research in barley, wheat, and dry beans, it appears uncommon for cultivar mixtures to exceed the yield of both monocultures (Coyne et al. 1978; Jeger et al. 1981b; Mundt et al. 1994; Newton et al. 1997). However it is more common for mixtures to out-yield the average of the cultivars used. Mixtures of cereal cultivars frequently yield more than the monoculture mean, and often yield similarly to the higher yielding cultivar (Jeger et al. 1981b; Mundt et al. 1994; Newton et al. 1997). Similarly, traits such as disease resistance, canopy leaf area, or pathogen inoculum suppression may be conferred to mixtures at levels greater than the average of the monocultures (Coyne et al. 1978; Mundt et al. 1994; Newton et al. 1997).

The current study concurs with other research in showing that mixtures may behave more similarly to one component cultivar than another. While the hypothesis that weed suppression and lodging resistance of mixtures would be superior to both monocultures was not true, mixtures behaved more similarly to the semi-leafless cultivar than one would expect based on the

percentage of each cultivar in the mixture. For example, weed biomass declined as the proportion of the semi-leafless cultivar relative to the leafed cultivar increased, then was maintained at similar levels between 50 and 100% semi-leafless pea. A similar relationship was observed with lodging resistance: although lodging responded to percentage semi-leafless pea with a significant quadratic effect ( $P = 0.003$ ), the predicted optimum (i.e., maximum lodging resistance) occurred in the monoculture of semi-leafless pea. In effect, then, lodging had an asymptotic relationship with percentage of semi-leafless pea, levelling off as the canopy composition approached 100% semi-leafless. These results confirm that one cultivar may contribute greater than its share of traits such as weed suppression and lodging resistance in mixture.

There is little doubt that the large difference in growth forms of pea used in this experiment contributed to the greater degree of yield enhancement observed. The development of semi-leafless pea was a significant advance in breeding because it greatly improved the crop's standing ability (Snoad 1974; Kielpinski and Blixt 1982). Mechanically induced lodging was previously used to demonstrate that semi-leafless pea suffered similar yield loss to leafed pea if similar levels of lodging were induced, and that yields of both were improved when lodging was prevented (Schouls and Langelaan 1994). The prominence of semi-leafless cultivars in seed production affirms the importance of standing ability in pea. Granting the upright growth habit of semi-leafless pea to leafed pea thus provides a significant advantage that was previously only available to semi-leafless sole crops. Based on research in other crops, it appears unlikely that yields of pea mixtures would exceed both monoculture yields if two leafed or two semi-leafless cultivars were combined, regardless of other cultivar differences.

The present study is unique in showing the transfer of weed suppression among cultivars in mixture, as no previous reports exist where leafed and semi-leafless pea mixtures were tested as a weed control tool. Previous studies where cereal mixtures were tested as a weed control technique found no advantage (Pridham et al. 2007). As for lodging, the sensitivity of pea yield to weeds has been previously established (Nelson and Nylund 1962; Wall et al. 1991). However, the extent to which weed suppression and lodging resistance each contributed to mixture yield is unknown. Weed-free controls would be needed to separate the effects of lodging resistance from weed suppression in the current study.

Regardless of causality, it was possible to identify the optimum combination of leafed and semi-leafless pea for yield enhancement under organic conditions. In the case of grain yield, the optimum was predicted in mixtures with near 75% semi-leafless pea. A similar peak was observed for biomass yield. This information is needed to provide meaningful recommendations to organic producers so that they can make use of this technique.

There are several reasons, however, to be cautious in recommending an exact ratio of leafed to semi-leafless pea based on this work. First, because the cultivars used were not isogenic, they differed in several respects unrelated to leaf type. These differences were discussed in the chapters, and included relative timing and rate of emergence, vine length, number of nodes, leaf area, and determinacy. In the present and other studies, these characteristics were associated with pest suppression, and thus indirectly affected yield. Since only a single cultivar of each leaf type was tested, and since commercial cultivars possess many possible combinations of these characteristics, it is unknown whether the optimum ratio of leafed to semi-leafless pea will be similar if different cultivars are used. Second, since the relative contributions of lodging resistance and weed suppression are unknown, it is difficult to predict the outcome if the same cultivar was not responsible for contributing both traits in mixture. For example, if the leafed rather than the semi-leafless cultivar was the more weed suppressive, it seems likely that the optimum ratio would incorporate more leafed pea than the current study suggests. Third, it is possible that other factors related to niche differentiation, for example foliage or rooting profile, contributed to the higher yield of mixtures of 75% semi-leafless pea.

