APPENDIX 1
Modelling Light Transmittance and Light Use Efficiency in Wheat

(Triticum aestivum) and Quackgrass (Elytrigia repens)

Grown in an Additive Series

Abstract. A line quantum sensor was used to monitor the transmission of photosynthetically active radiation (PAR\textsuperscript{13}) in a wheat-quackgrass additive series experiment at Portage la Prairie, Manitoba, in 1987 and 1988. PAR transmittance over time was described using a fourth order polynomial which partitioned the PAR transmittance pattern into five phases. In the first half of growing season the canopies of wheat-dominated mixtures transmitted less PAR than did quackgrass-dominated mixtures but the opposite was true during the last half of the season. PAR transmittance through mixture canopies was generally intermediate to PAR transmittance through the two monocultures. At all sampling dates PAR transmittance was negatively correlated with stand density. Minimum PAR transmittance values ranged from 4 to 16 % and averaged 9.6 % through the canopies of all treatments. Light use efficiency (LUE) was observed to vary with treatment and yield variable used. When based

\textsuperscript{13}Abbreviations: LUE, Light use efficiency; PAR, Photosynthetically active radiation; DAP, Days After Planting; TBIO, Community vegetative size; TSHT, Community vegetative dispersion; TREP, Community reproductive effort; TFEC, Community fecundity.
on biomass calculated LUE values did not significantly differ between treatments and averaged 1.9 g MJ\(^{-1}\). However, when based on reproductive effort, there was a positive correlation between the proportion of wheat in mixture and LUE. The opposite was true when LUE values were calculated based on vegetative dispersion. LUE values based on reproductive fecundity were an order of magnitude larger than values calculated using the other yield variables. When based on reproductive effort or vegetative dispersion, LUE values would decrease as stand density increased, whereas the LUE values would increase as stand density increased, when based on reproductive fecundity or biomass. At comparable stand densities the LUE of mixtures was generally superior to either species in monoculture. Superior LUE of mixtures was attributed to leaf positioning of quackgrass in mixture canopies during wheat senescence. It was hypothesized that the improved leaf positioning of quackgrass in mixtures during the last half of the season may largely offset any negative impacts on quackgrass productivity due to wheat competition for light during the first half of the season.


\(^{14}\)Letters following this symbol are a WSSA-approved computer code from Composite List of Weeds, Weed Sci. 32, Suppl. 2. Available from WSSA, 309 West Clark Street, Champaign, IL 61820.
INTRODUCTION

Quackgrass is recognized to be the most serious perennial grass weed of spring wheat in Manitoba (Thomas and Wise, 1984). Quackgrass infestations can cause severe yield losses in wheat. For example, in Manitoba, a quackgrass infestation of 100 shoots m² in the spring caused a 30 percent yield loss in spring wheat (Wilcox and Morrison, 1988). It is well established that quackgrass interferes with wheat but the mechanism(s) involved has yet to be determined.

Yield of a plant community is dependent on the amount of solar radiation intercepted. Light competition is often an important mechanism of interference except in situations with acutely limiting nutrient or water availability (Donald, 1963). In many studies of wheat-quackgrass interference competition for light has been reported to be the major interference mechanism (Cussans, 1968; Maillette, 1986; Skuterud, 1977; Thurston and Williams, 1968). Cussans (1968) attributed quackgrass etiolation and growth suppression by wheat to competition for light. Skuterud (1977) attributed the greater productivity of quackgrass under wheat than under oats to greater light penetration into the wheat canopy; 27 versus 21 % light penetration into wheat and oats, respectively. Maillette (1986) observed in glasshouse conditions that quackgrass was consistently shaded by wheat leaves and produced significantly less biomass than quackgrass in pure stands. It has also been stated that quackgrass is unlikely to affect cereals by shading them because quackgrass stems usually elongate slower than those of cereals (Thurston and Williams, 1968).

