COMPARISONS OF MALE STERILE CYTOPLASMS IN CANOLA (*BRASSICA NAPUS* L.)

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Gregory Ross Gingera

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ABSTRACT

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The effect of several male sterile cytoplasms on intercultivar canola hybrids was assessed over three years (1987-1989).

The nuclear genomes of several cultivars and hybrids of canola were transfered to the nap, ogu and pol male sterile cytoplasms. Days to first flower and to days to 50% flower were increased in the pol but not in the ogu cytoplasm. Seed yield and total dry matter were reduced for both open pollinated populations and hybrids in the ogu cytoplasm. Seed yield and total dry matter were significantly lower in pol than in the nap cytoplasm for hybrids and to a lesser degree for the open pollinated populations. Relative seed oil concentration was reduced in the pol cytoplasm by 1.8 and 2.3 percent; in ogu by 1.5 and 6.1 percent for 1988 and 1989 respectively. Relative seed protein was increased by the pol and ogu cytoplasms by 1.2 and 3.3 percent in both years.

The effect of the male sterile cytoplasms on classical growth characters was also assessed in the three years. The ogu cytoplasm had consistently lower crop growth rates, net

assimilation rates, relative growth rates and leaf area development than similar treatments in the nap and pol cytoplasms. Genotypes in the pol cytoplasm produced similar growth characters as those in nap, except the former produced a 10 % lower net assimilation rate early in the growing season. Hybrids in the nap cytoplasm produced greater levels of heterosis for leaf area and crop growth rates than the pol cytoplasm.

B. napus hybrids were heterotic for leaf area index and leaf area duration but appeared to exhibit little or no heterosis for crop growth rates, net assimilation rates or relative growth rates.

Carbon dioxide exchange rates of cultivars and hybrids in the three cytoplasms were determined in 1987, 1988 and 1989. In all three years, there were no significant differences between treatments in the nap and pol cytoplasms. As compared to nap cytoplasm treatments, ogu cytoplasm treatments reduced photosynthetic rates by approximately 20%. Genotypes in the ogu cytoplasm had approximately 65% of the leaf chlorophyll of the nap cytoplsam treatments early in the growing season and approached chlorophyll levels of the nap cytoplasm treatments later in the growing season. There were no significant differences in photosynthetic rate per unit chlorophyll between any of the cytoplasms. In the narrow range of genotypes tested there was no heterosis for photosynthetic rate or leaf chlorophyll content.

FOREWORD

The following thesis was written in manuscript style. The two manuscripts will be submitted to the Canadian Journal of Plant Science for publication.

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1. INTRODUCTION

Canadian rapeseed is derived from the seed of Brassica napus and Brassica campestris. In 1988, production of low erucic acid, low glucosinolate "canola" quality rapeseed in Canada was 4,243,000 tonnes on 3,652,000 hectares. Average Canadian canola rapeseed yields were 1160 kg ha^{-1} but in 1988, Manitoba yields were 980 kg ha^{-1}, a decline from 1987 yields of 1440 kg ha^{-1}.* Yield increases have primarily resulted from both genetic improvements and improved crop management; additional yield improvements may result from high levels of high parent heterosis present in canola quality B. napus hybrids (Sernyk and Stefansson 1983).

Before hybrid development is pursued in any crop species, economic levels of high parent heterosis must be available, pollination control mechanisms must be developed and proper seed production techniques must be devised. Reports of hybrid vigor in B. napus and B. campestris (Sernyk and Stefansson 1986, Zuberi and Ahmed 1973) have stimulated hybrid canola research. Canadian researchers have reported levels of 40% high parent heterosis in hybrids derived from crosses of B. napus canola quality cultivars (Sernyk and Stefansson 1983) and up to 120% in specific inbred line crosses (Brandle and McVetty 1989). In B.

* Handbook of Agricultural Statistics. 1988. Tables 41,42,43.

campestris Hutcheson et al. (1981) reported that high parent heterosis for seed yield of 46% occurred in a sub-species cross.

Studies of hybrid seed production techniques have been carried out in western Canada. Pinnisch (1988) suggested the use of 10:1 row ratios of sterile to fertile plants to produce adequate canola quality B. napus seed, which may be seeded at 3-6 kg ha^{-1} (Van Deynze 1989).

Several forms of pollination control presently exist in oilseed rape. Hand emasculation, gametocides, self-incompatibility and genic male sterility are at present ineffective for hybrid seed production in B. napus. The most promising system of producing hybrid seed appears to be cytoplasmic male sterility (CMS) as it is a simply inherited character and does not segregate for male fertility.

There are several CMS systems currently available for use in hybrid oilseed rape. Ogura (1968) reported male sterility in Raphanus sativus and transferred the nucleus of B. napus into this cytoplasm. The ogu cytoplasm has poor nectar production and a low temperature chlorosis (Bannerot et. al. 1977) which may affect plant growth rates. The lack of fertility restorer genes in B. napus germplasm presently limits the use of the ogu system in hybrid seed production. Thompson (1972) discovered the nap sterile cytoplasm which has maintainers in almost all B. napus genotypes and fertility is restored by a single Mendelian dominant gene. The pol system discovered by Fu (1981) has deep male

sterility and appears to be the most developed system. Dominant Mendelian genes restoring fertility to the pol cytoplasm have been discovered in B. napus germplasm (Fang and McVetty· 1987).

Both the nap and pol cms systems presently suffer from temperature induced male fertility reversion. Nap CMS anthers revert from male sterile to partially male fertile under temperatures of 26°/20° C (Fan and Stefansson 1986). Pol CMS anthers revert to partial male fertility under temperatures of 30°/24° C (Fan and Stefansson 1986).

There are indications that male sterile cytoplasms may have detrimental effects on plant growth. McVetty et al. (1990) suggested that hybrids in the pol cytoplasm have lower seed yield, harvest index and oil concentration as compared to similar hybrids in the nap cytoplasm. Poor plant performance associated with male sterile cytoplasms may decrease the economic benefits of high parent heterosis.

The objective of this research was to determine the effects of the nap, pol and ogu male sterile cytoplasms on the performance of several inter-cultivar hybrids by assessing the instantaneous photosynthetic rate, growth characteristics and seed quality of oilseed rape hybrids.

2. LITERATURE REVIEW

2.1 F1 HYBRID CULTIVARS

2.1.1 HYBRID SEED PRODUCTION

The development of hybrid cultivars requires significant levels of high parent heterosis, an effective pollination control mechanism and efficient hybrid seed production techniques.

Three distinct plant lines are required for hybrid seed production using cytoplasmic male sterility (CMS). The A-line has a male sterile cytoplasm and lacks fertility restoring nuclear alleles (S rfrf). The maintainer or B-line is genetically identical to the A-line except that it has a fertile cytoplasm (N rfrf). B-lines are planted adjacent to A-lines to increase male sterile line seed. The male sterile A-line is then planted next to the restorer or R-line which has a normal cytoplasm and male fertility restoring alleles (N RfRf), or more commonly, a male sterile cytoplasm and male fertility restoring alleles (S RfRf). All seed harvested on the A-line is theoretically hybrid and male fertility restored as all pollen is derived from male fertile R-lines. This seed is harvested and sold to be grown by producers (Burton 1983).

The presence of both A-lines and R-lines in the hybrid seed production field complicates seed production. Should too many R-lines be used in the field, hybrid seed yields

per unit area will be low due to fewer A-line rows. If insufficient R-line rows are used in the field, then poor cross-pollination will result and seed yields on A-line rows will be low, again reducing hybrid seed yield per unit area. Proper R-line to A-line row ratios must be developed for each crop and each set of environmental conditions (Smith 1978). R-lines also have to be removed after pollinating A-lines to prevent accidental contamination of A-line seed by non-hybrid seed from R-lines. The creation of triazine tolerant A-lines such as the ctr CMS system in B. napus allows for a post flowering application of atrazine to remove susceptible R-lines and allow A-line seed to be harvested without contamination (Grant 1984).

2.1.2 HETEROSIS

Hybrid vigor was first reported by Schull who defined it as an improvement in the crossbred as compared to pure breeding biotypes (Schull 1948). McDaniel (1986) described heterosis as the superiority of a hybrid over its parents.

Heterosis has several definitions. Positive or negative heterosis produces an offspring which has attributes greater or lesser than its parents. Low parent heterosis is displayed when the hybrid exceeds only the low parent involved; in high parent heterosis the offspring exceeds the better parent in the cross. The most common reference point for hybrid vigor is the mid-parent value, in

which the hybrid is superior to the mean of the two parents. For breeding purposes, however, high parent heterosis is the most logical reference point.

2.1.3 HETEROSIS IN OILSEED RAPE

Significant levels of high parent heterosis have been reported in B. campestris. Zuberi and Ahmed (1973) demonstrated 23% high parent heterosis existed for a cross involving B. campestris var 'Toria'. Hutcheson et al. (1981) described a spontaneous sub-species hybrid which produced seed yields 46% above the better parent in the cross. Although lower relative oil concentration accompanied this hybrid, seed yields was comparable to B. napus cultivars.

High parent heterosis for seed yield has also been documented in B. napus. Shiga (1976) demonstrated hybrid vigor in 98 of 131 inter-cultivar crosses. Sernyk and Stefansson (1983) identified two superior combinations of canola quality cultivars exhibiting 39% and 43% high parent heterosis; the former was a hybrid between an Australian cultivar, Marnoo and the Canadian cultivar Regent, the latter between Karat from Sweden and Regent. Grant and Beversdorf (1985) achieved 72% high parent heterosis between a hybrid of Westar and Hanna. Buson (1980) demonstrated 23% heterosis in winter oilseed rape inbred lines while Brandle

and McVetty (1989) reported 120% high parent heterosis in crosses of summer oilseed rape inbred lines.

Potential high parent heterosis for seed quality characteristics has been investigated. Swamyrao (1970) demonstrated up to 52% high parent heterosis for oil concentration in brown sarson (B. campestris var. Sarson). Grant and Beversdorf (1985), using B. napus hybrids, suggested little heterosis could be found for seed oil concentration but negative heterosis existed for protein levels. Sernyk and Stefansson (1983) reported fluctuations for oil and protein concentrations of about 1% around the level of the parent cultivar Regent. Brandle and McVetty (1989) indicated an increase of 0.8% for oil and a reduction of 0.5% in protein concentration in hybrids made using oilseed rape inbred lines.

High parent heterosis has been identified for plant growth characters. Johnson (1971) demonstrated up to 14% high parent heterosis for fresh weight production during the early vegetative growth phases of forage rape (B. napus) inbred line derived hybrids. Sernyk and Stefansson (1983) suggested that summer oilseed rape hybrids had greater leaf areas and closed the canopy more quickly than parental cultivars. An increase of 25 to 29% total dry matter and a 9 to 14% improvement in harvest index had been found for inter-cultivar hybrids (Sernyk and Stefansson 1983). Grant and Beversdorf (1985) and Lefort-Buson et al. (1987) did not demonstrate heterosis for thousand seed weight; Sernyk and

Stefansson (1983) suggested this character was intermediate between the two parents.

Oilseed rape hybrids were found to be taller than their parents (Sernyk and Stefansson 1983). Sernyk and Stefansson (1983) reported improved lodging resistance in hybrids but Grant and Beversdorf (1985) suggested that the increased lodging they observed was due to greater height and seed yield of hybrids. Grant and Beversdorf (1985) and Sernyk and Stefansson (1983) indicated that flowering date for hybrids was intermediate with respect to their parents.

Generally, greater levels of high parent heterosis have been realized between crosses of material with different genetic origins, such as Canadian by European (Sernyk and Stefansson 1983) and European by Asian crosses (Lefort-Buson et al. 1987). Similar conclusions have been drawn in Zea mays (Moll et al. 1962) and in Gossypium (Marani and Avieli 1973).

2.1.4 POLLINATION CONTROL MECHANISMS

B. napus has been reported as capable of producing up to 80% selfed seed under Western Canadian conditions (Rakow and Woods 1987). Proper hybrid seed production requires the production of a male sterile female line to achieve sufficient hybridity of the hybrid seed lot.

Several forms of pollination control exist in B. napus. Hand emasculation is useful for the development of small

quantities of seed, but is too labor intensive for field scale seed production. The use of gametocides such as GA_4 and GA_7 mixtures applied at the bud stage have been suggested for cole crops (Van Der Meer and Van Dam 1979), however, frequent applications (i.e. daily) of high concentrations of chemicals would be necessary to maintain male sterility. Rousselle et al. (1984) believed that gametocides would be ineffective in oilseed rape due to its indeterminate flowering habit.

Genetic male sterility (GMS) provides a simply inherited nuclear character conferring male sterility. Segregation for male fertility and sterility occurs in later generations requiring hand-roguing of field material (Lee and Yan 1983), making this pollination control mechanism uneconomical for Canadian seed producers.

Many Brassica species contain self-incompatibility or "SI" alleles. Although no R-lines are required with this system and seed may be bulk harvested, the major disadvantage of SI is that lines are difficult to maintain and increase (Burton 1983). Bud pollination (Thompson 1983) or exposing plants to 5% CO_2 will break down incompatibility and improve seed set. Alternatively, self-compatibility alleles could be placed in the lines during early testing to maintain seed quantities but later removed to produce hybrid seed (Burton 1983). Self-incompatibility may be successfully used in the production of synthetic varieties

to utilize a portion of available hybrid vigor (Banks and Beversdorf 1987).

Most recent research in pollination control has focused on cytoplasmic male sterility or CMS. CMS causes the flower to develop normal pistils while producing shrivelled, non-functional anthers through negative nucleo-cytoplasmic interactions (Burton 1983).

2.1.5 CYTOPLASMIC MALE STERILITY IN OILSEED RAPE

The first of several CMS systems in oilseed rape is the mur cytoplasm. Shiga (1980) created this system by backcrossing the nuclear genome of B. napus into the cytoplasm of an artificial amphidiploid hybrid of B. napus and Diplotaxis muralis. Pellan-Delourme et al. (1987) demonstrated that most B. napus lines were fertility restorers and only two maintainer lines were isolated. Ringdahl et al. (1987) reported the B. napus genotypes Bronowski and Karat are not sterilized by the mur cytoplasm. Male sterile plants produced virtually no nectar (Pellan-Delourme et al. 1987) and small seed (Ringdahl et al. 1987).

The nigra cytoplasm was successfully transfered from B. oleracea to B. napus. No nectar was produced on the deeply male sterile flowers and some twisted pods were formed on female plants. Maintainers have not been located and most B. napus lines appear to be restorers (Pellan-Delourme et al. 1987).

The ctr CMS system was developed by crossing the triazine resistant cultivar Tower by Bronowski; allowing for the removal of triazine susceptible male fertile R lines from a hybrid production field. No pollen appears to be produced on sterile plants and two to five fertility restorer genes have been identified in the cultivars Tower and Westar (Grant 1984).

Ogura (1968) found a male sterile cytoplasm in European radish (Raphanus sativus) and successfully transfered the nucleus of B. napus into this cytoplasm. The ogu cytoplasm has deep male sterility and produces no pollen under all temperature and photoperiod regimes (Polowick and Sawhney 1987). A low temperature chlorosis associated with the original ogu cytoplasm was removed by substituting B. napus chloroplasts into the Raphanus cytoplasm in summer (Pelletier et al. 1983) and winter oilseed rape cultivars (Jarl and Bjornman 1988). Poor nectar production on male sterile lines had resulted in low seed yields (Renard and Mesquida 1987), but the use of protoplast fusion techniques has produced male sterile regenerants with normal nectar levels and higher yields (Pelletier et al. 1987). Restorer genes are available in radish germplasm but none have been identified in oilseed rape (Shiga 1980). All oilseed rape cultivars are maintainers for ogu CMS and it appears as though restorer genes would have to be introgressed from Raphanus sativus (Fan et al. 1986). Heyn (1978) transfered restorer genes from radish but low female fertility

associated with male fertility restoration has been reported (Pellan-Delourme and Renard 1987).

The sterile nap cytoplasm is the standard B. napus cytoplasm. It was identified as a male sterile cytoplasm from a cross between Chisaya-natane and Hokuriku 23 (Shiga and Baba 1971) and from crosses involving a variety of rape strains using the Polish cultivar Bronowski as the male parent (Thompson 1972). Subsequent discovery of interchangeable maintainers indicated that these cytoplasms were identical. Thompson (1972) and Fan et al. (1986) tested rape strains from seven countries and found the cultivars Bronowski and Lergo were sterile and the rest were maintainers. Inheritance of male fertility restoration was attributed to a single Mendelian dominant gene. Yarrow et al. (1986) used protoplast fusion techniques tlo produce a triazine tolerant nap male sterile system.

The most promising male sterile cytoplasm appears to be the pol cytoplasm, originally derived from the Polish cultivar Polima (Fu 1981). Fan et al. (1986) reported that most cultivars functioned as maintainers but few sources of restorer genes are available. Male sterility was partially restored using an aneuploid line derived from the B. juncea cultivar Zem (Tai and McVetty 1987). Fang and McVetty (1987) later identified single Mendelian dominant restorer genes from a University of Manitoba winter oilseed rape accession line UM2353 and from the winter oilseed rape cultivar Italy.

Male fertility reversion induced by high temperatures has been reported in the nap and pol CMS systems. The nap CMS system produces partially fertile anthers under temperature regimes of 26°/20° C 10 to 14 days after treatment (Fan and Stefansson 1986). Reversion to partial fertility under such relatively low temperatures currently makes the nap CMS system impractical for hybrid seed production. The pol CMS system was slightly more temperature stable reverting to partial fertility at 30°/26° C (Fan and Stefansson 1986) 10 to 13 days after treatment (Burns 1989). Under partial male fertility, the incompletely male sterile A-lines pollinate their own flowers and little hybrid seed produced (Pinnisch 1988). Burns (1989) determined sufficient genetic variation existed for male sterility in the pol CMS system to initiate selection for more temperature stable inbred A-lines.

2.2 CYTOPLASM COST IN HYBRID CROPS

2.2.1 CYTOPLASM COST IN WHEAT

Kihara (1951) reported male sterility resulted from disharmony between the nucleus of Triticum vulgare and the cytoplasm of Aegilops caudata. The caudata cytoplasm induced temperature stable male sterility but several deleterious pleiotropic attributes have been observed. Decreased female fertility was frequently encountered, with

long days and late sowing intensifying the pistilloidy (Kihara 1951). Hughes and Bodden (1978) reported an increased incidence of germless grains, haploids and twin seedlings with genotypes in the caudata cytoplasm. Porter et al. (1965) indicated that reduced plant vigor and shrivelled, yellow seed were produced in this cytoplasm.