Despite the limitations, all available evidence suggests that mixtures of leafed with semi-leafless pea for grain yield should be comprised of at least 50% semi-leafless pea. In the present study, mixtures of 50% or greater semi-leafless pea yielded at least as well as the semi-leafless cultivar alone, and yield was greatly enhanced compared with the leafed cultivar alone. Under weed-free conditions, the optimum has been previously calculated to be within the range recommended here, falling between 53 and 67% semi-leafless pea (Schouls and Langelaan 1994).

The optimum mixture for biomass in the current study included 75% semi-leafless pea, the same composition as for optimum grain yield. The high biomass yield of the semi-leafless grain cultivar CDC Dakota appears unusual, since it was not bred for forage production.

However, evidence suggests that if a leafed and semi-leafless cultivar differed only in lodging resistance, the most beneficial mixtures would still be comprised of at least 50% semi-leafless pea. Biomass yield benefits have previously been observed in multiple combinations of 50:50 leafed and semi-leafless pea cultivars under weed-free conditions (Ćupina et al. 2010). If one cultivar produced biomass more prolifically or was more suppressive of weeds, the optimum may shift towards the cultivar that possesses these advantages. However since the transfer of lodging resistance to leafed pea appears to be a primary mechanism of yield increase, optimum mixtures will likely not favour leafed pea.

In the second experiment, the effects of mixtures on canopy microclimate and disease contrasted with their effects on weed suppression and lodging observed in the first experiment. In early 2012, moisture duration in mixtures was similar to the semi-leafless monoculture, indicating that mixtures were more conducive to disease than the average of the two monocultures. For the first week of 2012 contrasts showed that disease severity was consistent with this result; mixtures comprised of at least 50% semi-leafless pea had more disease than expected based on the average of the two cultivars. The result is perhaps not surprising: the same characteristics that were implicated in the improved weed suppression of mixtures (rapid canopy development) were also implicated in increased canopy humidity.

The two experiments in this thesis illustrate that the agronomic attributes of mixtures may lead to conflicting outcomes, and one outcome may need to be chosen over another. These results highlight the need to evaluate the integrated effects of any tools for organic or low-input production on the system as a whole so that erroneous conclusions are not made.

Under the conditions of the experiments described here, the effects of mixtures on ascochyta blight via microclimate appear to be less important than their effects on weeds. Although disease severity was not measured under organic conditions, final yield was maximized in mixtures of 75% semi-leafless pea despite the presence of disease. Fungicides were not applied to organic plots, and ascochyta blight symptoms were observed at all sites. Further, in the study of ascochyta blight development, microclimate was not responsible for differences in disease severity during the majority of the experiment.

Since microclimate and disease severity were not measured under organic conditions, the dynamics of ascochyta blight development are unknown. It is likely that disease development

will differ in the same mixtures under organic versus conventional conditions. In particular, there are many unanswered questions about the relationship between canopy traits and disease when weeds are present. For example, how do the microclimates of a sparse crop canopy with a dense weed community, and a dense crop canopy with a sparse weed community, compare with each other? Do weeds act as a barrier or enhance splash dispersal of *M. pinodes*? Although answers to such questions would not change the outcome of this experiment, they would enhance our understanding of the role of canopy traits in successful mixtures.

The study of mixtures on disease development under weed-free conditions refuted the hypothesis that disease suppression would be enhanced in mixtures. Mixtures did not lower disease severity compared with monocultures in any week. Further, there was no evidence that disease severity was lower than expected in mixtures based on the average disease reaction of the two monocultures. In fact, there were two weeks where it can be argued that the disease reaction of mixtures was more severe than expected: the last week of 2011, and the first week of 2012. In both weeks contrasts showed that mixtures of 50 or 75% semi-leafless pea developed ascochyta blight symptoms of similar severity to the semi-leafless cultivar. In remaining weeks, disease severity changed at a constant rate as the percentage of semi-leafless pea in the mixture increased. In other words, the concentration of each cultivar in the mixture adequately explained disease severity of mixtures.