Intra- and interspecific interference response interpretation is dependent on the yield
variable selected (Manuscript 1). Research with quackgrass grown under screens and in growth chambers at reduced light intensities has shown that rhizome production is more dependent on light than production of aerial parts (Hakansson, 1969; Palmer, 1958; Skuterud, 1984; Williams, 1970). In wheat it has been demonstrated that, depending on the timing and duration of shading, reductions in tillering, grains ear⁻¹ or 1000 kernel weight will occur (Fischer, 1985; Fischer and Stockman, 1980; Ford and Thorne, 1975; Puckridge, 1968; Willey and Holliday, 1971). This dependence of growth response on timing of light interference indicates that light use efficiency values will be dependent on yield variable measured.

The primary objective of this study was to determine the extent and duration of PAR transmittance in monocultures and mixtures of quackgrass and wheat. A secondary objective was to determine the comparative light use efficiencies of wheat and quackgrass in monocultures and mixtures and to determine the extent to which light use efficiency is dependent on the particular yield variable utilized.

**MATERIALS AND METHODS**

**Experimental Design**

A wheat-quackgrass additive series experiment was conducted in 1987 and repeated in 1988 at the University of Manitoba, Portage la Prairie research station. The site description and experimental design are the same as those described in Manuscript 1.
To assess the effect of the additive series treatments on PAR transmittance and LUE in the wheat-quackgrass additive series treatments the experimental data was grouped into indicators of biomass size and dispersion and indicators of reproductive effort and fecundity. Community biomass (TBIO) was defined as the sum of the dry matter of all above-ground plant portions and rhizomes. Community biomass dispersion (TSHT) was defined as the number of shoots per unit area including those of daughter quackgrass plants. Community reproductive effort (TREP) was defined as the combination of wheat grain mass and quackgrass spike and rhizome dry matter. Community fecundity (TFEC) was defined as the sum of the number of wheat kernels produced and the number of rhizome buds.

**Light Transmittance**

Except on overcast days, at weekly intervals at a time between 1200 to 1400 hours, the transmittance of photosynthetically active radiation (PAR) to the soil surface of each plot was determined using a 1 m long line quantum sensor\(^{15}\). The percentage light transmittance was calculated as

\[ T_\% = 100\left(\frac{I_t}{I_o}\right) \]

Where \( T_\% \) is the percentage transmittance, \( I_t \) is the PAR recorded at ground-level, and \( I_o \) is the PAR recorded above the canopy. Values of \( T_\% \) calculated in this fashion will often be overestimated as the quantum sensor measures both the direct and diffuse radiation and the diffuse radiation is generally greater within the canopy than above the canopy (Monteith,

\(^{15}\)LI-191SA LI-COR Inc., Lincoln, Nebraska.)
1973). However, for the comparative purposes of this manuscript, this quantitative error was not considered important.

The dynamics of canopy light transmittance was determined by fitting polynomials to the raw data for each of the 15 treatments from the 4 replicates using a linear regression procedure\textsuperscript{16}. The order of polynomial that consistently provided the best fit for all individual treatments in both years was then used for all plots. The coefficient of determination was calculated as recommended by Kvalseth (1985). Polynomial curves were compared to determine if there were significant differences using the nonlinear comparison procedure of Ratkowsky (1983). Significant differences were considered to be those at $\alpha = 0.05$.

**Light Use Efficiency**

Total daily solar radiation at the site was measured using a pyranometer sensor\textsuperscript{17} attached to a minimum dataset recorder. The total cumulative solar radiation over the growing seasons in 1987 and 1988 is presented in Figure 13. The pyranometer sensor has an operational wavelength response of 400 - 1100 nm. Although this sensor is not spectrally ideal (280 - 2800 nm), pyranometer calibration adjusts for the difference in spectral response and the pyranometer sensor gives a response that differs from the spectrally ideal irradiance.

\textsuperscript{16}PROC REG, SAS V5. SAS Institute, Cary, NC.