The ovata cytoplasm, identified by Fukasawa (Panayatov 1980), had fewer detrimental side effects. Porter et al. (1965) reported lines in this cytoplasm produced yellow seed and shrunken kernels and genotypes in the ovata cytoplasm flowered later than B-lines (Hughes and Bodden 1978). A low temperature chlorosis was associated with genotypes in the ovata cytoplasm (Mukai and Tsunewaki 1978).

T. timopheevi provided the next cytoplasm for hybrid wheat studies. Timopheevi A-lines flowered later than B-lines but female fertility was normal (Hughes and Bodden 1978). Although Rai (1976) suggested elevated seed protein in timopheevi lines, Sasaki et al. (1976) determined that the increased protein levels were due to poor seed set rather than the male sterile character itself. C.F. Hayward, as reported by Virmani and Edwards (1983) presented data indicating that hybrids in the normal cytoplasm outyielded timopheevi based hybrids by 7.1%. Johnson and Lucken (1986) reported reduced seedling germination and poor seedling vigor in timopheevi A-lines as compared with their B-lines.

Timopheevi A-lines were found to be susceptible to increased pre-harvest sprouting. Hand-emasculated B-lines had similar sprouting tendencies as fertile B-lines but were much lower than male sterile A-lines. Clayton and Ellis (1976) reported that A-lines had greater sprouting tendencies between two and four weeks prior to harvest.

Alpha-amylase levels were much higher in male sterile lines than in B-lines or self-pollinated lines (Doig et al. 1975). Jonsson (1976) found high levels of alpha-amylase in the F_1 but F_2 lines had similar enzyme levels as R-lines as long as complete fertility restoration was achieved. It was also noted that incompletely restored F_1 lines had greater alpha-amylase levels than more completly restored genotypes.

Rai (1976) indicated that a significant relationship between alpha-amylase levels and sprouting in wheat lines, a significant correlation between shrunken kernels and alpha-amylase activity, and concluded that alpha-amylase may be responsible for both kernel shrinkage and pre-harvest sprouting.

Although pollinator lines have an effect on pre-harvest sprouting in wheat (Ellis and Clayton 1976), the maternal genotype appeared to have major control over this character. Doig et al. (1975) reported that sufficient genetic variation existed for the selection of sprouting resistance.

Other sources of male sterility in wheat have been investigated. Mukai and Tsunewaki (1978) determined that the cytoplasms from T. umbellulata, T. triunculus and T.

biuncialis induced leaf variegation in a large number of common wheats. Maan and Lucken (1970) indicated that the T. boeticum cytoplasm produced weak plants, but that male fertility restoration also restored plant vigor. (Mukai and Tsunewaki 1979) indicated the Ae. kotschyi and Ae. variabilis cytoplasms decreased plant dry weights by 12 and 26% respecively. No other agronomic charcters were affected by the kotschyi cytoplasm but variabilis reduced plant height and tiller number (Mukai and Tsunewaki 1979).

2.2.3 CYTOPLASM COST IN CORN

Effects associated with male sterile cytoplasms have been described in Zea mays. Noble and Russell (1963) determined that the Texas (T) cytoplasm produced a 4.5% and 4.0% yield decrease for single cross and three-way cross hybrids respectively; a significant interaction was found to exist between nuclear genotype and cytoplasm. Stringfield (1958) observed that male sterile lines without fertility restoring genes (rfrf) yielded 11% less than completely restored material. Duvick (1958) and Noble and Russell (1963) indicated significant genotype by location interactions existed for T and S male sterile corn.

Grogan et al. (1965) found few differences in dry matter partitioning between male sterile and fertile lines, although Criswell (1974) found that tassel dry matter was greater in male fertile genotypes. $^{14}CO_2$ moved more rapidly

into the ears and husks of male sterile plants whereas fertile plants had $^{14}CO_2$ incorporated into ears later in the growing season. Total dry matter differences were not distinguishable until after six weeks after anthesis indicating that few differences exist in vegetative growth between male sterile and male fertile corn (Grogan et al. 1965).

Other aspects of the corn plant have been altered by male sterility. Duvick (1958) indicated that fewer tillers were associated with the T cytoplasm and Noble and Russell (1963) determined that fertility restoring (Rf) genes delayed pollen shedding. Stalk breakage was not affected by male sterility (Duvick 1958) despite the discovery that some male sterile T cytoplasm lines produced thinner stems (Sarvella and Grogan 1976). Both the T and S cytoplasms produced fewer barren plants than fertile lines (Duvick 1958). Male sterile plants have shorter internodes above the ear (Grogan et al. 1971). As a result, A-line plants are typically shorter than their fertile counterparts (Sarvella and Grogan 1965).

Disease susceptibility associated with male sterile cytoplasms has raised the most concern regarding the use of CMS in hybrid seed production. Grogan et al. (1971) described increased susceptibility of male sterile cytoplasms to Yellow Leaf Blight in corn. Yield reductions occurred even with the addition of fertility restoring alleles and were eventually attributed to the male sterile

mitochondria. These organelles were also the source of susceptibility to Southern Leaf Blight caused by Helminthosporium maydis. This organism caused a 15% yield reduction in 1971 and was responsible for the return to mechanical detasselling for hybrid seed production beginning in 1972.

2.2.3 CYTOPLASM COST IN OTHER CROPS

Pleiotropic effects associated with the msm1 cytoplasm from Hordeum spontaneum have been noted by hybrid barley breeders. Ahokas (1979) determined that slightly lighter kernels are produced on male-sterile spikes. Msm1 appears to produce 8% and 7% more protein in normal and high lysine lines respectively, but protein quality was unaffected by male sterility (Ahokas 1979). Sterile plants also produced leaves with greater levels of xanthophylls and more chlorophyll b, although no differences in total pigment concentrations were found (Ahokas 1978).

Studies in tobacco using the Nicotiana megalosiphon cytoplasm and the N. tabacum genome have demonstrated that male sterility affects plant development. Male sterile lines yielded from 7 to 14% less than fertile lines (Povilaitis 1972). Maan et al. (1962) indicated that male sterile plants were shorter, flowered later and weighed less than their fertile counterparts throughout the entire growing season. It was also determined that genotypes in

the megalosiphon cytoplasm produced fewer leaves until about 68 days after transplanting. Although Chaplin and Ford (1965) reported no significant differences in alkaloid content between sterile and fertile lines, Povilaitis (1972) suggested that male sterility may affect alkaloid levels. Maan et al. (1962) suggested that the additional seed yield benefit from tobacco hybrids was negated by detrimental effects associated with this male sterile cytoplasm.

Effects of the replacement of the Gossipyum hirsutum cytoplasm by the diploid cytoplasms G. anomalum and G. arboreum have been studied in cotton. No significant differences in yield were attributed to the diploid cytoplasms, but anomaleum lines had greater seedling vigor, fewer bolls and lighter lint levels (Thomson 1976). Although Meyer (1973) found yield reductions of 20% and 18% for the anomalum and arboreum cytoplasms as compared to male fertile lines, these differences may have resulted from poorer seedling establishment, the use of different restorer genes and smaller plots in Meyer's experiment.

2.2.4 CYTOPLASM COST IN OILSEED RAPE

The majority of the studies involving oilseed rape hybrids have been carried out in the nap cytoplasm. Since the pol cytoplasm is closer to utilization, it must be determined whether levels of heterosis may be maintained in this cytoplasm.

Some effects associated with the pol cytoplasm have been described by McVetty et al. (1990). Pol hybrids flowered one day later than hybrids in the nap cytoplasm. Both cytoplasms exhibited high parent heterosis for seed yield and total dry matter, but there were significant differences between them. The nap group of hybrids produced superior seed yield, total dry matter production and harvest index as compared similar hybrids in the pol cytoplasm. It was determined that oil content was lower by 1.3% in the pol cytoplasm as compared to the nap cytoplasm.

2.3 GROWTH ANALYSIS

2.3.1 GENERAL CONCEPTS

Net photosynthetic production of plant material may be assessed using plant growth analysis. The main measurements involved are leaf area (A) and mass (M) measured over a specific period of time (T). These primary values provide the basis for the calculation of the following secondary characters - relative growth rate (RGR), net assimilation rate (NAR), crop growth rate (CGR), leaf area index (LAI) and leaf area duration (LAD).

RGR is also described as the efficiency index, representing the efficiency of the plant to produce new material based on the resources already present (Hunt 1978). RGR is calculated as follows:

$$1\text{-}2\ RGR = \frac{\ln M2 - \ln M1}{T2 - T1} \qquad \text{(Radford 1967)}$$

where the RGR is determined by the change in the natural log of the mass divided by the time interval between T1 and T2.

RGR provides a convenient integration of the combined performances of various plant parts. Hunt (1978) suggested calculating the RGR for each plant component. Thus leaf relative growth rate is calculated as:

$$1\text{-}2\ RGRL = \frac{\ln LM2 - \ln LM1}{(T2 - T1)} \qquad \text{(Radford 1967)}$$

where LM1 and LM2 denote leaf weights at T1 and T2.

RGR is affected by NAR. NAR describes the productive efficiency of plants and estimates the carbon assimilatory capacity of its leaves (Hunt 1978). NAR is important as an estimate of plant growth as it is offset only to a small extent by changes in mineral uptake (Richards 1969). Sestak et al. (1971) indicated that ontogenetic shift is generally lower for NAR than for RGR. NAR tends to be closely related to incoming solar radiation, but decreases with greater water stress. NAR is derived as follows:

$$1\text{-}2\ NAR = \frac{(M2 - M1)}{(A2 - A1)} \times \frac{(\ln A2 - \ln A1)}{(T2 - T1)} \qquad \text{(Radford 1967)}$$

where NAR is calculated for the interval between T1 and T2.

LAI has been used to estimate the leafiness of a crop canopy. The optimum LAI is achieved when the lowest leaves

maintain a slight positive carbon balance (Sestak et al. 1971). All photosynthetically active radiation is being intercepted; with a further increase in LAI, lower leaves begin to import carbon and become a liability on further plant growth (Hunt 1978). LAI is a unitless value and is calculated as total leaf area (A) divided by the sample ground area (G):

$$1 \text{ LAI} = \frac{A1}{G} \qquad \text{(Radford 1967)}$$

LAD involves the integration of the LAI versus time curve. This parameter measures the ability of a crop to display leaf surface throughout the growing season and represents the opportunity to assimilate carbon (Richards 1969). Hunt (1978) indicated that LAD may be more important than NAR in determining final yield (Hunt 1978). Leaf area duration may be determined as follows:

$$1\text{-}2 \text{ LAD} = \frac{(A2\text{-}A1) \times (T2\text{-}T1)}{\ln A2 - \ln A1} \qquad \text{(Radford 1967)}$$

where LAD is calculated as the leaf area differences between the samples (A2 and A1) and related to the natural log of the leaf area divided by the time interval between sampling periods T1 and T2.

CGR combines LAI and NAR to represent of total plant size. CGR includes a value (G) that corrects for the total sample ground area and is derived by the following:

$$1\text{-}2\ CGR = \frac{W2-W1}{G(T2-T1)} \qquad \text{(Radford 1967)}$$

where total plant weight is related to the ground area covered (G) for the duration of time between samples T1 and T2.

2.3.2 GROWTH ANALYSIS OF OILSEED RAPE

Allen et al. (1971) observed several distinct phases of growth in winter B. napus. Phase one, about six to seven weeks after seeding, was associated with a high CGR and peak LAI at about five weeks after seeding. Superior CGR were associated with earlier maturing varieties (Kasa and Kondra 1986). Tayo and Morgan (1975) in a glasshouse study indicated peak LAI occurred two weeks prior to anthesis. Allen and Morgan (1975) observed later maturing cultivars typically achieved greater LAI toward the end of this period. NAR were also very high during early crop growth, particularly under low LAI and low seeding rates (Clarke and Simpson 1978). No large differences in NAR were found to exist between high and low yielding winter B. napus lines during the vegetative period (Allen and Morgan 1975).

The second growth phase arrived with initial flowering and lasted two to three weeks. Mendham and Scott (1975) suggested that plant size is limited at inflorescence

initiation because of a fixed number of leaves and axillary buds. Variation in leaf size contributed to the majority of the differences in leaf area between cultivars (Mendham and Scott 1975). A marked decrease in CGR was realized during early flowering (Allen and Morgan 1971). High yielding cultivars generally maintained high LAI throughout this phase (Allen and Morgan 1975). Although there was a decline in NAR associated with early flowering, Allen and Morgan (1975) showed no significant differences between high and low yielding cultivars. Jenkins and Leitch (1986) suggested that lower NAR during flowering may be due to light interception by non-photosynthetically active floral parts.

Phase three began once the plants stopped flowering. This period lasted one to two weeks and was characterized by increased CGR despite a declining LAI. Jenkins and Leitch (1986) indicated that LAI decreased due to the shading of leaves by the upper pods. Large increases in pod and total plant dry weight were reported during this phase (Allen et al. 1971). Clarke and Simpson (1978) indicated an enhanced NAR is achieved before flowering but as it was attained prior to maximum pod area, it was not due to increased pod photosynthesis. They suggested that the increased demand for assimilates from the expanding pods may have increased the export of photosynthate from remaining leaves and enhanced their photosynthetic production.

The last phase of crop growth lasted about five weeks during which plant dry weights decreased due to pod and seed

shattering (Allen and Morgan 1971) and the LAI declined to near zero (Major 1977).

Cultivars differed in their ability to maintain LAI. Major (1977) determined that B. napus maintained greater LAD than B. campestris. Clarke and Simpson (1978) suggested that differences in LAD after anthesis contributed to superior yields in both rain-fed and irrigated trials.

Significant differences in plant dry matter accumulation have also been recorded. Major (1977) observed that summer B. napus varieties produce 60% of their dry matter prior to flowering whereas B. campestris produces 40% prior to anthesis. Clarke and Simpson (1978) determined that rain-fed material produced half of its dry matter prior to flowering, while material not limited by moisture continued to increase in mass until pod ripening. Tayo and Morgan (1975) observed that higher yielding winter B. napus cultivars were superior at producing dry matter during early flowering and during pod development.

2.3.3 FLOWER AND POD DEVELOPMENT

Mendham and Scott (1975) suggested that plant size at floral initiation limited later growth stages. Flower production in B. napus typically extended over three weeks (Allen and Morgan 1975); with earlier, lower yielding cultivars flowering earlier than higher yielding, later maturing genotypes. For spring cultivars, days to first

flower contributed significantly to early maturity and that earliness of the initial growth stages contributed to earliness of later growth stages (Campbell and Kondra 1977).

Assimilate flow to young pods was critical to normal seed development. Tayo and Morgan (1975) demonstrated that shading plants one week after anthesis reduced flower and pod numbers whereas later shading had no effect on flower numbers. Short periods of assimilate stress during flowering produced plants with fewer pods but more seeds per pod, but that extended periods of stress severely reduced pod expansion and seeds per pod. Leaf removal at flowering caused lower yields than shading as the expansion of bracts and axillary shoots compensated for decreased assimilate production (Tayo and Morgan 1975). The plants that experienced stress during the bud stage or early flowering appeared to be most severely affected.

2.4 PHOTOSYNTHESIS

2.4.1. GENERAL CONCEPTS

Research into photosynthetic processes demonstrate the net productivity of various plant organs using both infra-red gas analysis (IRGA) equipment and radioactive isotopes such as ^{14}C.

There have been conflicting reports regarding cultivar differences in net photosynthesis. Mahon and Hobbs (1981) indicated that there were no differences for photosynthetic rate among high and low yielding pea genotypes. They also

indicated that although small differences may exist, many measurements would be required to establish statistical significance. Peet et al. (1977) indicated that differences in photosynthetic rate were observed in dry beans, but that performance changed with developmental phase. Dornhoff and Shibles (1970) indicated that higher yielding soybean varieties have a tendency to produce greater photosynthetic rates later in the season and as in dry beans, the greatest rates may be found at anthesis.

Reports of heterosis for photosynthetic rate appear to be crop specific. In Sorghum, Blum (1989) indicated mid parent heterosis was found for three of four hybrids over a specific temperature range. Khanna-Chopra (1982) found positive, negative or a lack of heterosis for Sorghum hybrids at anthesis, but indicated that the leaves may have been at different stages of physiological maturity. Hoffman et al. (1984) indicated that hybrid vigor in Sorghum was more apparent under high stress conditions. In corn, Heichel and Musgrave (1969) found significant mid parent heterosis for a series of unrelated inbred lines, but no high parent heterosis was found. Lupton (1976) indicated that differences in photosynthetic rates between wheat parents and hybrids could be found. Yamauchi and Yoshida (1985) suggested little hybrid vigor could be found for a series of 35 rice hybrids. Muramoto et al. (1965) working with cotton showed no consistent differences in

photosynthetic rate between interspecific hybrids and parental varieties.

Chlorophyll concentration has been used as an indicator of photosynthetic productivity. (Buttery and Buzzell 1977) suggested that early screening for lines with greater photosynthetic rates may be done using chlorophyll concentration as a selection criteria as there was a close association between these two parameters. Buttery et al. (1981) indicated that there was a significant relationship between July leaf chlorophyll levels and net photosynthesis among a set of 48 cultivars and lines of soybeans. Planchon (1976) indicated that certain wheat hybids contain greater levels of chlorophyll a which may be related to greater photosynthetic rates.

Chlorophyll deficiencies resulting in leaf variegation have been reported in several male sterile cytoplasms. Fukasawa (1953) reported leaf color variegation was associated with the ovata male sterile cytoplasm in wheat. Mukai and Tsunewaki (1978) reported that variegation also occured in the umbellulata and biuncialis cytoplasms and that the effects appeared to be temperature dependent.

Differences for leaf characters have been described within the genus Brassica. Significant differences were found for photosynthetic rates and total leaf chlorophyll concentration among B. napus, B. campestris, B. juncea, B. carinata and B. hirta (Hobbs 1988). Banga et al. (1983) reported the cam cytoplasm from B. campestris increased the

chlorophyll a content of leaves relative to a similar genotype in B. napus. Differences appeared to be greater across species than within a single species as no differences in the chlorophyll a/b ratio were found for four B. napus genotypes (Hobbs 1988).

2.4.2 INFRA-RED GAS ANALYSIS OF OILSEED RAPE

Hozyo et al. (1972) determined that pods were active in carbon assimilation and Major (1975) indicated that B. napus stems, pods and leaves all contain stomates and could be capable of photosynthesis.

Studies have been conducted in B. napus using IRGA equipment. Donnelly and Hume (1984) reported depressed photosynthetic rates in triazine tolerant rapeseed at 25°/20° C but not at 15°/10° C. Hobbs (1986) used the Li-6000 closed system to assess field-grown triazine tolerant canola. Photosynthetic rates were lower for resistant plants over all sampling dates. In a subsequent study, Hobbs (1988) determined heterosis did not exist for leaf photosynthetic rate in a Westar/Cresor B. napus hybrid. Paul and Eagles (1988) as well as Hobbs (1988) found no significant differences existed for photosynthetic rate within a series of four B. napus varietes.