While there are no strong sources of resistance to ascochyta blight in current field pea breeding lines, studies of non race-specific, splashed-dispersed pathogens in cereal mixtures suggest that even small differences in susceptibility may lower disease severity of mixtures below the mean. Jeger et al. (1981b, 1981a) used mathematical models and field studies to illustrate how small differences in pathogen infection frequency and sporulation rate on different wheat and barley cultivars most often lead to either similar or lower disease severity than expected based on dilution alone. The model predicts that a lower infection frequency or sporulation rate in one cultivar would lead to disease control benefits in mixture by reducing the inoculum available to cause infections in the other cultivar.

Since infection frequency and sporulation rate were not measured for CDC Sonata and CDC Dakota, it is unknown whether these factors differed for the two cultivars. The lack of differences in ascochyta blight severity between the two cultivars in greenhouse studies does not

suggest that they differed in infection frequency. The presence of disease severity differences between monocultures on the first sampling date in 2012, before repeated infection cycles could occur, is also not supportive of sporulation differences. If the two cultivars did differ in infection frequency and/or sporulation rate, there are three possible explanations for the lack of mixture benefit in the current study. The first is that the difference between cultivars was not large enough to affect total spore abundance in mixture canopies. A second possibility is that infection severity was not limited by inoculum availability. Previously, dry bean cultivar mixtures were observed to reduce *Sclerotinia sclerotiorum* apothecia production beneath canopies, but not to lower infection severity in the same mixtures (Coyne et al. 1978). Similarly, ascospore abundance has been shown not to be the major limiting factor in the initiation of ascochyta blight epidemics (Schoeny et al. 2007). A third explanation is that one cultivar had a higher infection frequency, and the other had a similarly higher sporulation rate, which would allow the effects of both to be cancelled out. Measuring infection frequency and sporulation rate for the two pea cultivars used would clarify whether cultivar-specific inoculum differences affected disease development in mixtures.

In the absence of infection frequency and sporulation data for the two cultivars, the most convincing explanation for the lack of mixture benefit on disease suppression is that the characteristics that reduced disease were not transferable to the canopy level. Individual plant characteristics such as vine length, number of nodes, and tissue senescence were correlated with disease in weeks where no leaf area or microclimate differences were observed. Simple dilution of these characteristics by adding a different cultivar accounts for the linear response of disease to mixture observed in most weeks.

Based on the results of this thesis, mixtures of leafed and semi-leafless pea increase yield under organic conditions. Both grain and biomass yield of CDC Sonata (leafed) and CDC Dakota (semi-leafless) mixtures were optimized with 25% leafed and 75% semi-leafless pea. Unlike yield, canopy characteristics such as weed suppression, lodging resistance, canopy microclimate, and disease suppression did not exceed both component cultivars in the mixture. Instead, mixtures expressed these characteristics at the mean level of the two cultivars, or adopted characteristics more similar to one cultivar than the other.

Given the limited number of crop management tools available to organic producers, the value of cultivar mixtures in organic systems is immediately apparent. However, the limited selection of leafed pea cultivars constrains the application of this technique. Since no leafed grain cultivars are available, use of leafed and semi-leafless mixtures for seed production is not feasible at the present time. While leafed forage cultivars do exist, only two very tall cultivars, 40-10 and Trapper, are available in Saskatchewan. No seed is available for CDC Sonata, the cultivar used in these experiments. Further, emergence problems have been noted with CDC Sonata regardless of seed source, making the cultivar poorly suited to organic production.

With currently limited field application, perhaps the results of this thesis are best applied as a model system for pea breeders. Since mixtures may provide beneficial traits to a cultivar which does not possess them, a cultivar's yield potential may be higher in mixture than in monoculture. Based on the results of this thesis, selecting leafed and semi-leafless pea lines together in mixtures can increase yield compared with selecting single lines of high-yielding semi-leafless pea. Developing lines that are isogenic for leaf type may produce beneficial combinations, while maintaining similar seed size and controlling for other differences that may affect interactions with weeds and disease. As a continuation of this thesis project, several pairs of pea lines isogenic for leaf type that were obtained from pea breeders will be studied alone and in mixtures for their effects on yield, weeds, and disease.

The optimum mixture of isogenic leafed and semi-leafless pea combinations may differ from the ratio established in this thesis, due to the unique abilities of the cultivars used to suppress weeds and disease, and their competitive interactions with each other. Since the transfer of lodging resistance to leafed pea by semi-leafless pea appears to be the primary mechanism in the yield enhancements observed, a mixing ratio with a minimum of near 50% semi-leafless pea is recommended as a starting point for future evaluations. Because the same canopy characteristics may have opposite effects on weeds and disease, optimum ratios of leafed to semi-leafless pea for organic production should be determined under organic management.