\textsuperscript{17}LI-200SA LI-COR Inc., Lincoln, Nebraska.
Figure 13. Cumulative incident light (pyranometer sensor) received by the wheat-quackgrass additive series experiments at Portage la Prairie, Manitoba, in 1987 and 1988.
by less than 5\%^{18}. Light use efficiency was determined as

\[ \text{LUE} = \frac{y_k}{Qc} = \frac{y_k}{Qc} \sum_{k=1}^{n} \{100 - T_{\%k}\}[0.5(I_{opk})]\]

where \( y_k \) is the yield variable yield, \( Qc \) is the cumulative sum of intercepted solar irradiance over each intervals quanta use, \( T_{\%k} \) is the mean percent transmittance of the interval, and \( I_{opk} \) is the cumulative incident radiation recorded for the interval on the pyranometer sensor. Monteith (1973) indicates that for practical purposes the PAR fraction can be assumed to average 50\% of solar irradiance. \( I_{opk} \) is multiplied by the scaler 0.5 to convert the pyranometer values to PAR. Treatment results from both years were pooled following validation by an F-Test for homogeneity of variance. Results were analyzed by ANOVA as a randomized complete block and when treatments were significant at \( \alpha=0.05 \), treatment means were separated by the least significant difference test at \( \alpha=0.05 \).

RESULTS AND DISCUSSION

PAR Transmittance

Incident solar radiation reaching the top of the canopy was similar in 1987 and 1988 (Figure 13). Additionally, the general form of the canopy PAR transmittance curves were

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similar in 1987 (Figure 14) and 1988 (Figure 15). A fourth order polynomial most consistently provided the best fit to the canopy PAR transmittance versus time plots. Over both years the $R^2$ values ranged from 0.84 to 0.98. Canopy PAR transmittance patterns for each year were significantly different and therefore corresponding polynomial curves for each treatment could not be pooled.

Canopy PAR transmittance gradually changed with mixture proportion (Figures 14 and 15). A nonlinear curve testing procedure (Ratkowsky, 1983) determined that for adjacent pairs of treatments, at any stand density in either year, the canopy PAR transmittance curves were often not significantly different. In contrast, only rarely were any three adjacent curves at any particular stand density and year not significantly different. Canopy PAR transmittance curves for wheat and quackgrass monocultures were always significantly different.

In 1988 the cumulative daily solar radiation was greater than in 1987 for the last half of the growing season (Figure 13). This extra light availability may have been reflected in wheat having matured six days earlier in 1988 than in 1987. Similarly the dynamics of PAR transmittance through the canopies was such that, on average, curve inflections occurred six days earlier in 1988 (Figure 15) than in 1987 (Figure 14).

Canopy PAR transmittance dynamics in the wheat-quackgrass mixtures was characterized into five phases:

**Phase 1.** Vegetative growth phase - A steady decline in PAR transmittance associated with increased vegetative growth of wheat and/or quackgrass.
Figure 14. Photosynthetically active radiation (PAR) transmittance dynamics of the various mixture proportions and total stand densities in the 1987 wheat-quackgrass additive series experiment.
Figure 15. Photosynthetically active radiation (PAR) transmittance dynamics of the various mixture proportions and total stand densities in the 1988 wheat-quackgrass additive series experiment.
Phase 2. Maximum leaf area index phase - The transition point between phase 1 and 2 associated with the least PAR transmittance and late anthesis in both wheat and quackgrass.

Phase 3. Early maturation phase - A steady increase in PAR transmittance associated with increasing leaf senescence in wheat and rapid stem elongation and more erect habit in quackgrass.

Phase 4. Late maturation phase - The transition point between phase 3 and 5 associated with complete senescence and grain ripening in wheat and the most erect habit of quackgrass.

Phase 5. Displacement phase - A slight decline in canopy PAR transmittance to the ground associated with displacement of wheat culms by heavy heads and increased lodging in quackgrass.

Similar multiphase canopy irradiance transmittance patterns have been shown under both pasture ryegrass (*Lolium rigidum*) (Stearn and Donald, 1962) and wheat (Fischer, 1983; Skutterud, 1977).

During growth phase 2 the interpolated minimum canopy PAR transmittance to the soil surface ranged from 4 to 16 % and averaged 9.6 % over the two years (Figures 14 and 15). The PAR transmittance indicated in these experiments is less than those obtained by Skuterud (1977). He observed that spring wheat intercepted all but 15 % of the sunlight to
5 cm above the soil.

In both years there was a trend that the more quackgrass present in the mixture the later the interpolated minimum PAR transmittance value occurred. For example in 1988 the date of minimum light transmittance for the 75 plants m$^2$ stand density occurred 52 days after planting (DAP) for monoculture wheat versus 62 DAP for monoculture quackgrass (Figure 15). This indicates that quackgrass was slower to achieve its maximum leaf area index than was wheat.