Field conditions have been shown to affect photosynthetic rates in B. napus. Hobbs (1988) demonstrated lower photosynthetic rates existed for plants grown under

moisture stress. Clarke and McCraig (1982) indicated that the uptake of $^{14}CO_2$ was fairly consistent during periods of low water stress but as water stress intensified, increases in leaf diffusive resistance appeared to produce a diurnal pattern of photosynthetic rate. Hobbs (1988) reported that light saturation occurred at 1700 uE m^{-2} sec^{-1}. Singh et al. (1983) suggested that a diurnal patterns in mustard (B. juncea) photosynthetic rates was produced if light levels were below 1400 uEm^{-2} sec^{-1}. Peak photosynthetic rates were registered at 20° C but under cool days is lower in the morning, whereas under warmer days the photosynthetic rates were greater in the morning (Singh et al. 1988). Large deviations from optimum temperatures may produce varied responses in photosynthetic measurements (Hobbs 1988).

2.4.3. ^{14}C TRANSLOCATION STUDIES IN OILSEED RAPE

The second major source of photosynthesis research has involved radioactive labelling studies to trace translocation in plants. Brar and Thies (1979) determined the second fully expanded leaf exports assimilates to young leaves and root tissue. Major et al. (1978) demonstrated that photosynthetic products are not translocated from lower leaves to pods or seeds. The fifth leaf exported the majority of its products to the rapidly elongating stem (Brar and Thies 1979). Freyman et al. (1973) suggested that leaf photosynthesis was responsible for 35.2% of the

photosynthate produced in field grown B. campestris. There also was an inverse relationship between leaf area and photosynthetic rate per unit leaf area.

B. napus stems are also active in photosynthesis. Major et al. (1978) hypothesized the lower stem was responsible for plant maintenance as it retained a greater level of $^{14}CO_2$ with only a small portion exported to upper leaves, pods or seeds. Very little $^{14}CO_2$ was translocated to the root. Upper stems and leaves transported greater levels of assimilates to seed and lesser amounts to the pods (Major et al. 1978). Nalborczyk et al. (1986) reported that at initial seed formation leaves and shoots contribute 60% and 30% respectively to $^{14}CO_2$ fixation. Stems tended to import less material for their own growth after stem elongation ceased (Addo-Quaye et al. 1986). Chapman et al. (1983) found photosynthetically active stems in winter oilseed rape but little CO_2 fixing activity in buds or flowers.

Chapman et al. (1984) also believed the ultimate leaf had a considerably smaller effect on final yield than in cereals. Brar and Thies (1979) considered the ultimate leaf to be extremely important as it contributed 37% of the photosynthate in seed. This apparent contradiction may be due to the discovery that $^{14}CO_2$ levels decreased in later seed development due to increased seed respiration (Brar and Thies 1979) as a result of oil formation. Addo-Quaye et al. (1986) determined that the ultimate leaf of the main stem

did not translocate much of its assimilates to axillary branches. Transport to other stems may be unnecessary as axillary branches usually have their own ultimate leaves.

Differences in CO_2 translocation were determined for individual racemes and for positions on racemes. Addo-Quaye et al. (1986) demonstrated lower pods imported more assimilates than those on the upper two thirds of the raceme. This may be due to the greater light penetration and fixing ability of upper pods or as Wardlaw (1968) suggested, the proximity of the sink to the source enabled greater transport of fixed carbon from the upper leaves to lower pods.

3.0 GROWTH ANALYSIS OF HYBRID OILSEED RAPE

3.1 Abstract

The effect of three male sterile cytoplasms on the growth characters of oilseed rape cultivars and their hybrids was studied at five locations over three years. Treatments in the pol cytoplasm flowered one to two days later than similar material in the nap and ogu cytoplasms; hybrids were intermediate to their parents in flowering date. Genotypes in the pol and ogu cytoplasms produced 75% and 50% the seed yield of nap cytoplasm treatments. Heterosis for seed yield and total dry matter of 30 to 40% was found in the nap and pol cytoplasms, but not in the ogu cytoplasm. Relative seed oil concentration was reduced in the pol cytoplasm by approximately 2.1% and in ogu by approximately 5.4%; there was no heterosis for seed quality. Hybrids exhibited superior LAI, LAD, CGR and NAR but not RGR. Treatments in the ogu cytoplasm had reduced CGR, NAR, RGR, LAI and LAD by 40, 30, 10, 25 and 20 percent respectively as compared to similar genotypes in the nap cytoplasm. Treatments in the nap and pol cytoplasms appeared to produce similar growth rates except that the pol cytoplasm produced lower levels of heterosis and a 10% reduction in NAR early in the growing season. The use of the ogu male sterile cytoplasm decreased plant performance whereas the pol cytoplasm had fewer detrimental effects on plant growth characters.

3.2 Introduction

Recent reports of high parent heterosis in oilseed rape suggests that hybrid oilseed rape cultivars may be produced on a field scale. Canadian researchers discovered levels of 40-50% (Sernyk and Stefansson 1983) and 75-120% (Brandle and McVetty 1989) high parent heterosis for intercultivar and inbred-line derived oilseed rape hybrids, respectively.

Cytoplasmic male sterility (CMS) appears to be the most efficient mechanism to develop hybrid canola quality oilseed rape. The nap (Thompson 1972) and pol (Fu 1981) cytoplasms have temperature sensitive male sterility producing a temperature induced partial male fertility reversion under field temperatures of 26° C and 30° C respectively (Fan and Stefansson 1986). The ogu cytoplasm (Ogura 1968) lacks fertility restoring genes in B. napus, is susceptible to a low temperature seedling chlorosis (Bannerot et al. 1977) and appears to be less attractive to honeybee pollinators than conventional nap cytoplasm oilseed rape (Renard and Mesquida 1987). Protoplast fusion techniques have removed the chlorosis (Pelletier et al. 1987) and increased the attractiveness to pollinating insects.

The biological cost of male sterile cytoplasms has also been documented in corn (Noble and Russell 1963, Stringfield 1958) and wheat (Virmani and Edwards 1983). McVetty et al. (1990) indicated that the pol cytoplasm decreased seed

yield, total dry matter and oil concentration in a series of oilseed rape hybrids and open pollinated populations.

This study was established to assess the effects of the nap, ogu, and pol cytoplasms on classical growth analysis characters in several summer oilseed rape hybrids and their parental cultivars.

3.3 Materials and Methods

3.3.1 Experimental and Field Design

Three geographically diverse cultivars of summer oilseed rape (B. napus spp. oleifera) were used as parents in this study: Marnoo (Australia), Karat (Sweden) and Regent (Canada). Sernyk and Stefansson (1983) and McVetty et al. (1990) have demonstrated significant high parent heterosis among hybrids involving these cultivars.

A-lines with the pol cytoplasm were produced by crossing Karat, Regent and Marnoo to the B. napus cv. Polima and then backcrossing six times to recover the nuclear genotype of the recurrent parent.

Ogu A-lines were produced by crossing the cultivars Regent, Karat and Marnoo to Raphanus sativus L. and then backcrossing six times to recover the genotype of the male parent.

The trials consisted of 21 entries: the three cultivars (Regent, Karat and Marnoo) and four reciprocal cross hybrids (Regent/Karat, Karat/Regent, Regent/Marnoo, Marnoo/Regent)

in each of the three cytoplasms (nap, ogu, pol). A split-plot design was used to randomize the entries with each cultivar or hybrid considered a main factor and cytoplasm type the sub-factor.

The experiments were planted at the Cottage Field site at the Plant Breeding Institute, Cambridge, England in 1987 and the Point, Arboretum and Bison Block fields of the University of Manitoba, Winnipeg, Canada in 1988 and 1989. At Cambridge, 150 kg N ha^{-1} was applied as 34-0-0 (14%S) and 1 kg ha^{-1} Benazalox WP (50g clopyralid (3,6-dichloropyridine-2-carboxylic acid) + 300g benazolin (4-chloro-2,3-dihydro-2-oxo-1,3-benazolin-3-ylacetic acid) was applied at the fifth true leaf stage. In 1988 and 1989, trifluralin (a,a,a-trifloro-2,6-dintro-N,N-dipropyl-p-toluidine) granules were fall-incorporated at a rate of 0.35 kg a.i. ha^{-1} for broadleaf and grass weed control. Fertilizer was applied at a rate as recommended by soil tests. Carbofuran (2,3-Dihydro-2,2-dimethyl-7-benzofuranyl methyl carbamate) (10%) granules were banded with the seed at a rate of 1.0 kg a.i. ha^{-1} to control flea beetles (Phyllotrea cruciferae G. and P. striolata F.). Malathion (0,0-dimethyl phosphorodithioate of diethyl mercaptosuccinate) (50% EC) was applied throughout the latter half of the growing seasons at the University of Manitoba sites to control diamondback moths (Plutella spp.) in 1988 and flea beetles in 1988 and 1989. Plots were hand weeded throughout the growing seasons at all locations.

The plots were designed as follows. The Cottage Field, Cambridge site had six replicates and the University of Manitoba sites had four replicates at each location. Plots consisted of three rows of experimental material in 1987 and 1988; while in 1989, four rows of each treatment were seeded per plot. The three metre long rows were seeded at a rate of 6 kg ha^{-1} on 30 cm spacings. Adjacent plots were separated by one guard row of Fido and Regent seed at the Cambridge and University of Manitoba sites, respectively. Edge effects were minimized by seeding four border rows of Fido and Regent at each end of the experiment.

The treatments were seeded into summerfallowed land using a Hege belt-cone seeder at Cambridge and a double disc belt-cone 8-row seeder at the University of Manitoba sites. The Cottage Field Cambridge location was seeded April 13, 1987; in 1988 the Point location was planted on May 16 and the Arboretum on May 25. In 1989, the Point was seeded May 9 and the Bison Block location on May 17. The Cottage Field had a clay soil, the Point a Riverdale Clay, while the Arboretum and Bison Block were classified as Red River Clay soil types.

Seasonal temperatures and rainfall in 1987 were cool and dry in April and May, but cool and wet in June, July and August. 1988 levels of rainfall were below average in May and August and close to normal in June and July (Appendix 1 Table 1). On June 11, 1988 10.5 mm irrigation was applied

to the Point location. Temperatures were 3.3° C and 5.2° C above long term averages in May and June respectively with July and August 1.5° C and 1.7° C warmer than normal. In 1989, mean June temperatures were similar to climatic averages; May, July and August were 3° C above long term temperatures. May and July were drier than normal, August was near long term averages and in June there was twice the normal rainfall.

3.3.2 Growth Analysis Sampling Procedure

All material used for growth analysis studies were collected from the outer two rows of each plot. Samples one two and three were removed on 14, 28 and 42 days respectively after crop emergence. Equal emergence was considered to have occurred 8, 8 and 14 days after planting in 1987, 1988 and 1989 respectively. The longer period required for emergence to occur in 1989 may be attributed to depressed spring soil moisture levels in 1989.

After emergence, three representative 50 cm row lengths in each plot were staked to provide homogeneous sampling material throughout the growing season. All samples were at least 25 cm from the ends of plot rows and from earlier samples to reduce edge effects. During sampling, plants were pulled from the ground and any remaining root tissue was excised at the root/shoot interface. The shoots were placed into cold storage at 4° C until they could be dried

at 80° C for 48 hours. Total shoot dry mass was then recorded.

One replicate at each location was selected on the basis of uniform emergence for a more detailed study. Within this replicate, each sample was separated into leaf and stem tissue. Leaf area determinations were made using a photocopy and cut procedure in Cambridge and a Delta-T Instruments camera and monitor system at the University of Manitoba. Leaves that were over 50 percent chlorotic were not included in leaf area assessments. Leaf and stem material were dried separately for 48 hours at 80° C using a forced air drier before being weighed. Linear regression was used to relate the leaf and stem mass and leaf area to the other treatments in each location.

3.3.3 Yield and Quality Measurements

Days to first flower after planting and days to 50% flower were recorded at all locations in 1988 and 1989. Yield data were collected from the inner row in 1987 and 1988 and from the inner two rows in 1989. The center row(s) were hand-harvested, deposited in burlap bags and air dried for three weeks. The bags were weighed to determine total dry matter, threshed using a stationary thresher and the seed weighed. Harvest index was calculated as a ratio between sed yield and total dry matter.

Seed quality was assessed in 1988 and 1989. Harvested seed was passed through a spiral column; 25g and 1g samples were used to measure seed oil and protein concentration respectively. Oil content was measured using Nuclear Magnetic Resonance (Robertson and Morrison 1979) and seed protein at 0% moisture was determined using the macro-kjeldahl method.

3.3.4 Statistical Analysis

All statistical analyses were performed on the Ahmdahl mainframe computer system at the University of Manitoba using standard analysis of variance procedures. The chi-square test of homogeneity of error variances was applied using procedures as outlined in Gomez and Gomez (1984). Data were combined within years when possible but not over years due to the heterogeneity of error variances. Means separation tests were performed using the Least Significant Differences (LSD) test on individual subplots (cytoplasms) within each mainplot (cultivar or hybrid) and of each mainplot within each subplot. Heterosis was determined to exist at the high parent level based on significant separation using the LSD test on cultivars; cytoplasm cost was determined based on LSD separation of cytoplasms within particular cultivars or hybrids. Linear regressions were performed to correlate growth analysis characters to yield and total dry matter at each location.

As suggested by Campbell and Kondra (1978) and Sernyk and Stefansson (1983), hybrids were intermediate to their parents in days to first flower in the nap cytoplasm, and appear to be intermediate in the ogu and pol cytoplasms as well.

3.4.1.2 Days to Fifty Percent Flower

Location differences were found to be significant in 1988 (Appendix 1. Table 2), but cultivars, cytoplasms and cultivar by cytoplasm interactions were significant in both years. As with days to first flower, nap cytoplasm treatments were the earliest to flower (Table 3.3 and Table 3.4). Ogu cytoplasm treatments were similar to nap cytoplasm treatments, with the exception of ogu Regent, which took longer to reach 50% flower. In 1988, Karat and Marnoo in the pol cytoplasm were equivalent to similar genotypes in the nap cytoplasm, but all other pol cytoplasm treatments flowered up to four days later in 1988 and reached 50% flower one to two days later in 1989.

3.4.2 Seed Yield

Cambridge 1987 seed yields had a significant cytoplasm and cultivar effect as well as a significant cytoplasm by cultivar interaction (Appendix 1. Table 3). In 1987, cultivars in the pol and nap cytoplasms produced similar

yields, except for Karat and the Karat/Regent hybrid which produced more seed in the pol cytoplasm than in the nap (Table 3.6). Ogu cytoplasm cultivar yields were similar to those found in the other cytoplasms, but hybrids in the ogu cytoplasm yielded significantly lower than hybrids in the pol or nap cytoplasms. Significant levels of high parent heterosis were found in nap Karat hybrids, but not for nap Marnoo hybrids. Karat/Regent was the sole pol cytoplasm hybrid which was heterotic for yield.

Significant cultivar by cytoplasm interactions were found for all locations in 1988 and 1989 (Appendix 1. Table 4). Due to the heterogeneity of error variances, data were not combined and individual locations will be discussed in separate experiments.

In 1988, cultivar seed yields were equivalent in the nap and pol cytoplasms (Table 3.7 and Table 3.8). All ogu cytoplasm treatments produced significantly lower seed yield as compared to the treatments in the pol and nap cytoplasms.

All intercultivar hybrids tested in 1988 had lower seed yield in the pol cytoplasm as compared to similar hybrids in the nap cytoplasm. Hybrids in the ogu cytoplasm had significantly lower seed yield as compared to hybrids in the pol or nap cytoplasms.

Significant levels of high parent heterosis were demonstrated in all nap hybrids for both 1988 locations. At the Point, only the Regent/Karat and Karat/Regent hybrid produced significant high parent heterosis for seed yield in

the pol cytoplasm, while at the Arboretum, only hybrids containing Regent as a female parent had significant high parent heterosis in the pol cytoplasm.

Average 1988 yields were 1387 kg ha^{-1} while in 1989, yields were 1906 kg ha^{-1}. Arboretum 1988 yields were very poor as compared to yields at the Point 1988 as a result of flea beetle and diamondback moth infestations. The Point was also irrigated on June 11 which may have increased seed yield.

In 1989, improved growimg conditions and fewer insect problems allowed for greater seed yields than in 1988. Cultivars and hybrids in the nap cytoplasm produced significantly greater seed yield than those in the pol cytoplasm at both locations (Table 3.9 and Table 3.10). All cultivars and hybrids in the ogu cytoplasm produced lower seed yield than in the nap or pol cytoplasms.

In 1989 high parent heterosis was found for all hybrid combinations in the nap cytoplasm at both locations, for Regent/Karat and Karat/Regent in the ogu cytoplasm at Bison and for all Regent/Karat based hybrids at the Point. Only hybrids involving Karat and Regent exhibited heterosis at both locations in 1989.

Differences in seed yield between locations in 1989 may be attributed to several factors. The Bison Block was a newly cultivated land area which had quackgrass (Agropyron repens) and Canada thistle (Cirsium arvense) infestations early in the year, whereas the Point location had relatively

fewer weed problems. The Bison site was also prone to flooding as it appeared that the surface drainage was poorer than at the Point location.

3.4.3 Total Dry Matter

Significant cytoplasm effects and cultivar by cytoplasm interactions were found in all years at all locations (Appendix 1. Table 3 and Appendix 1. Table 5).

In 1987, high parent heterosis was found in the nap and pol cytoplasm treatments but not for the ogu cytoplasm treatments (Table 3.11). The nap and pol cytoplasms produced similar total dry matter except for the Karat/Regent and Karat genotypes which produced less material when in the pol cytoplasm. Ogu cytoplasm parents and hybrids produced the least total dry matter; except for Regent, which all three cytoplasms produced similar total dry matter.

In 1988 no significant differences were found to exist between cultivars in any cytoplasm, but the nap and pol cytoplasm hybrids at the Point 1988 location were superior to the ogu hybrids (Table 3.12). Additionally, no significant differences were found between the nap and pol cytoplasm treatments at the Arboretum site, but hybrids produced significantly lower total dry matter when in the ogu cytoplasm (Table 3.13). High parent heterosis was found for all combinations of hybrids in the nap cytoplasm, but only for Regent/Karat and Karat/Regent in the pol cytoplasm.

No high parent heterosis for total dry matter was found to exist in the ogu cytoplasm.