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# **APPENDIX: PRELIMINARY COMPARISON OF CDC DAKOTA AND CDC SONATA REACTION TO WHOLE-PLANT INOCULATION WITH *MYCOSPHAERELLA PINODES***

## **A.1 Materials and Methods**

### **A.1.1 Experimental Setup**

A repeated measures experiment was conducted to test the disease reaction of a semi-leafless and leafed pea cultivar, CDC Dakota and CDC Sonata, respectively, prior to their use in field epidemiology experiments. The experiment was conducted twice, with four replications in each run. A replicate consisted of a pot of each cultivar sown with four seeds.

### **A.1.2 Inoculation**

Plants were inoculated approximately two weeks after planting. Each cultivar averaged four to five nodes at the time of inoculation.

Inoculum of the Saskatchewan *M. pinodes* isolate Mp25 was grown for approximately 11 days on oatmeal agar. For each run, a suspension of  $2 \times 10^5$  conidia ml<sup>-1</sup> in sterile deionized water with a drop of tween was prepared and airbrushed onto whole plants at a pressure of 10 psi. Spore suspension was delivered to each pot for approximately 11 seconds. After inoculation, pots were placed in a humidity chamber overnight, then moved to a misting chamber for the remainder of the experiment.

### **A.1.3 Disease Ratings and Calculations**

Ratings of ascochyta blight severity were conducted twice, seven and fourteen days after inoculation. Disease severity was rated on each plant using a 1-10 scale that represented percentage necrosis on whole plants in 10% increments. For example, a score of 1 represented a range of 0 to 10% necrosis, and a score of 10 represented a range of 90 to 100% necrosis. For analysis, the disease rating for each plant was converted to the midpoint of the represented range, for example, for a score of 1 the disease severity was 5%, and for a score of 10 the disease severity was 95%. Analyses were performed on the average percentage necrosis of the emerged plants in each pot.

#### A.1.4 Statistical Analysis

Statistical analyses were performed using the MIXED procedure of SAS. Cultivar, scoring date, and their interaction were treated as fixed effects, and run, replicate, and interactions of run with treatment were treated as random effects. The variables run, cultivar, scoring date, and replicate were entered as class variables. Scoring date was initially treated as a repeated factor, but resulted in over-parameterization of the model (Kiernan et al. 2012). Eliminating the repeated statement simplified the model, lowered IC values, and resulted in similar levels of significance to the more complex model for all variables.

Disease data were tested for homogeneity of variances and normality of residuals, and were log-transformed prior to analysis to meet these assumptions. Since pots with fewer emerged plants may have received greater volumes of spore suspension on a per plant basis, the number of emerged plants in each pot was tested as a possible covariate for disease severity. However, this variable was excluded from the final model as it did not account for disease severity differences either alone or in combination with cultivar ( $P > 0.5745$ ).

#### A.2 Results

The cultivars CDC Dakota and CDC Sonata did not differ in the percentages of necrotic tissue when whole plants were inoculated with *M. pinodes* (Tables A1 and A2), nor did the two cultivars show any differences in the rate of symptom development over time (Table A1). Only scoring date had a significant effect on disease severity (Table A1). Disease severity increased, from 22 to 44% plant necrosis, between the two assessments.

**Table A1:** Analysis of variance for ascochyta blight severity in preliminary greenhouse tests as affected by pea cultivar (CDC Dakota or CDC Sonata) and scoring date (7 or 14 days after inoculation).

Source	df	P value
Cultivar	1	0.5841
Scoring Date	1	0.0028
Cultivar x Scoring Date	1	0.3991
Run†	1	0.2641
Run x Cultivar†	1	.
Run x Scoring Date†	1	.
Run x Cultivar x Scoring Date†	1	0.2861

†Significance of random effects calculated using the COVTEST option in the MIXED procedure of SAS

**Table A2:** Average severity of ascochyta blight in two-week preliminary greenhouse tests for pea cultivars CDC Dakota and CDC Sonata (combined for the two rating dates 7 and 14 days after inoculation).

<b>Cultivar</b>	<b>Disease Severity</b>
CDC Dakota	32.072 a
CDC Sonata	30.035 a

Means followed by the same letter are not significantly different at  $P = 0.05$