At the 1989 Point location, no differences could be established for total dry matter production between the nap and pol cytoplasms, except with the Regent/Marnoo hybrid (Table 3.14). Cultivars in all three cytoplasms produced equal total dry matter; hybrids in the ogu cytoplasm produced significantly lower dry matter than hybrids in the other two cytoplasms. High parent heterosis was found for the Karat/Regent and Regent/Karat combinations in all three cytoplasms, but heterosis was not discovered for Marnoo and Regent hybrids.

The Bison 1989 site produced only a significant cytoplasm effect with the nap cytoplasm similar to the pol cytoplasm and the pol cytoplasm equal to the ogu cytoplasm for total dry matter production (Table 3.15). Heterosis for total dry matter could not be established at this site.

3.4.4 Harvest Index

Significant cytoplasm differences were not found at the Cambridge site (Appendix 1. Table 3), but differences in harvest index (HI) existed in 1988 and 1989 (Appendix 1 Table 6).

In 1988 and 1989 nap cytoplasm treatments produced greater HI than pol cytoplasm treatments. Ogu cytoplasm treatments produced the lowest HI values.

Differences in pollination among the cytoplasms may explain differences in harvest index. The nap cytoplasm produced fully functional anthers with long filaments under the warm field conditions in 1988 and 1989, whereas the pol cytoplasm produced smaller anthers with shorter filaments. Shorter filaments do not allow the anthers to extend above the stigma and may reduce pollen transfer. The ogu cytoplasm is fully sterile and pollen would have to be transferred from adjacent gauard rows.

The University of Manitoba sites usually have very little insect pollination and wind pollination would be the most important mode of pollen transfer. Under these conditions, the fully fertile nap and the partially fertile pol cytoplasm would develop greater seed yield than the male sterile ogu cytoplasm.

3.4.5 Seed Quality

Significant cytoplasm effects were found in both 1988 for seed oil and seed protein content (Appendix 1. Table 7). A slight cultivar by cytoplasm interaction was discovered for seed oil content in 1989.

The pol cytoplasm produced a lower relative seed oil concentration by approximately 1.8 and 2.4% for 1988 (Table 3.16) and 1989 (Table 3.17) respectively, but produced greater seed protein levels by 0.9% (Table 3.16) and 1.5% (Table 3.18). Lower seed oil content had been associated

with the pol cytoplasm (McVetty et al. 1990). The ogu cytoplasm reduced relative seed oil by as much as 5.9 and 6.3%, but increased seed protein by 3.1 and 3.5% for 1988 and 1989 respectively.

Both the ogu and pol male sterile cytoplasms appeared to have a detrimental effect on seed oil concentration. The presence of a significant cultivar by cytoplasm interaction indicates that selection for greater seed oil levels within individual cytoplasms may improve oil concentration in the pol and ogu cytoplasms.

In 1988, warm temperatures combined with low precipitation during pod development produced seed with lower oil and greater protein concentration. Oil levels were lowered by approximately 1% and protein content was increased by about 0.5% for 1988 as compared to 1989.

3.4.6 Growth Characters

3.4.6.1 Crop Growth Rate

In all three years, significant cytoplasm differences were discovered for all three sampling periods (Appendix 1. Table 8, Appendix 1. Table 9 and Appendix 1. Table 10). Highly significant cultivar by cytoplasm interactions were found to exist in 1988 until approximately 14 days after emergence (DAE) (Appendix 1. Table 9).

In 1987, ogu cytoplasm treatments had a significantly lower crop growth rate (CGR) throughout the growing season (Table 3.19). No significant differences in CGR were noted between genotypes in the nap and pol cytoplasms.

In 1988 cultivars in the nap and pol cytoplasms produced similar CGR1 (Table 3.20). Karat and Regent produced equal CGR1 when in the nap or pol cytoplasms; Marnoo produced the greatest CGR1 in the pol cytoplasm and significantly lower CGR1 in the nap and ogu cytoplasms. The Karat/Regent hybrid was the only hybrid which produced greater CGR1 in the nap cytoplasm as compared to the pol cytoplasm. In other hybrids, the nap and pol cytoplasm treatments produced equal CGR1; hybrids in the ogu cytoplasm produced significantly lower CGR1.

No evidence of heterosis for CGR1 could be found for any of the cytoplasms.

In 1989, Karat and Marnoo produced similar CGR1 in the nap and pol cytoplasms (Table 3.21). Marnoo genotypes in the nap Karat and nap Marnoo cytoplasm were found to be equal to similar genotypes in the pol cytoplasm. Regent in the nap cytoplasm developed greater CGR1 than in the pol cytoplasm. In all cases, cultivars in the ogu cytoplasm produced lower CGR1 than in the other two cytoplasms. Hybrids in the nap cytoplasm produced greater CGR1 as pol cytoplasm hybrids in all cases except for the Marnoo/Regent hybrid. All hybrids in the ogu cytoplasm produced inferior crop growth rates as compared to the nap or pol cytoplasms.

In 1989 high parent heterosis was found for three of four nap cytoplasm hybrids but not for any of the other nuclear cytoplasm combinations.

As with the Cambridge 1987 location, treatments in the ogu cytoplasm produced lower CGR throughout the growing season as compared to the nap or pol treatments (Table 3.23).

Although CGR may not be adversely affected by the pol cytoplasm in the cultivars, the absence of high parent heterosis for CGR may limit the productivity of hybrids in this cytoplasm.

As Clarke and Simpson (1978) reported, CGR was relatively low in the early sampling periods of all three years but increased as the season progresed. Major (1977) determined that CGR increased as flowering approached and as the plants attained maximum leaf area. Leaf production did not appear to be excessive as CGR continued to increase throughout the growing season for all three years (Clarke and Simpson 1978).

CGR was lowest at the Cambridge site early in the year (Table 3.19), suggesting that CGR may be adversely affected by cool, wet weather. There was an upsurge in CGR later in the growing season, indicating compensatory growth may occur.

3.4.6.2 Net Assimilation Rate

Although no significant cytoplasm differences were found between cytoplasms or cultivars for net assimilation rate (NAR) in the Cambridge trial (Appendix 1. Table 8), significant cytoplasm effects were found in the first sampling periods of 1988 (Appendix 1. Table 11) and the first and second sampling periods of 1989.

In 1988 and 1989 NAR1 nap cytoplasm treatments produced greater NAR than the pol cytoplasm treatments (Table 3.24). Genotypes in these two cytoplasms produced signficantly greater NAR1 than ogu cytoplasm treatments. In 1988 detrimental effects of the ogu cytoplasm on NAR were still evident 28 days after emergence (DAE), suggesting that this cytoplasm is less efficient in net photosynthetic production. Under better growing cvonditions such as in 1989, ogu cytoplasm treatments maintained inferior NAR for at least 42 DAE. It may be possible that the use of distantly related cytoplasms such as the ogu cytoplasm from Raphanus may reduce the net assimilation rate or photosynthetic efficiency of canola hybrids.

Although significant cultivar effects were discovered in 1989, no significant levels of high parent heterosis for NAR were discovered (Table 3.25) for any of the three years.

The nature of the growing season appeared to affect the pattern of NAR development. The cool, wet conditions found in 1987 produced non-significant cytoplasm and cultivar

effects. A hot, dry season such as 1988 produced a significant cytoplasm effect only early in the growing season when moisture conditions were close to long term averages. The warm, wet season of 1989 produced greater differences among cytoplasms. The detrimental effect of male sterile cytoplasms appear to be more pronounced under ideal growing conditions.

Net assimilation rates were greatest during seedling development and declined throughout the growing season as suggested by Hunt (1978). Decreases in NAR may be due to the mutual shading of leaves as canopy closure nears completion (Clarke and Simpson (1978).

3.4.6.3. Relative Growth Rate

Cultivar effects were found to be significantly different for RGR (relative growth rate) at the Cambridge 1987 site (Appendix 1. Table 12). Significant cultivar by cytoplasm interactions, cultivars and cytoplasms were found significant for relative growth rate 1 in 1988 and 1989 (Appendix 1. Table 13). Cytoplasm effects were significant for RGR2 in 1988 and RGR3 and for RGR3 in 1989.

In all three years, pol and nap cytoplasm treatments produced equivalent RGR1, but ogu cytoplasm treatments developed lower RGR1 throughout the sampling period (Table 3.26, Table 3.27 and Table 3.28).

Although the ogu cytoplasm treatments produced significantly lower RGR1, they developed significantly greater RGR2 and RGR3 as compared to nap and pol cytoplasm treatments .(Table 3.29).

Relative growth rate appears to be relatively stable and not severely affected by the adverse environmental conditions of 1988. Clarke (1977) suggested that weather conditions may affect RGR; it may be possible that the cool and wet conditions encountered at Cambridge may have decreased relative growth rates.

There was no indication of heterosis for RGR in any of the years tested.

As the ogu cytoplasm is subject to a low temperature chlorosis (Bannerot et al. 1977), it may produce a lower growth rate than the other two cytoplasms and may continue to invest energy into vegetative tissue later in the season while similar genotypes in the nap and pol cytoplasms are allocating dry matter to reproductive organs. Treatments in the ogu cytoplasm may develop dry matter at a slower rate and delay plant development.

3.4.6.4 Leaf Area Index

Cytoplasm effects were significantly different for leaf area index (LAI) in 1987 (Appendix 1. Table 12). The 1988 and the 1989 locations (Appendix 1. Table 14 and Appendix 1. Table 15) produced cytoplasm differences in both years as

well as significant cultivar by cytoplasm interactions for LAI.

At the Cambridge 1987 locations the ogu cytoplasm treatments produced significantly lower LAI than the other cytoplasms for all three sampling periods (Table 3.27). No significant differences appeared to exist for LAI between the nap or pol cytoplasm treatments.

In 1988, cultivars in the nap and pol cytoplasms generally produced equal LAI1 (Table 3.28). Ogu cytoplasm treatments generally produced lower LAI1 as compared to the other cytoplasms. Hybrids in the nap cytoplasm generally produced greater LAI than pol cytoplasm hybrids; hybrids in the pol cytoplasm produced equal or greater LAI as hybrids in the ogu cytoplasm. In 1989, nap and pol cytoplasm treatments the greatest LAI1 while ogu cytoplasm treatments produced lower LAI in both cultivars and hybrids (Table 3.29).

In 1988, hybrids in the nap cytoplasm produced greater LAI2 when Regent was a female parent and pol hybrids produced greater LAI when Regent was the male parent (Table 3.30). Ogu cytoplasm treatments produced significantly lower LAI2 than the other cytoplasms.

In 1989, the nap and pol cytoplasm treatments produced significantly greater LAI2 than ogu cytoplasm treatments (Table 3.31).

In 1988, LAI3 was greater in the pol cytoplasm treatments than treatments in the nap or ogu cytoplasms

(Table 3.32). In 1989 there were no significant differences between the nap or pol cytoplasm treatments (Table 3.33). In 1989, treatments in the ogu cytoplasm produced significantly lower LAI3 than in the other two cytoplasms.

Heterosis for leaf area was only expressed in 1988. The Karat/Regent, Regent/Karat Regent/Marnoo hybrids were heterotic for leaf area index in the nap cytoplasm (Table 3.38). Two of these hybrids continued to produce heterosis for LAI until 28 DAE. No significant levels of heterosis for leaf area were found at Cambridge as the cool, moist conditions may have limited hybrid leaf area production. In 1989, excellent growing conditions appeared to favor cultivar growth and reduced heterosis for LAI as no significant levels of heterosis were discovered at any stage.

3.4.6.5 Leaf Area Duration

Cytoplasm effects were significant for leaf area duration (LAD) in 1987 (Appendix 1. Table 23). The 1988 and 1989 locations (Appendix 1. Table 17 and Appendix 1. Table 18) produced significant cytoplasm and cultivar by cytoplasm interactions for LAD.

The nap and pol cytoplasms produced equal LAD for the 1987 Cambridge location (Table 3.34); ogu cytoplasm treatments developed lower LAD for the entire growing season.

In 1988 and 1989 the pattern of LAD was as follows. In most cases the nap and pol cytoplasms produced similar LAD for the open pollinated varieties (Table 3.35 to Table 3.40). Ogu material consistently produced inferior LAD for both parents and hybrids.

The primary difference between the pol and nap cytoplasms occured with the levels of heterosis for LAD. Nap cytoplasm treatments were heterotic for LAD1 in 1988 and for LAD2 in 1989. Pol cytoplasm treatments were not heterotic for LAD. Ogu cytoplasm treatments produced heterotic LAD for only two hybrids at one location. Heterosis was expressed for LAD in 1988 during the first sampling dates but was expressed in 1989 during the second period. The delay of heterosis may be due to the unfavorable conditions during emergence and crop establishment in 1989.

3.4.7 Relationships Between Growth Parameters and Yield

Many of the growth parameters were significantly related to crop yield (Appendix 1. Table 19 and Table 3.41). CGR was significantly correlated to yield for all sampling periods over all locations. RGR during early seedling growth is important as all five locations had significant relationships between this growth parameter and crop yield. NAR assessments during periods one and two produced significant correlations in three of five environments. LAI

also provided a close relationship with yield as four of five locations in each sampling period were significantly related. LAD is an important determinant of crop yield as all three sampling periods for all locations were significantly related to crop yield.

There were also significant relationships between total dry matter and the growth parameters (Apendix 1. Table 20 and Table 3.42). LAI and LAD provided a significant relationship with 11 and 15 of the 15 sample periods significantly related to total dry matter production, respectively. NAR for sample periods one and two produced two and three sites related to total dry matter. RGR in sample one provided relationships in all of the sites and relative growth rate two in two of the locations. CGR was related to total dry matter in fourteen of the fifteen sample periods.

Although the majority of the growth analysis parameters calculated in this work would provide estimates of cytoplasm cost and heterosis, several of these are more applicable to standard research programs than others. The use of NAR, LAI and LAD, while useful to provide relative estimates of plant development, also require tremendous amounts of labor to obtain accurate leaf area assessments. RGR and CGR are simply acquired by sequential destructive harvests and drying of plant material which would be far less costly to a research program.

In addition, the majority of the parameters were highly correlated during the early portion of crop development i.e. during seedling development and early bolting. In studies such as this, it may be useful to sample more frequently earlier in the season to examine the effects of early crop development on crop yield.

3.5. Summmary and Conclusions

The effect of three male sterile cytoplasms on the classical growth parameters of hybrid oilseed rape was studied to determine the biological cost of hybrid seed production using CMS.

The pol cytoplasm delayed flowering in both hybrid and parental cultivars by 1 to 2 days, but the ogu cytoplasm did not delay flowering. Hybrids flowered intermediate to their parents in both years.

There were significant cultivar by cytoplasm differences for seed yield and total dry matter. Treatments in the nap cytoplasm had greater seed yield and total dry matter than pol treatments and ogu material had the lowest seed yield and total dry matter production. Yield penalties for the pol and ogu cytoplasms were approximately 25 and 50% respectively. Greater levels of yield heterosis were found in nap cytoplasm material, as there appeared to be a cytoplasm cost associated with the pol and ogu cytoplasms.

Seed quality was affected by cytoplasm type. Pol material lowered relative seed oil concentration by approximately 2.1% and increased seed protein by 1.2%. The ogu cytoplasm decreased relative oil concentration by 6.1% and increased seed protein by 3.3%.

Growth analysis characters were also affected by cytoplasm type. The ogu cytoplasm reduced CGR, NAR, RGR, LAI and LAD by 40, 30, 10, 25 and 20% throughout the growing season, respectively. The pol cytoplasm had similar growth rates as the nap cytoplasm, except that pol had a 10% lower NAR early in the growing season and that lower levels of heterosis were found for CGR, LAI and LAD.

3.6 Acknowledgements

The author wishes to express his thanks to the National Sciences and Engineering Research Council of Canada for their financial assistance.

Table 3.1. Mean days to first flower 1988.

cultivar/hybrid	cytoplasm nap	ogu	pol
Karat	41.2 a	41.5 a	42.2 a
Marnoo	40.3 a	41.6 a	42.5 b
Regent	37.8 a	40.0 b	41.3 c
Karat/Regent	40.6 a	41.3 a	42.5 b
Regent/Karat	40.5 a	41.5 a	41.7 b
Marnoo/Regent	40.7 a	41.0 b	42.0 b
Regent/Marnoo	40.1 a	40.5 b	42.0 b

Means followed by the same letter within rows are not significantly different at the 5% level of probability, LSD.

Table 3.2. Mean days to first flower 1989.

cultivar/hybrid	cytoplasm nap	ogu	pol
Karat	43.8 a	44.2 a	44.8 b
Marnoo	43.6 a	44.7 b	46.0 c
Regent	42.3 a	43.5 b	44.0 b
Karat/Regent	43.1 a	43.5 a	44.7 b
Regent/Karat	43.5 a	44.0 a	44.7 b
Marnoo/Regent	43.7 a	44.0 a	45.0 b
Regent/Marnoo	43.1 a	43.5 a	45.0 b

Means followed by the same letter within rows are not significantly different at the 5% level of probability, LSD.

Table 3.3. Mean days to fifty percent flower 1988.

cultivar/hybrid	cytoplasm		
	nap	ogu	pol
Karat	46.8 a	47.3 a	48.2 a
Marnoo	47.0 a	48.1 a	49.0 a
Regent	43.2 a	44.7 a	47.0 b
Karat/Regent	44.8 a	46.2 a	48.2 b
Regent/Karat	44.7 a	46.3 a	47.8 b
Marnoo/Regent	45.1 a	45.5 a	47.6 b
Regent/Marnoo	45.5 a	46.3 a	47.8 b

Means followed by the same letter within rows are not significantly different at the 5% level of probability, LSD.

Table 3.4. Mean days to fifty percent flower 1989.

cultivar/hybrid	cytoplasm		
	nap	ogu	pol
Karat	49.1 a	49.0 a	50.5 b
Marnoo	47.1 a	50.8 a	51.3 b
Regent	46.0 a	47.8 b	48.6 b
Karat/Regent	47.6 a	48.5 a	49.6 b
Regent/Karat	47.3 a	47.8 a	49.1 b
Marnoo/Regent	48.0 a	49.1 a	49.7 b
Regent/Marnoo	47.8 a	49.0 a	49.5 b

Means followed by the same letter within rows are not significantly different at the 5% level of probability, LSD.

Table 3.5. Mean seed yield (kg ha^{-1}) Cambridge 1987.

cultivar/hybrid	cytoplasm nap	ogu	pol
Karat	1892 b	1459 c	2888 a
Marnoo	2716 a	1690 c	3175 a
Regent	1775 a	1567 a	1875 a
Karat/Regent	3437 b*	2392 c	4361 a*
Regent/Karat	2486 a*	1925 b	2808 a
Marnoo/Regent	3129 a	1990 b	2494 a
Regent/Marnoo	2427 a	1897 b	2670 a

Means followed by the same letter within rows are not significantly different at the 5% level of probability, LSD.
* denote significant levels of high parent heterosis at the 5% level of probability.

Table 3.6. Mean seed yield (kg ha^{-1}) Point 1988.

cultivar/hybrid	cytoplasm nap	ogu	pol
Karat	1831 a	1151 b	1451 ab
Marnoo	1458 a	1193 b	1501 a
Regent	1893 a	549 b	1484 a
Karat/Regent	2869 a*	1539 c	2213 b*
Regent/Karat	2909 a*	1439 c	2205 b*
Marnoo/Regent	2540 a*	1213 c	1897 b
Regent/Marnoo	2513 a*	1447 c	1978 b

Means followed by the same letter within rows are not significantly different at the 5% level of probability, LSD.
* denote significant levels of high parent heterosis at the 5% level of probability.

Table 3.7. Mean seed yield (kg ha^{-1}) Arboretum 1988.

cultivar/hybrid	cytoplasm nap	ogu	pol
Karat	758 a	96 c	718 a
Marnoo	806 a	268 b	785 a
Regent	1070 a	601 b	807 a
Karat/Regent	1778 a*	543 c	1136 b
Regent/Karat	1912 a*	354 c	1319 b
Marnoo/Regent	1651 a*	511 c	1003 b
Regent/Marnoo	1518 a*	308 c	1216 b*

Means followed by the same letter within rows are not significantly different at the 5% level of probability, LSD.
* denote significant levels of high parent heterosis at the 5% level of probability.

Table 3.8. Mean seed yield (kg ha^{-1}) Point 1989.

cultivar/hybrid	cytoplasm nap	ogu	pol
Karat	2027 a	715 c	1095 b
Marnoo	2825 a	772 c	1891 b
Regent	2809 a	336 c	1970 b
Karat/Regent	4010 a*	2150 c*	2092 b*
Regent/Karat	4106 a*	1803 c*	2055 b*
Marnoo/Regent	3841 a	1741 c	2943 b
Regent/Marnoo	3674 a	1587 c	2871 b

Means followed by the same letter within rows are not significantly different at the 5% level of probability, LSD.
* denote significant levels of high parent heterosis at the 5% level of probability.

Table 3.9. Mean seed yield (kg ha^{-1}) Bison 1989.

cultivar/hybrid	cytoplasm nap	ogu	pol
Karat	1905 a	890 c	1613 b
Marnoo	1558 a	838 c	1165 b
Regent	1718 a	938 c	1129 b
Karat/Regent	2767 a*	1218 c*	1534 b
Regent/Karat	2204 a*	1294 c*	1672 b
Marnoo/Regent	2417 a*	1041 c	1671 b*
Regent/Marnoo	2239 a*	1079 c	1873 b*

Means followed by the same letter within rows are not significantly different at the 5% level of probability, LSD.
* denote significant levels of high parent heterosis at the 5% level of probability.

Table 3.10. Mean total dry matter production (kg ha^{-1}) Cambridge 1987.

cultivar/hybrid	cytoplasm nap	ogu	pol
Karat	10833 b	8527 c	16322 a
Marnoo	11031 a	7244 c	13110 a
Regent	11088 a	9889 a	11744 a
Karat/Regent	15877 b*	11075 c	20322 a*
Regent/Karat	15293 a*	11922 b	17177 a
Marnoo/Regent	15822 a*	10199 b	16566 a*
Regent/Marnoo	15159 a*	11977 b	16677 a*

Means followed by the same letter within rows are not significantly different at the 5% level of probability, LSD.
* denote significant levels of high parent heterosis at the 5% level of probability.

Table 3.11. Mean total dry matter production (kg ha^{-1}) Point 1988.

cultivar/hybrid	cytoplasm nap	ogu	pol
Karat	7616 a	5456 a	6841 a
Marnoo	6966 a	5516 a	6424 a
Regent	8041 a	6107 a	7213 a
Karat/Regent	9850 a*	6580 b	8744 a*
Regent/Karat	9633 a*	6407 b	8833 a*
Marnoo/Regent	9457 a*	6596 b	8933 a*
Regent/Marnoo	9713 a*	6738 b	8650 a*

Means followed by the same letter within rows are not significantly different at the 5% level of probability, LSD.
* denote significant levels of high parent heterosis at the 5% level of probability

Table 3.12. Mean total dry matter production (kg ha^{-1}) Arboretum 1988.

cultivar/hybrid	cytoplasm nap	ogu	pol
Karat	5783 a	3592 b	4333 ab
Marnoo	6033 a	4000 b	5066 ab
Regent	5655 a	4024 a	4466 a
Karat/Regent	8711 a*	3441 b	7133 a*
Regent/Karat	8694 a*	5183 b	7566 a*
Marnoo/Regent	8111 a*	3574 b	5907 a
Regent/Marnoo	8027 a*	4727 b	6022 ab

Means followed by the same letter within rows are not significantly different at the 5% level of probability, LSD.
* denote significant levels of high parent heterosis at the 5% level of probability.

Table 3.13. Mean total dry matter production (kg ha^{-1}) Point 1989.

cultivar/hybrid	cytoplasm nap	ogu	pol
Karat	17688 a	17611 a	16621 a
Marnoo	27666 a	23855 a	26179 a
Regent	24055 a	13388 a	21549 a
Karat/Regent	32027 a*	22585 b*	29005 a*
Regent/Karat	31111 a*	19777 b*	28949 a*
Marnoo/Regent	29355 a	18611 b	25338 a
Regent/Marnoo	30000 a	22188 b	24632 b

Means followed by the same letter within rows are not significantly different at the 5% level of probability, LSD. * denote significant levels of high parent heterosis at the 5% level of probability.

Table 3.14. Mean total dry matter production (kg ha^{-1}) Bison 1989.

cultivar/hybrid	cytoplasm nap	ogu	pol
Karat	6869 a	6762 a	6018 b
Marnoo	6546 a	4629 c	6096 b
Regent	6068 b	5705 c	6805 a
Karat/Regent	8668 a*	7458 b	4339 c
Regent/Karat	7509 b*	7094 c	9335 a*
Marnoo/Regent	8121 a*	7377 b*	6019 c
Regent/Marnoo	8077 a*	6358 c*	7259 b*

Means followed by the same letter within rows are not significantly different at the 5% level of probability, LSD. * denote significant levels of high parent heterosis at the 5% level of probability.

Table 3.15. Mean cytoplasm effects on harvest index 1988 and 1989.

cytoplasm	1987	1988		1989	
	Cambridge	Point	Arb	Point	Bison
nap	.187 a	.283 a	.189 a	.263 a	.283 a
ogu	.184 a	.198 c	.097 c	.121 c	.162 c
pol	.183 a	.253 b	.164 b	.165 b	.240 b

Means followed by the same letter within rows are not significantly different at the 5% level of probability, LSD.

Table 3.16. Mean seed oil (%) and protein (%) combined experiments 1988.

cytoplasm	seed oil	seed protein
nap	39.86 a	30.01 c
ogu	33.91 c	33.16 a
pol	38.00 b	31.95 b

Means followed by the same letter are not significantly different at the 5% level of probability. LSD.

Table 3.17. Mean seed oil concentration (%) 1989.

cultivar/hybrid	cytoplasm		
	nap	ogu	pol
Karat	40.83 a	34.58 c	37.83 b
Marnoo	39.23 a	33.53 b	38.82 a
Regent	41.83 a	35.98 c	38.43 b
Karat/Regent	42.10 a	36.30 c	37.71 b
Regent/Karat	41.90 a	35.33 c	39.12 b
Marnoo/Regent	41.45 a	34.37 c	39.66 b
Regent/Marnoo	41.13 a	34.03 c	39.71 b

Means followed by the same letter within rows are not significantly different at the 5% level of probability, LSD.

Table 3.18. Mean seed protein concentration (%) 1989.

cultivar/hybrid	cytoplasm		
	nap	ogu	pol
Karat	30.06 a	33.18 c	31.10 b
Marnoo	29.90 a	32.32 b	30.36 a
Regent	29.17 a	32.77 c	31.40 b
Karat/Regent	29.36 a	32.50 c	31.60 b
Regent/Karat	29.48 a	32.55 c	31.12 b
Marnoo/Regent	29.07 a	33.68 c	31.11 b
Regent/Marnoo	29.05 a	33.72 c	30.12 b

Means followed by the same letter within rows are not significantly different at the 5% level of probability, LSD.

Table 3.19. Mean crop growth rate (mg cm^{-2}) Cambridge 1987.

cytoplasm	CGR1	CGR2	CGR3
nap	.058 a	.982 a	4.45 a
ogu	.042 b	.594 b	3.00 b
pol	.056 a	.970 a	4.82 a

Means followed by the same letter within rows are not significantly different at the 5% level of probability, LSD.

Table 3.20. Mean crop growth rate 1 (mg cm^{-2}) 1988.

cultivar/hybrid	cytoplasm		
	nap	ogu	pol
Karat	.120 a	.076 b	.141 a
Marnoo	.094 b	.074 c	.176 a
Regent	.189 a	.076 b	.166 a
Karat/Regent	.235 a	.099 c	.122 b
Regent/Karat	.158 a	.082 b	.152 a
Marnoo/Regent	.186 a	.092 b	.166 a
Regent/Marnoo	.178 a	.115 b	.190 a

Means followed by the same letter within rows are not significantly different at the 5% level of probability, LSD.

Table 3.21. Mean crop growth rate 1 (mg cm^{-2}) 1989.

cultivar/hybrid	cytoplasm		
	nap	ogu	pol
Karat	.108 a	.057 b	.105 a
Marnoo	.156 a	.069 b	.174 a
Regent	.143 a	.047 c	.119 b
Karat/Regent	.171 a*	.062 c	.120 b
Regent/Karat	.172 a*	.044 c	.134 b
Marnoo/Regent	.157 a	.050 b	.144 a
Regent/Marnoo	.189 a*	.073 c	.148 b

Means followed by the same letter within rows are not significantly different at the 5% level of probability, LSD.
* denote significant levels of high parent heterosis at the 5% level of probability.

Table 3.22. Mean cytoplasm effects on crop growth rate (mg cm^{-2}) 1988 and 1989.

cytoplasm	1988		1989	
	CGR2	CGR3	CGR2	CGR3
nap	.974 a	1.99 a	1.314 a	3.00 a
ogu	.714 b	1.69 b	0.577 b	1.98 b
pol	1.021 a	2.05 a	1.357 a	2.96 a

Means followed by the same letter within rows are not significantly different at the 5% level of probability, LSD.

Table 3.23. Mean cytoplasm effects on net assimilation rate (g m^{-2}) 1988 and 1989.

cytoplasm	1988	1989	1989
	NAR1	NAR1	NAR2
nap	2.85 a	2.93 a	1.06 a
ogu	1.96 c	2.03 c	0.92 b
pol	2.35 b	2.69 b	1.07 a

Means followed by the same letter within rows are not significantly different at the 5% level of probability, LSD.

Table 3.24. Mean relative growth rate 1 (g day^{-1}) 1988.

cultivar/hybrid	cytoplasm		
	nap	ogu	pol
Karat	.556 a	.512 b	.570 a
Marnoo	.539 a	.523 b	.583 a
Regent	.559 a	.518 b	.579 a
Karat/Regent	.586 a	.542 b	.560 b
Regent/Karat	.577 a	.531 b	.572 a
Marnoo/Regent	.588 a	.536 b	.581 a
Regent/Marnoo	.589 a	.552 b	.589 a

Means followed by the same letter within rows are not significantly different at the 5% level of probability, LSD.

Table 3.28. Mean leaf area index 1 combined 1988 locations (log transformed).

cultivar/hybrid	cytoplasm nap	ogu	pol
Karat	.101 a	.057 b	.108 a
Marnoo	.081 b	.056 b	.135 a
Regent	.102 a	.061 b	.121 a
Karat/Regent	.179 a*	.075 b	.097 b
Regent/Karat	.128 a	.063 b	.120 a
Marnoo/Regent	.151 a*	.074 c	.125 b
Regent/Marnoo	.142 a*	.061 b	.137 b

Means followed by the same letter within rows are not significantly different at the 5% level of probability, LSD.
* denote significant levels of high parent heterosis at the 5% level of probability.

Table 3.29. Mean leaf area index 1 combined 1989 locations (log transformed).

cultivar/hybrid	cytoplasm nap	ogu	pol
Karat	.090 a	.060 b	.091 a
Marnoo	.120 b	.070 c	.146 a
Regent	.112 a	.050 c	.103 b
Karat/Regent	.127 a	.064 c	.105 b
Regent/Karat	.107 b	.048 c	.144 a
Marnoo/Regent	.119 a	.053 b	.123 a
Regent/Marnoo	.137 a	.074 c	.126 b

Means followed by the same letter within rows are not significantly different at the 5% level of probability, LSD.

Table 3.30. Mean leaf area index 2 combined 1988 locations (log transformed).

cultivar/hybrid	cytoplasm nap	ogu	pol
Karat	.226 b	.054 c	.303 a
Marnoo	.203 b	.185 b	.338 a
Regent	.285 b	.252 b	.355 a
Karat/Regent	.306 b	.239 c	.322 a
Regent/Karat	.362 a*	.184 c	.320 b
Marnoo/Regent	.284 b	.278 b	.359 a
Regent/Marnoo	.383 a*	.248 c	.327 b

Means followed by the same letter within rows are not significantly different at the 5% level of probability, LSD.
* denote significant levels of high parent heterosis at the 5% level of probability.

Table 3.31. Mean leaf area index 2 combined 1989 locations (log transformed).

cultivar/hybrid	cytoplasm nap	ogu	pol
Karat	.210 b	.149 c	.298 a
Marnoo	.200 b	.163 c	.260 a
Regent	.236 a	.171 b	.258 a
Karat/Regent	.313 a	.283 b	.322 a
Regent/Karat	.320 a	.276 b	.331 a
Marnoo/Regent	.312 a	.256 b	.315 a
Regent/Marnoo	.318 a	.264 b	.317 a

Means followed by the same letter within rows are not significantly different at the 5% level of probability, LSD.

Table 3.32. Mean leaf area index 3 combined 1988 locations (log transformed).

cultivar/hybrid	cytoplasm nap	ogu	pol
Karat	.351 a	.273 b	.392 a
Marnoo	.299 b	.257 c	.363 a
Regent	.368 b	.376 b	.400 a
Karat/Regent	.404 b	.391 c	.415 a
Regent/Karat	.423 b	.365 c	.432 a
Marnoo/Regent	.385 a	.336 b	.403 a
Regent/Marnoo	.386 b	.372 b	.410 a

Means followed by the same letter within rows are not significantly different at the 5% level of probability, LSD.

Table 3.33. Mean leaf area index 3 combined 1989 locations (log transformed).

cultivar/hybrid	cytoplasm nap	ogu	pol
Karat	.741 a	.618 b	.750 a
Marnoo	.788 a	.629 b	.771 a
Regent	.792 a	.626 b	.759 a
Karat/Regent	.784 a	.624 b	.777 a
Regent/Karat	.735 b	.690 c	.849 a
Marnoo/Regent	.804 a	.595 c	.736 b
Regent/Marnoo	.827 a	.595 b	.812 a

Means followed by the same letter within rows are not significantly different at the 5% level of probability, LSD.

Table 3.34. Mean cytoplasm effects on leaf area duration (cm^2 days) Cambridge 1987.

cytoplasm	LAD1	LAD2	LAD3
nap	275.2 a	5401 a	31250 a
ogu	200.4 b	3421 b	21084 b
pol	268.2 a	5359 a	33230 a

Means followed by the same letter within rows are not significantly different at the 5% level of probability, LSD.

Table 3.35. Mean leaf area duration 1 combined 1988 locations log transformed (cm^2 days).

cultivar/hybrid	cytoplasm		
	nap	ogu	pol
Karat	2.949 a	2.728 b	2.991 a
Marnoo	2.870 b	2.722 c	3.079 a
Regent	2.949 a	2.747 b	3.033 a
Karat/Regent	3.204 a*	2.817 c	2.943 b
Regent/Karat	3.052 a	2.763 b	3.023 a
Marnoo/Regent	3.119 a*	2.834 c*	3.048 b
Regent/Marnoo	3.101 a*	2.887 b*	3.086 a

Means followed by the same letter within rows are not significantly different at the 5% level of probability, LSD.
* denote significant levels of high parent heterosis at the 5% level of probability.

Table 3.36. Mean leaf area duration 1 combined 1989 locations log transformed (cm^2 days).

cultivar/hybrid	cytoplasm nap	ogu	pol
Karat	2.901 a	2.748 b	2.903 a
Marnoo	3.032 a	2.791 b	3.112 a
Regent	3.002 a	2.675 b	2.972 a
Karat/Regent	3.046 a	2.785 b	2.978 a
Regent/Karat	2.985 a	2.676 b	3.109 a
Marnoo/Regent	3.019 a	2.681 b	3.039 a
Regent/Marnoo	3.083 a	2.839 b	3.049 a

Means followed by the same letter within rows are not significantly different at the 5% level of probability, LSD.

Table 3.37. Mean leaf area duration 2 combined 1988 locations log transformed (cm^2 days).

cultivar/hybrid	cytoplasm nap	ogu	pol
Karat	4.281 a	4.093 b	4.335 a
Marnoo	4.217 b	4.112 b	4.414 a
Regent	4.306 b	4.178 b	4.386 a
Karat/Regent	4.500 a*	4.211 b*	4.314 b
Regent/Karat	4.408 a*	4.144 b	4.370 a
Marnoo/Regent	4.436 a*	4.236 c	4.398 b
Regent/Marnoo	4.441 a*	4.252 b*	4.426 a

Means followed by the same letter within rows are not significantly different at the 5% level of probability, LSD.
* denote significant levels of high parent heterosis at the 5% level of probability.

Table 3.38. Mean leaf area duration 2 combined 1989 locations (cm^2 days).

cultivar/hybrid	cytoplasm nap	ogu	pol
Karat	4.318 a	4.155 b	4.398 a
Marnoo	4.441 b	4.186 b	4.491 a
Regent	4.433 a	4.109 b	4.384 a
Karat/Regent	4.480 a	4.183 b	4.453 b
Regent/Karat	4.439 a	4.118 b	4.504 a
Marnoo/Regent	4.436 a	4.113 b	4.455 a
Regent/Marnoo	4.535 a*	4.200 b	4.476 a

Means followed by the same letter within rows are not significantly different at the 5% level of probability, LSD.
* denote significant levels of high parent heterosis at the 5% level of probability.

Table 3.39. Mean leaf area duration 3 1988 combined locations log transformed (cm^2 days).

cultivar/hybrid	cytoplasm nap	ogu	pol
Karat	5.445 b	4.550 c	5.061 a
Marnoo	5.283 b	4.871 c	5.225 a
Regent	5.107 a	5.225 c	5.300 b
Karat/Regent	5.352 a	5.205 c	5.270 b
Regent/Karat	5.474 b	5.163 c	5.057 a
Marnoo/Regent	5.312 a	5.395 b	5.565 a
Regent/Marnoo	5.370 a	5.575 c	5.338 b

Means followed by the same letter within rows are not significantly different at the 5% level of probability, LSD.

Table 3.40. Mean leaf area duration 3 combined 1989 locations log transformed (cm^2 days).

cultivar/hybrid	cytoplasm nap	ogu	pol
Karat	5.168 b	4.985 c	5.362 a
Marnoo	5.279 c	4.989 b	5.267 a
Regent	5.265 b	4.959 b	5.208 a
Karat/Regent	5.350 a	5.005 c*	5.356 b
Regent/Karat	5.346 a	4.988 c	5.267 b
Marnoo/Regent	5.254 a	4.973 b	5.311 a
Regent/Marnoo	5.423 a	5.001 b	5.414 a

Means followed by the same letter within rows are not significantly different at the 5% level of probability, LSD.
* denote significant levels of high parent heterosis at the 5% level of probability.

Table 3.41. Correlation values for growth analysis parameters and crop yield.

	Location				
Parameter	1987 Cambridge	1988 Point	1988 Arb	1989 Point	1989 Bison
NAR1	.000	.035	.202 **	.357 **	.493 **
NAR2	.001	.215 **	.003	.442 **	.124 **
NAR3	.005	.000	.044	.366 **	.033
RGR1	.135 **	.412 **	.294 **	.392 **	.261 **
RGR2	.028 **	.219 **	.001	.007	.016
RGR3	.005 **	.001	.006	.201 **	.136 **
LAI1	.135 **	.432 **	.331 **	.353 **	.153
LAI2	.232 **	.036	.259 **	.441 **	.351 **
LAI3	.201 **	.417 **	.020	.297 **	.076 *
CGR1	.122 **	.340 **	.308 **	.416 **	.210 **
CGR2	.239 **	.166 **	.223 **	.388 **	.337 **
CGR3	.143 **	.183 **	.162 **	.174 **	.062 **
LAD1	.134 **	.440 **	.335 **	.357 **	.161 **
LAD2	.269 **	.430 **	.418 **	.442 **	.275 **
LAD3	.307 **	.237 **	.108 **	.442 **	.289 **

*,** significant at 0.05 and 0.01 levels of probability respectively, LSD.

Table 3.42. Correlation values for growth analysis parameters and total dry matter by location.

	Location				
Parameter	1987 Cambridge	1988 Point	1988 Arb	1989 Point	1989 Bison
NAR1	.000	.207	.136 **	.305 **	.048
NAR2	.025 *	.532 **	.002	.355 **	.053
NAR3	.001	.004	.051 *	.100 **	.000
RGR1	.069 **	.119 **	.245 **	.387 **	.065 **
RGR2	.077 **	.048 **	.000	.022	.014
RGR3	.001	.002	.004	.348 **	.012
LAI1	.001 **	.040 **	.169 **	.250 **	.045
LAI2	.056 **	.055 **	.218 **	.459 **	.040
LAI3	.209 **	.225 **	.021	.275 **	.022
CGR1	.051 **	.121 **	.240 **	.291 **	.040
CGR2	.232 **	.077 *	.191 **	.502 **	.049 **
CGR3	.167 **	.123 **	.119 **	.115 **	.012
LAD1	.057 **	.168 **	.254 **	.318 **	.048 *
LAD2	.215 **	.200 **	.329 **	.419 **	.053 *
LAD3	.316 **	.101	.048	.367 **	.000

*,** significant at 0.05 and 0.01 levels of probability respectively, LSD.

4. INFRA-RED GAS ANALYSIS OF OILSEED RAPE HYBRID CULTIVARS

4.1 Abstract

Three male sterile cytoplasms nap, ogu and pol were tested in a series of summer oilseeed rape hybrids to examine whether the biological cost associated with male sterile cytoplasms extended to leaf characters such as photosynthetic rate and leaf characters. The treatments with the nap and pol male sterile cytoplasms had similar photosynthetic rates over the five sites and three or four leaf stages. The treatments with the ogu cytoplasm were associated with approximately 20% lower photosynthetic rates, especially early in the growing seasons. No heterosis appeared to exist for photosynthetic rate in any of the cytoplasms. Depressed photosynthetic rates were observed in the drought conditions of 1988 as compared to the more favorable environments of 1987 and 1989. Total leaf chlorophyll of leaves 3, 4 and 6 was approximately 35% lower in the ogu cytoplasm than in the nap or pol cytoplasms. There were usually non significant differences between the cytoplasms for total chlorophyll in leaf 8. Although significant differences in photosynthetic rate per unit leaf area were found, no differences in photosynthetic rate per unit chlorophyll were discovered.

4.2 Introduction

Yield heterosis has been reported in hybrid cultivars of oilseed rape (Brassica napus spp. oleifera) involving crosses of Canadian and European cultivars (Sernyk and Stefansson 1983) and inbred lines (Brandle and McVetty 1989).

The development of hybrid seed production requires the use of a pollination control mechanism in perfectly flowered plants such as B. napus. Cytoplasmic male sterility or CMS has been suggested as the most developed pollination control mechanism at present (McVetty et al. 1990). Several CMS systems are at various stages of development for use in hybrid oilseed rape production. The nap cytoplasm, discovered by Shiga and Baba (1971) and Thompson (1971) is the standard sterile cytoplasm in which most B. napus cultivars are contained. The pol cytoplasm was discovered in the B. napus cultivar 'Polima' by Fu (1981). The ogu cytoplasm, transfered from radish (Raphanus sativus) by Ogura (1968) also sterilizes B. napus genotypes.

There are indications that male sterile cytoplasms may have a biological cost relative to male fertile cytoplasms. Yield decreases associated with male sterile cytoplasms have been noted in corn (Noble and Russell 1963) and wheat (Virmani and Edwards 1983).

The pol cytoplasm of B. napus appears to have a cost associated with its use as well; hybrid cultivars in the pol cytoplasm had lower yield and total dry matter as compared

to similar hybrids in the standard nap cytoplasm (McVetty et al. 1990). The biological cost of the pol and ogu male sterile cytoplasms compared to the nap cytoplasm has been previously assessed using classical growth analysis parameters.

Gas exchange has been suggested as a physiological character which may show promise as a screening tool for breeding programs (Buttery and Buzzell 1977). It has been indicated that the use of gas exchange may allow for the selection of productive hybrids in breeding materials. Hybrids in crops such as corn (Zea mays) (Heichel and Musgrave 1969), wheat (Triticum aestivum) (Lupton 1976), and Sorghum (Blum 1989) have demonstrated heterosis for gas exchange rates. However, Hobbs (1988) indicated that heterosis was not found for gas exchange rates for a B. napus intercultivar hybrid of Westar and Cresor.

The objective of this study was to determine the effects of the pol and ogu male sterile cytoplasms on the gas exchange capabilities of field grown B. napus hybrids. This study also assessed whether heterosis for photosynthetic rate existed for unrelated B. napus intercultivar hybrids.

4.3 Materials And Methods

4.3.1. Experimental and Field Design

Three cultivars of summer oilseed rape (B. napus spp. oleifera) were used as parents in this study, Marnoo (Australia), Karat (Sweden) and Regent (Canada). Previous studies (Sernyk and Stefansson 1983, McVetty et al. 1990) have demonstrated significant high parent heterosis in hybrids involving these cultivars.

Ogu cytoplasm A-lines were produced by crossing the cultivar Regent, Karat and Marnoo to R. sativus and then backcrossing six times to recover the genotype of the male parent.

A-lines with the pol cytoplasm were produced by crossing Karat, Marnoo and Regent to the B. napus cv. Polima and then backcrossing six times to recover the nuclear genotype of the recurrent parent.

Reciprocal cross hybrids of Regent/Karat and Regent/Marno were made in each of the male sterile cytoplasms. Twenty plants of each cultivar were used to provide necessary genetic variation. Female flowers were emasculated, bud pollinated and then covered with cellulose crossing bags.

The trials consisted of 21 entries: the three cultivars (Regent, Karat and Marnoo) and four reciprocal cross hybrids (Regent/Karat, Karat/Regent, Regent/Marnoo, Marnoo/Regent) in the three cytoplasms (nap, ogu, pol). A split-plot

split-plot design was used to randomize the entries with each cultivar or hybrid considered a main factor and the cytoplasm type a sub-factor.

The experiments were planted at the Cottage Field site at the Plant Breeding Institute, Cambridge, England in 1987 and the Point, Arboretum and Bison Block fields of the University of Manitoba campus, Winnipeg, Manitoba in 1988 and 1989. At Cambridge, 150 kg N ha^{-1} was applied as 34-0-0 (14%S) and 1 kg ha^{-1} Benazalox WP (50g clopyralid (3,6-dichloropyridine-2-carboxylic acid) + 300g benazolin (4-chloro-2,3-dihydro-2-oxo-1,3-benazolin-3-ylacetic acid) was applied at the fifth true leaf stage. In 1988 and 1989, trifluralin (a,a,a-trifloro-2,6-dintro-N,N-dipropyl-p-toluidine) granules were fall-incorporated at a rate of 0.35 kg a.i. ha^{-1} for broadleaf and grass weed control. Fertilizer was applied at a rate as recommended by soil tests. Carbofuran (2,3-Dihydro-2,2-dimethyl-7-benzofuranyl methyl carbamate) (10%) granules were banded with the seed at a rate of 1.0 kg a.i. ha^{-1} to control flea beetles (Phyllotrea cruciferae G. and P. striolata F.). Malathion (0,0-dimethyl phosphorodithioate of diethyl mercaptosuccinate) (50% EC) was applied throughout the latter half of the growing seasons at the University of Manitoba sites to control diamondback moths (Plutella spp.) in 1988 and flea beetles in 1988 and 1989. Plots were hand weeded throughout the growing seasons at all locations.

The experiments were seeded into summerfallowed land using a Hege belt-cone seeder at Cambridge and a double disc belt-cone 8-row seeder at the University of Manitoba sites. The Cottage Field was seeded April 13, 1987 while in 1988, the Point location was planted on May 16 and the Arboretum on May 25. In 1989, the Point was seeded May 9 and the Bison Block location on May 17. The Cottage Field had a clay soil, the Point a Riverdale Clay, while the Arboretum and Bison Block were classified as Red River Clay soil types.

Plots were arranged as follows. The Cottage Field site had six replicates and the University of Manitoba sites had four replicates at each location. Plots consisted of three rows of experimental material in 1987 and 1988; in 1989, four rows of each treatment were seeded per plot. Rows were three metres long and seeded at a rate of six kg ha^{-1} on 30 cm row spacings. Adjacent plots were separated by one guard row of Fido and Regent at the Cottage and University of Manitoba sites, respectively. Edge effects were minimized by seeding four border rows of Fido or Regent at each end of the experiment.

Seasonal rainfall and temperatures for the Cottage Field were cool, cloudy, dry in April and cool and wet in June, July and August. In 1988, rainfall was below average in May and August and close to normal in June and July. Temperature were 3.3°C and 5.2°C above long term averages in May and June respectively with July and August 1.5 and 1.7

1.7 degrees warmer than normal. In 1989, mean June temperatures were similar to long term averages; May, July and August were 3°C above long term temperatures. May and July were drier than normal, August was near long term averages and in June, the University of Manitoba sites received twice the normal rainfall.

4.3.2 Gas Analysis Sampling Procedure

Carbon dioxide exchange rates were measured with the ADS open infra-red gas analysis (IRGA) system at the Cambridge Plant Breeding Institute and the closed Li-6000 Portable Photosynthesis System at the University of Manitoba. Leaves 4, 6, and 8 were measured during 1987; leaf numbers 3, 4, 6, and 8 at the Point location and leaves 3, 4 and 6 were sampled at the Arboretum in 1988. Fewer measurements were possible at the Arboretum due to premature leaf senescence promoted by extreme heat and water stress. In 1989, leaves 3, 4, 6, and 8 were tested at both the Point and Bison Block locations.

All gas exchange measurements were made on the outside two rows of each plot. Recordings were made between 7:00 AM and 12:00 PM to reduce the effects of water stress on stomatal aperature. Only fully expanded leaves of the appropriate leaf stage were used in carbon dioxide exchange measurements. Sunlit leaves with quantum sensor values exceeding 1500 uE m^{-2} s^{-1} were manoeuvered inside the leaf

chamber for 30 second readings. The leaves were then excised and immediately placed on ice to prevent loss of turgor. Leaf areas were measured using a photocopy, cut and weigh procedure at Cambridge and a Delta-T camera and monitor system at the University of Manitoba.

Leaf discs were punched out of the sample sections for chlorophyll assessments. The disc was immediately frozen at -20° C until the extractions could be carried out. Leaf chlorophyll concentration was determined as per the procedure outlined by Arnon (1949) using Acetone (80% v/v). Absorbances were measured at 645 nm, 663 nm and 710 nm using a Beckman spectrophotometer. The following relationships determined leaf chlorophyll concentration:

M=A663-A710
N=A645-A710
C=((M*12.7)-(N*2.69))/12.7
D=((N*22.9)-(M*4.68))/2.69

Chltot=C+D
ChlA/B=C/D.

4.3.3 Statistical Analysis

All statistical analyses were carried out using Statistical Analysis System programs on the University of Manitoba mainframe computer system. Analysis of variance procedures and Least Significant Difference (LSD) procedures were performed to analyze the data (Gomez and Gomez 1984). Significant cytoplasm effects were indicated by a significant difference in the LSD test and high parent

heterosis was indicated by significant LSD separation of a hybrid and its highest parent.

4.4 Results And Discussion

4.4.1 Photosynthetic Rate

Significant cytoplasm effects were encountered in all locations and years (Appendix 2. Tables 1-5). The photosynthetic determinations indicated that a cytoplasm cost is associated with the ogu male sterile cytoplasm (Tables 4.1 to 4.5). This cytoplasm caused a decrease in the photosynthetic rate during all three years of observation. The depression occured in leaves 3,4 and 6 and occasionally in leaf 8 suggesting that ogu material is subject to a lower instantaneous photosynthetic rate throughout the growing season. This depression in gas exchange may account for its decreased performance in growth analysis trials. Farineau et al. (1990) using a series of protoplast derived cybrids indicated that material in the ogu cytoplasm with nap chloroplasts did not demonstrate a photosynthetic rate depression in laboratory tests. This study along with the work of Farineau et al. (1990) appears to indicate that it is the ogu chloroplast which may produce the majority of the biological cost associated with the ogu cytoplasm.

There were no significant differences between the pol and nap cytoplasms for any of the gas exchange parameters indicating that the biological cost associated with the pol

cytoplasm does not extend to instantaneous gas exchange. It may be possible that the nuclear genome of B. napus may be more compatible in the B. napus derived pol cytoplasm than in the radish derived ogu cytoplasm. Nevertheless, the availability of corrective protoplast fusion techniques in Brassica (Pelletier et al. 1987) suggests that the search for alternative sources of male sterility does not have to be confined to the genus Brassica.

There appeared to be no significant cultivar differences in photosynthetic rate per unit leaf area (Tables 4.1-4.5). Hobbs (1988) found no significant differences existed for photosynthetic rate within a series of four B. napus varietes. Similar results have been discovered by Mahon and Hobbs (1981) who found no differences between high and low yielding pea cultivars. As Peet et al. (1977) indicated, there may be differences in cultivar photosynthetic rates, but these differences may change with developmental phase and the ideal sampling stage may yet have to be determined for B. napus genotypes. Alternatively, as Mahon and Hobbs (1981) have suggested, small differences may be present, but that many measurements on a single leaf may be necessary to establish statistical significance. The presence of a significant replicate effect for all locations (Appendix 2. Tables 1-5) appears to suggest that a large number of readings is necessary to produce accurate results.

The variability of photosynthetic rate measurements increased later in the growing season. This may be due to the shading of the upper leaves by the stems and flowers. Shading would also tend to decrease the maximum photosynthetic rate of leaf 8, which was found in 1989 (Tables 4.4 and 4.5).

Greater variability in photosynthetic rate was found in 1988 as compared to 1989 due to the increased water stress experienced during the growing season. Clarke and McCraig (1982) indicated that the uptake of $^{14}CO_2$ was fairly consistent during periods of low water stress. As water stress was increased, increases in leaf diffusive resistance appeared to produce a diurnal pattern of photosynthetic rate. This diurnal pattern has also been described by Singh et al. (1988). Thus, under the water limiting conditions of 1988 increased variability of photosynthetic measurements would be expected.

Temperature also had an effect on photosynthetic measurements. Hobbs (1988) determined that the temperature response for B. napus produced a maximum around 28°C. Therefore under higher field temperatures in 1988, photosynthetic rates would be lower than in the cooler years of 1987 and 1989. The detrimental effect of the ogu male sterile cytoplasm also appeared to be less severe later in the growing season of 1988 and 1989. It may be possible that the increased variability of measurements later in the season masked real differences or that material in the ogu

narrow range of genotypes tested, Hobbs (1988) also found no differences in total leaf chlorophyll for four B. napus genotypes. Similarly, no evidence of heterosis for leaf chlorophyll content was discovered.

Significant differences existed for total leaf chlorophyll content among the male sterile cytoplasms (Tables 4.6-4.9). In all three years, material in the nap and pol cytoplasms produced similar amounts of leaf chlorophyll. The decreased total leaf chlorophyll in the ogu cytoplasm for leaves 3 and 4 in all years is consistent with the temperature dependent decrease reported by Bannerot et al. (1977). The upper leaves 6 and 8 may not be subjected to the chlorosis as air temperatures are above 12°C during their development. Locations seeded early in the season such as the Point 1989 may demonstrate chlorosis, while the leaves at the Bison location may have experienced warmer temperatures during leaf development and may not subject the the low temperature chlorosis.

Temperature sensitive chlorosis has previously been reported in male sterile cytoplasms. Fukasawa (1953) reported leaf color variegation was associated with the ovata male sterile cytoplasm in wheat. Mukai and Tsunewaki (1978) reported that variegation also occured in the umbellulata and biuncialis cytoplasms and that the effects appeared to be temperature dependent.

4.4.3. Photosynthetic Rate per Unit Chlorophyll

There appeared to be no significant differences between any of the cytoplasms for photosynthetic rate per unit leaf chlorophyll (Appendix 2. Tables 10-13 and Tables 4.10 to 4.13). The lack of significance may suggest that the photosynthetic apparatus in the ogu chloroplast is similar to that in the nap and pol cytoplasms. Farineau (1990) discovered similar photosynthetic rates between male fertile cytoplasms and protoplast fusion corrected ogu cybrids. This indicates that perhaps leaf chlorophyll content is the limiting vigor in the ogu cytoplasm.

4.5 Summary and Conclusions

The effect of three male sterile cytoplasms on instantaneous gas exchange rates and leaf chlorophyll content were studied to assess the cytoplasmic cost of hybrid seed production using CMS.

The nap and pol cytoplasms produced similar photosynthetic rates, but material in the ogu cytoplasm had decreased photosynthetic rates, particularly early in the growing season. There was no evidence of heterosis or cultivar differences in photosynthetic rate.

The nap and pol cytoplasms also produced significantly greater total leaf chlorophyll as compared to the ogu

cytoplasm. There appeared to be no heterosis for total leaf chlorophyll for the hybrids.

The photosynthetic rate per unit leaf chlorophyll was equal for all three cytoplasms. This indicates that the three cytoplasms may contain a similar photosynthetic apparatus and that the lower total leaf chlorophyll content of the ogu cytoplasm may be limiting its productivity.

4.6 Acknowlegements

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Table 4.1. Means of cytoplasm effects on photosynthetic rate (mg CO_2 dm^{-2} hr^{-1}) Cambridge 1987.

cytoplasm	Leaf 4	Leaf 6	Leaf 8
nap	35.27 a	39.57 a	42.00 a
ogu	32.23 b	32.62 b	39.56 a
pol	35.79 a	40.23 a	43.03 a

Means followed by the same letter are not significantly different at the 5% level of probability, LSD.

Table 4.2. Means of cytoplasm effects on photosynthetic rate (mg CO_2 dm^{-2} hr^{-1}) Point 1988.

cytoplasm	Leaf 3	Leaf 4	Leaf 6	Leaf 8
nap	24.56 a	27.94 a	21.93 a	26.16 a
ogu	24.30 a	26.58 a	18.76 b	24.12 a
pol	23.10 a	28.58 a	21.20 a	26.57 a

Means followed by the same letter are not significantly different at the 5% level of probability, LSD.

Table 4.3. Means of cytoplasm effects on photosynthetic rate (mg CO_2 dm^{-2} hr^{-1}) Arboretum 1988.

cytoplasm	Leaf 3	Leaf 4	Leaf 6
nap	28.43 a	28.21 a	26.43 a
ogu	26.16 a	24.17 b	22.26 b
pol	27.29 a	29.18 a	27.08 a

Means followed by the same letter are not significantly different at the 5% level of probability, LSD.

Table 4.4. Means of cytoplasm effects on photosynthetic rate (mg CO_2 dm^{-2} hr^{-1}) Point 1989.

cytoplasm	Leaf 3	Leaf 4	Leaf 6	Leaf 8
nap	34.10 a	43.13 a	44.92 a	34.74 a
ogu	26.50 b	33.37 b	36.64 b	30.39 b
pol	36.81 a	43.12 a	43.68 a	34.52 a

Means followed by the same letter are not significantly different at the 5% level of probability, LSD.

Table 4.5. Means of cytoplasm effects on photosynthetic rate (mg CO_2 dm^{-2} hr^{-1}) Bison 1989.

cytoplasm	Leaf 3	Leaf 4	Leaf 6	Leaf 8
nap	34.63 a	33.51 a	29.13 a	33.57 a
ogu	24.24 b	22.19 b	26.50 a	25.09 b
pol	35.86 a	31.14 a	28.48 a	33.81 a

Means followed by the same letter are not significantly different at the 5% level of probability, LSD.

Table 4.6. Means of cytoplasm effects on total leaf chlorophyll (mg l^{-1}) Point 1988.

cytoplasm	Leaf 3	Leaf 4	Leaf 6	Leaf 8
nap	3.71 a	3.67 a	3.85 a	4.02 a
ogu	3.55 a	3.48 a	3.52 a	3.86 a
pol	3.65 a	3.75 a	3.67 a	3.93 a

Means followed by the same letter are not significantly different at the 5% level of probability, LSD.

Table 4.7. Means of cytoplasm effects on total leaf chlorophyll (mg l^{-1}) Cambridge 1987 and Arboretum 1988.

cytoplasm	Cambridge Leaf 4	Arboretum Leaf 3	Arboretum Leaf 4	Arboretum Leaf 6
nap	3.38 a	3.03 a	3.33 a	2.99 a
ogu	2.74 b	2.73 b	2.85 b	2.60 b
pol	3.38 a	3.06 a	3.25 a	2.95 a

Means followed by the same letter are not significantly different at the 5% level of probability, LSD.

Table 4.8. Means of cytoplasm effects on total leaf chlorophyll (mg l^{-1}) Point 1989.

cytoplasm	Leaf 3	Leaf 4	Leaf 6	Leaf 8
nap	3.26 a	3.05 a	2.90 a	2.70 a
ogu	2.69 b	2.49 b	2.36 b	2.81 a
pol	3.44 a	2.95 a	2.84 a	2.63 a

Means followed by the same letter are not significantly different at the 5% level of probability, LSD.

Table 4.9. Means of cytoplasm effects on total leaf chlorophyll (mg l^{-1}) Bison 1989.

cytoplasm	Leaf 3	Leaf 4	Leaf 6	Leaf 8
nap	2.64 a	2.97 a	2.60 a	1.56 a
ogu	1.73 b	1.79 b	2.49 a	1.53 a
pol	2.72 a	2.91 a	2.57 a	1.56 a

Means followed by the same letter are not significantly different at the 5% level of probability, LSD.

Table 4.10. Means of cytoplasm effects on photosynthetic rate per unit leaf chlorophyll ($mgCO_2$ $mgchl^{-1}$ hr^{-1}) Point 1988.

cytoplasm	Leaf 3	Leaf 4	Leaf 6	Leaf 8
nap	5.56 a	6.52 a	4.80 a	5.49 a
ogu	5.77 a	6.44 a	4.53 a	5.32 a
pol	5.45 a	6.44 a	4.75 a	5.81 a

Means followed by the same letter are not significantly different at the 5% level of probability, LSD.

Table 4.11. Means of cytoplasm effects on total leaf chlorophyll ($mgCO_2$ $mgchl^{-1}$ hr^{-1}) Cambridge 1987 and Arboretum 1988.

	Cambridge	Arboretum	Arboretum	Arboretum
cytoplasm	Leaf 3	Leaf 4	Leaf 6	Leaf 8
nap	7.22 a	5.50 a	5.02 a	5.14 a
ogu	7.24 a	5.68 a	5.00 a	5.05 a
pol	7.52 a	5.22 a	5.26 a	5.35 a

Means followed by the same letter are not significantly different at the 5% level of probability, LSD.

Table 4.12. Means of cytoplasm effects on total leaf chlorophyll ($mgCO_2$ $mgchl^{-1}$ hr^{-1}) Point 1989.

cytoplasm	Leaf 3	Leaf 4	Leaf 6	Leaf 8
nap	5.37 a	4.73 a	4.81 a	6.15 a
ogu	5.19 a	4.57 a	4.48 a	6.09 a
pol	5.64 a	4.84 a	4.40 a	6.11 a

Means followed by the same letter are not significantly different at the 5% level of probability, LSD.

Table 4.13. Means of cytoplasm effects on total leaf chlorophyll ($mgCO_2$ $mgchl^{-1}$ hr^{-1}) Bison 1989.

cytoplasm	Leaf 3	Leaf 4	Leaf 6	Leaf 8
nap	5.49 a	4.06 a	4.00 a	5.23 a
ogu	5.42 a	5.05 a	3.71 a	5.17 a
pol	6.68 a	4.18 a	3.96 a	4.91 a

Means followed by the same letter are not significantly different at the 5% level of probability, LSD.

5. GENERAL DISCUSSION

High parent heterosis, a pollination control mechanism and field techniques for hybrid seed production are all necessary for hybrid canola seed production. A central concern is the effect of a male sterile cytoplasm on the growth of field produced plant material. The effects of three male sterile cytoplasms were studied at five locations over three years from 1987 to 1989.

5.1 Growth Analysis

The ogu and pol cytoplasms affected plant growth. Crop yield and total dry matter were reduced by 50% in the ogu cytoplasm. The pol cytoplasm reduced seed yield by approximately 25%. Despite the yield penalties, a large amount of heterosis was available for use in pol. Days to first and to fifty percent flower were increased in the pol cytoplasm and unaffected by the ogu cytoplasm. Seed oil was reduced by 1.8 and 5.9 percent respectively in pol and the ogu cytoplasms. Seed protein was elevated by 0.9 and 3.3 percent in these two cytoplasms.

The use of the ogu and pol cytoplasms altered classical growth analysis parameters. As compared to genotypes in the nap cytoplasm, material in the ogu cytoplasm reduced LAI, LAD, RGR, CGR and NAR by approximately 25, 30 10, 40 and 30 percent during the growing season. The nap and pol

cytoplasms produced similar LAI, LAD, RGR and CGR thorughout the growing seasons; pol produced 10% lower NAR during the early part of growing the season. The pol cytoplasm often demonstrated lower levels of heterosis for LAI, LAD and CGR. The decreased growth associated with ogu and the lower levels of heterosis available in the pol cytoplasm may be identified as the biological cost associated with these male sterile cytoplasms.

5.2 Infra-Red Gas Analysis

The effect of the ogu and pol male sterile cytoplasms was assessed by instantaneous gas exchange measurements conducted in field plots trials. The ogu cytoplasm reduced gas exchange by approximately 35% for leaves 3, 4 and 6 in most years. The nap and pol cytoplasms had similar gas exchange capabilities in all three years. Material in the ogu cytoplasm reduced leaf chlorophyll by approximately 35%, particularly early in the growing seasons; the ogu cytoplasms generally produced equal levels of leaf chlorophyll by the eighth leaf. No significant differences were found to exist for total leaf chlorophyll between the nap and pol cytoplasms. No significant differences in photosynthetic rate per unit leaf chlorophyll were found in any of the male sterile cytoplasms tested.

6. CONCLUSIONS

Studies on the effect of male sterile cytoplasms on the growth of several intercultivar hybrids revealed a biological cost associated with CMS. Material in the pol cytoplasm generally demonstrated lower levels of heterosis for yield and total dry matter. Pol cytoplasm material decreased seed oil content and elevated seed protein by 1.8 and 0.9 percent respectively. A 1-2 day delay in flowering was associated with the pol cytoplasm. Ogu material had low seed yield and total dry matter, but no increase in days to first flower. Seed oil was decreased by 5.9 and seed protein was increased by 3.3% in this cytoplasm.

Classical growth analysis parameters were affected by these cytoplasms. Material in the ogu cytoplasm had decreased LAI, LAD, NAR, RGR, CGR throughout the growing season as compared to nap cytoplasm treatments. The pol cytoplasm treatments had no decrease in LAI, LAD, CGR or RGR, but slight decreases were found in NAR early in the growing season. Heterosis for classical growth parameters was not as prevalent in ogu and pol as compared to the nap cytoplasm.

Gas exchange parameters were also affected by male sterile cytoplasms. Lower photosynthetic rates and lower total leaf chlorophyll were found in the ogu cytoplasm as

compared to the nap or pol cytoplasms. No difference was found in the photosynthetic rate per unit leaf chlorophyll.

7. CONTRIBUTIONS TO KNOWLEDGE

There have been published reports of a yield penalty associated with the T male sterile cytoplasm in corn (Noble and Ross 1963), the timopheevi cytoplasm (Virmani and Edwards 1983) in wheat and the pol cytoplasm in canola (McVetty et al. 1990). Male sterile cytoplasms alter other plant characters such as leaf quality in tobacco (Povilaitis 1972) seed quality in wheat (Doig et al. 1975) and disease susceptibility in corn (Grogan et al. 1971). A study of the effects of a male sterile cytoplasm is necessary to ensure that radical changes in plant biology are not produced by using CMS in hybrid oilseed rape production.

Studies of other Brassica cytoplasms may provide an estimate of the cytoplasm cost of the nap cytoplasm. The investigation of other cytoplasms such as the fertile cam cytoplasm may identify possible cytoplasmic heterosis.

An interesting investigation would involve assessing the improved ogu cytoplasm; i.e. comparing the protoplast fusion derived ogu cytoplasm and the nap cytoplasm as they perform under Western Canadian conditions.

Further studies should be conducted examining the effects of restorer genes to the pol male sterile cytoplasms as fertility restoring genes may affect plant development either positively or negatively.

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APPENDIX 1.

Appendix 1. Table 1. Weather conditions for 1988 and 1989 as compared to long term climatic averages.

Month	1988		1989		Normal[1]	
	temp	ppt	temp	ppt	temp	ppt
May	14.6	29.9	15.3	35.3	11.3	65.7
June	22.0	94.9	21.2	44.9	16.8	80.1
July	21.1	70.8	22.2	69.3	19.6	75.9
August	20.1	8.5	20.1	16.5	18.3	75.2

[1] Long term averages, 1951-1980. Environment Canada Monthly Meteorolgical Summary. 1989.

Appendix 1. Table 2. Mean squares and degrees of freedom for flowering data of growth analysis experiments.

Source	df	First Flower		50% Flower	
		1988	1989	1988	1989
loc	1	68.14 *	14.88 *	70.72 *	4.33
rep	3	8.59	.48	6.62	2.48
loc*rep	3	6.14	2.45	4.06	1.78
cv	6	13.03	16.07 **	28.32 **	25.51 **
rep*cv	18	5.41	.57	3.78	.79
loc*cv(rep)	24	7.20 *	1.14 *	2.84	.90
cyto	2	10.16 **	4.18 **	50.14 **	17.79 **
rep*cyto	6	3.77	1.24	2.41	.45
cv*cyto	12	7.92 *	2.32	9.64 **	3.50 **
rep*cv*cyto	36	4.67	1.08	1.71	.82
error c	56	3.16	.84	2.29	.71

*,** significant at 0.05 and 0.01 levels of probability respectively, LSD.

Appendix 1. Table 3. Mean squares and degrees of freedom for yield, total dry matter and harvest index in 1987 Cambridge growth analysis experiment.

Source	df	Yield	TDM	HI[1]
rep	5	3990	114846	.72335
cv	6	3327 **	645550 **	.75368
rep*cv	30	8456 **	43957	.42858 **
cyto	2	141106 **	2983968 **	.00854
cv*cyto	12	3655 *	92040 **	.00032
error b	72	1867	35473	.00778

[1] vlues multiplied by 100
*,** significant at 0.05 and 0.01 levels of probability respectively, LSD.

Appendix 1. Table 4. Mean squares and degrees of freedom for yield in 1988 and 1989 growth analysis experiments.

		1988		1989	
Source	df	Point	Arb	Point	Bison
rep	3	2893 *	873	6716	1371
cv	6	1822 **	6259 **	128662 **	157732 **
rep*cv	18	1444	568	982	122365
cyto	2	57783 **	54185 **	1005030 **	218609 **
cv*cyto	12	2963 **	2336 **	49462 **	128033 **
error b	42	818	299	10449	59516

*,** significant at 0.05 and 0.01 levels of probability respectively, LSD.

Appendix 1. Table 5. Mean squares and degrees of freedom for total dry matter in 1988 and 1989 growth analysis experiments.

		1988				1989			
Source	df	Point		Arb		Point		Bison	
rep	3	46103	*	14609		72594		168329	
cv	6	78470	**	98712	**	890055	*	157732	
rep*cv	18	12959		10941		222891	*	122365	*
cyto	2	106534	*	538513	**	3755336	**	218609	*
cv*cyto	12	1970		41886	*	296752	**	128033	*
error b	42	12710		12710		101545		59516	

*,** significant at 0.05 and 0.01 levels of probability respectively, LSD.

Appendix 1. Table 6. Mean squares and degrees of freedom for harvest index in 1988 and 1989 growth analysis experiments.

		1988[1]				1989[1]			
Source	df	Point		Arb		Point		Bison	
rep	3	.7237		.0812		.0375		.8962	
cv	6	1.3528		.9276	*	1.5924		.7924	
rep*cv	18	.4018		.2085		.1266		1.0860	
cyto	2	5.2699	**	6.3813	**	14.8209	**	10.7263	**
cv*cyto	12	.4836		.2887		.8394		.6998	
error b	42	.2747		.2059		.0845		.7160	

[1] values multiplied by 100
*,** significant at 0.05 and 0.01 levels of probability respectively, LSD.

Appendix 1. Table 7. Mean squares and degrees of freedom for seed quality characteristics 1988 and 1989 growth analysis experiments.

Source	df	% oil 1988	% oil 1989	% protein 1988	% protein 1989
loc	1	3.37	7.04	.00	2.23
rep	3	.20	.84	.14	.36
loc*rep	3	.40	4.62 *	.22	1.66
cv	6	.39	8.60	.22	1.35
rep*cv	18	.38	3.67	.09	1.81
loc*cv(rep)	24	.36	3.70	.09	2.14
cyto	2	496.43 **	571.43 **	146.33 **	182.92 **
rep*cyto	6	.72	6.35	.13	4.45
cv*cyto	12	.77	6.34 *	.14	3.86
rep*cv*cyto	36	.97	2.10	.18	2.47
error c	56	1.02	3.01	.17	1.61

*,** significant at 0.05 and 0.01 levels of probability respectively, LSD.

Appendix 1. Table 8. Mean squares and degrees of freedom for crop growth rate and net assimilation rate 1987 Cambridge growth analysis experiment.

Source	df	CGR1[1]	CGR2	CGR3	NAR1	NAR2	NAR3
rep	5	.668	.097	1.500	1.634 **	.332 **	.093
cv	6	.188	.098	3.967	.104	.032	.075
rep*cv	30	.266	.082	2.024	.068	.058	.095
cyto	2	3.335 **	2.122 **	37.637 **	.001	.071	.028
cv*cyto	12	.299	.093	1.849	.054	.101	.107
error b	70	.248	.059	1.772	.004	.084	.002

[1] Values for CGR1 were multiplied by 1000
*,** significant at 0.05 and 0.01 levels of probability respectively, LSD.

Appendix 1. Table 9. Mean squares and degrees of freedom for crop growth rate 1988 growth analysis experiments.

Source	df	CGR1[1]		CGR2[1]		CGR3[1]	
loc	1	.689		8.807		25.31	
rep	3	.071		4.843		8.47	
loc*rep	6	.833		2.731	**	287.42	**
cv	6	.917	**	1.352		185.80	**
rep*cv	18	.138		8.029		29.05	
loc*cv(rep)	24	.083		9.507		26.29	
cyto	2	9.390	**	100.552	**	211.55	**
rep*cyto	6	.094		1.446		56.68	
cv*cyto	12	.750	**	5.310		19.39	
rep*cv*cyto	36	.113		4.497		28.53	
error c	56	.167		5.561		31.89	

[1] Values for CGR1, CGR2 and CGR3 were multiplied by 100
*,** significant at 0.05 and 0.01 levels of probability respectively, LSD.

Appendix 1. Table 10. Mean squares and degrees of freedom for crop growth rate 1989 growth analysis experiments.

Source	df	CGR1[1]		CGR2		CGR3	
loc	1	1.637	**	5.900	**	35.491	**
rep	3	.114		.003		.328	
loc*rep	6	.033		.053		.288	
cv	6	.627	**	.041	**	.834	
rep*cv	18	.034		.029		.462	
loc*cv(rep)	24	.225		.093		.651	
cyto	2	14.722	**	10.611	**	18.686	**
rep*cyto	6	.104		.029		.424	
cv*cyto	12	.297		.154		.614	
rep*cv*cyto	36	.073		.025		.412	
error c	56	.140		.147		.681	

[1] Values for CGR1 were multiplied by 100
*,** significant at 0.05 and 0.01 levels of probability respectively, LSD.

Appendix 1. Table 11. Mean squares and degrees of freedom for net assimilation rate 1988 and 1989 growth analysis experiments.

Source	df	1988 NAR1		1988 NAR2		1988 NAR3		1989 NAR1		1989 NAR2		1989 NAR3	
loc	1	23.383	*	.001		.207		.278		.280		.035	*
rep	3	.360		.269		.115		.047		.039		.012	*
loc*rep	6	.647		.231	*	.142		.035		.022		.001	
cv	6	.208		.047	*	.167		.194		.152		.047	*
rep*cv	18	.076		.063		.064		.013		.015		.014	
loc*cv(rep)	24	.085		.046		.084		.085		.039		.014	
cyto	2	4.392	**	.028		.054		12.145	**	.417		.040	
rep*cyto	6	.334		.007		.072		.052		.017		.028	
cv*cyto	12	.209		.099		.036		.084		.089		.031	
rep*cv*cyto	36	.115		.047		.05		.030		.023		.011	
error c	56	.419		.055		.071		.045		.049		.023	

*,** significant at 0.05 and 0.01 levels of probability respectively, LSD.

Appendix 1. Table 12. Mean squares and degrees of freedom for relative growth rate and leaf area index for 1987 Cambridge growth analysis experiment.

Source	df	RGR1[1]		RGR2[1]		RGR3		LAI1[1]		LAI2		LAI3	
rep	5	.094		.163		1.037		1.506	*	.289		2.193	
cv	6	.036		.063		.069		.050		.333		7.453	
rep*cv	30	.039		.701		.011		.203		.269		3.133	
cyto	2	7.479	**	.203	*	1.070		2.617	**	5.099	*	67.797	**
cv*cyto	12	.058		.113	*	.013		1.839		.190		3.280	
error b	70	.050		.053		.015		1.583		.209		2.355	

[1] values multiplied by 100
*,** significant at the 0.05 and 0.01 levels of probability respectively, LSD.

Appendix 1. Table 13. Mean squares and degrees of freedom for relative growth rate 1988 and 1989 growth analysis experiments.

Source	df	RGR1[1]	RGR2[1]	RGR3[1]	RGR1[1]	RGR2[1]	RGR3[1]
loc	1	5.30	21.40 **	.874	3.83 *	3.24	.55 *
rep	3	2.81	4.66	.555	.95	1.23	.17
loc*rep	6	2.21	1.22	.627	3.05	.60	.04
cv	6	3.18 **	.88	.903	2.74 *	1.54	1.50 **
rep*cv	18	4.02	.61	.521	.23	2.35	.27
loc*cv(rep)	24	3.11	.69	.536	.98	.65	.29
cyto	2	36.88 **	5.12 *	1.636 *	87.33 **	1.27	102.9 **
rep*cyto	6	.09	.17	.460	.99 *	.73	.41
cv*cyto	12	1.67 **	1.19	.235	1.11 **	.98	.80
rep*cv*cyto	36	.27	.48	.380	.48	.51	.22
error c	56	.64	1.10	.429	.42	.60	.45

[1] values multiplied by 1000
*,** significant at 0.05 and 0.01 levels of probability respectively, LSD.

Appendix 1. Table 14. Mean squares and degrees of freedom for log transformed leaf area index combined 1988 growth analysis experiments.

Source	df	LAI1	LAI2	LAI3
loc	1	.0046	.4930 *	.6520 *
rep	3	.0023	.0332	.0261
loc*rep	6	.0032 *	.0048	.0542 **
cv	6	.0047 *	.0490	.0319 **
rep*cv	18	.0006	.0102	.0033 **
loc*cv(rep)	24	.0006	.0210	.0046
cyto	2	.0577 **	.2526 **	.0568 **
rep*cyto	6	.0006	.0086	.0170
cv*cyto	12	.0036 **	.0158	.0003
rep*cv*cyto	36	.0005	.0082	.0035
error c	56	.0008	.0168	.0066

*,** significant at 0.05 and 0.01 levels of probability respectively, LSD.

Appendix 1. Table 15. Mean squares and degrees of freedom for log transformed leaf area index combined 1989 growth analysis experiments.

Source	df	LAI1	LAI2	LAI3
loc	1	.0068 **	.0655 **	.8798 **
rep	3	.0008	.0098	.0359
loc*rep	6	.0001	.0095	.0073
cv	6	.0032 *	.0873	.0083
rep*cv	18	.0002	.0128	.0046
loc*cv(rep)	24	.0010	.0076	.0135
cyto	2	.0066 **	.1371 **	.4492 **
rep*cyto	6	.0006	.0239	.0086
cv*cyto	12	.0014 **	.0935 **	.0103
rep*cv*cyto	36	.0004	.0364	.0065
error c	56	.0005	.0128	.0134

*,** significant at 0.05 and 0.01 levels of probability respectively, LSD.

Appendix 1. Table 23. Mean squares and degrees of freedom for leaf area duration Cambridge growth analysis experiment.

Source	df	LAD1	LAD2	LAD3
rep	5	40653 *	378453	39250992
cv	6	1196	195484	143044595
rep*cv	30	5194	223392	56375162
cyto	2	72064 **	54823288 **	1764932765 **
cv*cyto	12	4926	1122155	30184223
error b	70	4270	1727272	32147113

*,** significant at 0.05 and 0.01 levels of probability respectively, LSD.

Appendix 1. Table 17. Mean squares and degrees of freedom for log transformed leaf area duration combined 1988 growth analysis experiments.

Source	df	LAD1	LAD2	LAD3
loc	1	.0965*	.2769 **	6.8001 **
rep	3	.0511*	.0164	.1258
loc*rep	6	.0488*	.0479 **	.2220
cv	6	.0737**	.0659 **	.2159
rep*cv	18	.0126	.0079	.1406
loc*cv(rep)	24	.0119	.0105	.1249
cyto	2	1.1352**	.7270 **	3.6771 **
rep*cyto	6	.0096	.0043	.2034
cv*cyto	12	.0433**	.0302 **	.1821
rep*cv*cyto	36	.0083	.0053	.1448
error c	56	.0136	.0087	.5657

*,** significant at 0.05 and 0.01 levels of probability respectively, LSD.

Appendix 1. Table 18. Mean squares and degrees of freedom for log transformed leaf area duration combined 1989 growth analysis experiments.

Source	df	LAD1	LAD2	LAD3
loc	1	.0866 **	.2633 **	.2465 **
rep	3	.0203	.0050	.0061
loc*rep	6	.0048	.0015	.0073
cv	6	.0587 **	.0376 **	.0030
rep*cv	18	.0505	.0021	.0081
loc*cv(rep)	24	.0198 **	.0102	.0164
cyto	2	1.4059 **	1.6168 **	1.7853 **
rep*cyto	6	.0207	.0073	.0213
cv*cyto	12	.0249 **	.0124 *	.0245
rep*cv*cyto	36	.0103	.0034	.0746
error c	56	.0085	.0063	.0165

*,** significant at 0.05 and 0.01 levels of probability respectively, LSD.

Appendix 1. Table 19. F values for regressions on growth analysis parameters and crop yield of growth analysis experiments.

	Location									
Parameter	1987 Cambridge		1988 Point		1988 Arb		1989 Point		1989 Bison	
NAR1	.01		3.04		20.75	**	79.84	**	23.63	**
NAR2	.16		22.56	**	.24		18.18	**	11.61	**
NAR3	.70		.02		3.81		18.54	**	2.80	
RGR1	19.47	**	57.48	**	34.24	**	52.98	**	29.04	**
RGR2	3.61	**	23.10	**	.01		.60		1.37	
RGR3	31.30	**	.13		.49		20.67	**	12.91	**
LAI1	19.35	**	64.44	**	40.68	**	44.89	**	14.85	**
LAI2	37.57	**	3.07		28.68	**	64.89	**	44.41	**
LAI3	31.30	**	58.78	**	1.71		34.65	**	6.79	*
CGR1	17.38	**	42.40	**	36.49	**	58.44	**	21.91	**
CGR2	39.03	**	46.36	**	23.63	**	52.08	**	41.88	**
CGR3	21.76	**	18.45	**	45.94	**	17.38	**	5.47	*
LAD1	19.24	**	64.61	**	41.42	**	45.63	**	15.78	**
LAD2	45.82	**	61.93	**	59.07	**	64.97	**	31.14	**
LAD3	54.95	**	34.57	**	35.02	**	47.42	**	28.87	**

*,** significant at 0.05 and 0.01 levels of probability respectively, LSD.

Appendix 1. Table 20. F values for correlations on growth analysis parameters and total dry matter of growth analysis experiments.

	Location				
Parameter	1987 Cambridge	1988 Point	1988 Arb	1989 Point	1989 Bison
NAR1	.04	.22	12.96 **	36.10 **	3.59
NAR2	3.29 *	4.60 **	.21	45.14 **	3.86
NAR3	.14	.66	4.42 *	9.17 **	.76
RGR1	9.30 **	11.14 **	26.70 **	51.80 **	5.76 **
RGR2	10.40 **	4.18 **	.01	.48	1.16
RGR3	.19	.17	.33	43.86 **	2.81
LAI1	7.45 **	16.75 **	27.34 **	36.25 **	3.90
LAI2	35.61 **	4.81 *	22.94 **	69.61 **	3.44
LAI3	32.86 **	23.85 **	1.82	31.15 **	1.88
CGR1	6.71 **	11.30 **	25.90 **	33.76 **	3.45
CGR2	38.75 **	6.83 *	19.36 **	82.96 **	4.25 **
CGR3	24.89 **	11.58 **	11.17 **	10.73 **	1.03
LAD1	7.59 **	16.63 **	27.92 **	38.23 **	4.18 *
LAD2	33.97 **	20.56 **	40.33 **	59.31 **	4.63 *
LAD3	57.52 **	22.37 **	39.81 **	47.56 **	5.38 *

*,** significant at 0.05 and 0.01 levels of probability respectively, LSD.

Appendix 2.

Appendix 2. Table 1. Mean squares and degrees of freedom for photosynthetic rate and leaf clorophyll content 1987 Cambridge.

Source	df	Leaf 4	Leaf 6	Leaf 8	chlorophyll
rep	5	139.84 **	50.19 *	72.60 *	29.80
cv	6	55.05 *	33.80	43.48	117.71
rep*cv	30	7.15	22.43	22.92	44.59
cyto	2	156.26 **	788.76 **	130.44 **	2229.63 **
cv*cyto	12	14.38	13.76	9.15	48.59 *
error b	70	4.94	18.71	25.29	31.93

*,** significant at the 0.05 and 0.01 levels of probability respectively, LSD.

Appendix 2. Table 2. Mean squares and degrees of freedom for photosynthetic rate per unit leaf area 1988 Point.

Source	df	Leaf 3	Leaf 4	Leaf 6	Leaf 8
rep	3	210.79 **	326.31 **	62.65 **	78.24
cv	6	69.21 *	52.86	31.76	15.74
rep*cv	18	51.37	17.26	18.55	39.35
cyto	2	17.08	29.45	76.87 **	48.47
cv*cyto	12	23.32	68.72	20.12	27.07
error b	42	28.10	20.62	10.32	36.53

*,** significant at the 0.05 and 0.01 levels of probability respectively, LSD.

Appendix 2. Table 3. Mean squares and degrees of freedom for photosynthetic rate per unit leaf area 1988 Arboretum.

Source	df	Leaf 3	Leaf 4	Leaf 6
rep	3	26.63	116.34 **	264.65 **
cv	6	27.93	42.63	34.89
rep*cv	18	23.53	70.16 **	39.34
cyto	2	36.15	197.95 **	191.52 **
cv*cyto	12	39.00	45.66	56.97
error b	42	27.23	24.44	29.30

*,** significant at the 0.05 and 0.01 levels of probability respectively, LSD.

Appendix 2. Table 4. Mean squares and degrees of freedom for photosynthetic rate per unit leaf area 1989 Point.

Source	df	Leaf 3	Leaf 4	Leaf 6	Leaf 8
rep	3	917.33 **	70.77 **	49.91	130.16 **
cv	6	156.34 *	42.49	50.71	30.17
rep*cv	18	49.46	38.86	60.14 *	39.49
cyto	2	800.07 **	888.57 **	557.86 **	168.17 **
cv*cyto	12	52.07	105.28	24.76	45.48
error b	42	57.82	53.15	37.05	37.92

*,** significant at the 0.05 and 0.01 levels of probability respectively, LSD.

Appendix 2. Table 5. Mean squares and degrees of freedom for photosynthetic rate per unit leaf area 1989 Bison.

Source	df	Leaf 3	Leaf 4	Leaf 6	Leaf 8
rep	3	72.52	211.27 **	43.50	157.34 **
cv	6	47.21	8.26	29.92	34.13
rep*cv	18	41.28	33.02	20.55	23.22
cyto	2	1418.11 **	998.46 **	52.36	691.08 **
cv*cyto	12	36.71	41.47	18.35	14.92
error b	42	27.77	40.86	29.72	22.53

*,** significant at the 0.05 and 0.01 levels of probability respectively, LSD.

Appendix 2. Table 6. Mean squares and degrees of freedom for total leaf chlorophyll content 1988 Point.

Source	df	Leaf 3	Leaf 4	Leaf 6	Leaf 8
rep	3	1.666 **	1.897 **	2.141 **	4.376 **
cv	6	.611 **	.793 *	.652	1.210 *
rep*cv	18	.138	.288	.400	.395
cyto	2	.188	.450	.756	.182
cv*cyto	12	.111	.244	.208	.147
error b	42	.248	.224	.406	.224

*,** significant at the 0.05 and 0.01 levels of probability respectively, LSD.

Appendix 2. Table 7. Mean squares and degrees of freedom for total leaf chlorophyll content 1988 Arboretum.

Source	df	Leaf 3	Leaf 4	Leaf 6
rep	3	.190	.007	.261
cv	6	.201	.048	.084
rep*cv	18	.098	.060	.159
cyto	2	.995 **	1.893 **	1.312 **
cv*cyto	12	.056	.005	.043
error b	42	.069	.074	.045

*,** significant at the 0.05 and 0.01 levels of probability respectively, LSD.

Appendix 2. Table 8. Mean squares and degrees of freedom for total leaf chlorophyll content 1989 Point.

Source	df	Leaf 3	Leaf 4	Leaf 6	Leaf 8
rep	3	2.543	1.548 **	.666	.105
cv	6	6.315	.291	.441	.321
rep*cv	18	2.683	.166	.092	.132
cyto	2	4.266 **	2.554 **	2.418 **	.231
cv*cyto	12	.259	.097	.117	.403
error b	42	.258	.105	.133	.197

*,** significant at the 0.05 and 0.01 levels of probability respectively, LSD.

Appendix 2. Table 9. Mean squares and degrees of freedom for total leaf chlorophyll content 1989 Bison.

Source	df	Leaf 3	Leaf 4	Leaf 6	Leaf 8
rep	3	.049	.387	.815	.024
cv	6	.064	.092	.243	.021
rep*cv	12	.078	.082	.189	.033
cyto	2	8.469 **	12.360 **	.094	.009
cv*cyto	12	.072	.209	.223	.036
error b	42	.047	.111	.213	.022

*,** significant at the 0.05 and 0.01 levels of probability respectively, LSD.

Appendix 2. Table 10. Mean squares and degrees of freedom for photosynthetic rate per unit leaf chlorophyll 1988 Point.

Source	df	Leaf 3	Leaf 4	Leaf 6	Leaf 8
rep	3	21.071 **	4.781 *	13.457	14.835 **
cv	6	1.882	1.057	4.703	2.465
rep*cv	18	3.657 **	3.547 **	10.125	1.683
cyto	2	.734	.064	2.794	1.688
cv*cyto	12	1.219	12.797	3.889	.957
error b	42	1.872	1.372	5.943	1.312

*,** significant at the 0.05 and 0.01 levels of probability respectively, LSD.

Appendix 2. Table 11. Mean squares and degrees of freedom for photosynthetic rate per unit leaf chlorophyll 1987 Cambridge and 1988 Arboretum.

	Cambridge		Arboretum			
Source	df[1]	Leaf 4	df[2]	Leaf 3	Leaf 4	Leaf 6
rep	5	6.257 **	3	3.733	7.649 **	7.983 **
cv	6	1.976	6	.612	1.946	1.022
rep*cv	30	.855	12	1.679	3.000 **	2.610
cyto	2	.517	2	1.528	.605	.647
cv*cyto	12	1.252	12	1.861	1.662	3.137
error b	70	1.127	42	1.399	.926	1.473

[1,2] degrees of freedom for Cambridge and Arboretum locations respectively
*,** significant at the 0.05 and 0.01 levels of probability respectively, LSD.

Appendix 2. Table 12. Mean squares and degrees of freedom for photosynthetic rate per unit leaf chlorophyll 1989 Point.

Source	df	Leaf 3	Leaf 4	Leaf 6	Leaf 8
rep	3	32.682 **	9.578 **	2.930	1.285
cv	6	9.811	2.060	1.610	1.942
rep*cv	12	3.476 **	.933	1.049	1.547
cyto	2	1.440	.515	.055	1.009
cv*cyto	12	1.994	1.205	.906	1.745
error b	42	1.666	.779	1.723	2.333

*,** significant at the 0.05 and 0.01 levels of probability respectively, LSD.

Appendix 2. Table 13. Mean squares and degrees of freedom for photosynthetic rate per unit leaf chlorophyll content 1989 Bison.

Source	df	Leaf 3	Leaf 4	Leaf 6	Leaf 8
rep	3	3.433 *	7.345 **	2.370 *	.035 **
cv	6	.702	.748	1.035	.010
rep*cv	12	1.237	1.067	.619	.004
cyto	2	.681	1.640	.730	.001
cv*cyto	12	1.152	.377	1.399	.005
error b	42	2.823	1.035	.972	.006

*,** significant at the 0.05 and 0.01 levels of probability respectively, LSD.