The maximum canopy PAR transmittance during growth phase 4 ranged from 11 to 37 % and averaged 24 % over both years (Figures 14 and 15). On average the interpolated phase 4 values for 1987 were 3 % more than the 1988 values. This is likely the result of the more rapid maturation, due to hotter dryer conditions, in 1988 compared to 1987.

For all growth phases, in all mixture proportions, there was a trend towards higher densities transmitting less PAR than the lower densities. For example, in 1988 monoculture wheat at 30 DAP had intercepted 40, 65, and 82 % at 75, 150, and 300 plants m$^2$, respectively (Figure 15). Maillelle (1986) similarly observed that low density stands of wheat and quackgrass grew slower and produced fewer leaves than at higher densities.

During the vegetative growth phase (phase 1) the larger the quackgrass proportion in mixture the more PAR was transmitted through the canopies. However, the opposite was true during phase 4 growth. For example at 75 plants m$^2$ at 40 DAP in 1987 PAR transmittance was 37 and 56 % whereas at 80 DAP PAR transmittance was 33 and 23 %, for wheat and quackgrass monocultures, respectively. The temporal difference in PAR transmittance indicates that wheat is more effective at PAR interception during the first half
of the growing season whereas quackgrass is more efficient at PAR interception during the later half. In wheat-quackgrass mixtures the superior PAR interception by quackgrass late in the growing season may explain the marked dry weight increases that have been observed to occur in quackgrass during the crop ripening phase (Cussans, 1968; Rauber and Bottger, 1984; Skutterud, 1984).

PAR transmittance in the wheat-quackgrass mixtures was comparable to that for the species in monoculture. A similar result for species in monocultures and mixtures has been noted by Willey (1979) for intercrops.

**Light Use Efficiency**

Light use efficiency (LUE) values varied with yield variable used in its calculation. When based on TBIO, TREP, TSHT and TFEC the LUE values ranged from 1.68 to 2.00 g MJ⁻¹, 0.31 to 0.67 g MJ⁻¹, 1.08 to 1.99 # MJ⁻¹, and 5.70 to 24.95 # MJ⁻¹, respectively (Table 24). TREP is a major component of TBIO and this explains the smaller and similar range of LUE values for TREP relative to TBIO. LUE values based on TFEC were an order of magnitude larger than LUE values based on the other yield variables. This difference in magnitude is simply a reflection of the scale of the fecundity values being in the thousands, whereas the other yield variables were in the hundreds.

When calculated using TBIO there was no significant difference between LUE values between treatments (Table 24). This lack of difference can be explained by the complementary light use patterns of wheat and quackgrass over the growing season. Wheat intercepts more light for the first half of the growing season, whereas quackgrass intercepts
Table 24. Wheat-quackgrass additive series light use efficiency (LUE) values calculated using selected variables.

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<th>Mixture Proportion</th>
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<tr>
<td>S.E.M.</td>
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<td>(0.066)</td>
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</table>

^ Average of the 1987 and 1988 experiments LUE values.
^TBIO = community biomass, TREP = community reproductive effort, TSHT = community vegetative dispersion, and TFEC = community reproductive fecundity
^c Standard error of mean (S.E.M.) for column values.
more light over the last half (Figures 14 and 15). The net effect of this complementary PAR interception pattern is similar LUE values for the treatments when based on vegetative biomass. LUE values on the scale of 1.9 g MJ⁻¹ for TBIO are comparable to LUE values reported by other researchers in other crops.

When calculated using TREP there were significant differences in LUE values between treatments (Table 24). The dominant effect was that the monoculture quackgrass treatments resulted in lower LUE values compared to any of the mixtures or monoculture wheat. There was also a trend that the greater the proportion of wheat the greater was the LUE value. Thus in terms of reproductive effort wheat was more efficient in using PAR over the growing season than was quackgrass. There were no significant mixture or mixture by density interactions for LUE based on TREP. The LUE of the mixtures, particularly the mixtures with higher proportions of quackgrass, was often greater than could be accounted for by the greater LUE of wheat present alone. It was observed that quackgrass stood more erect in mixtures because of the mechanical support of the wheat. That quackgrass is supported by wheat in mixtures was also reported by Maillette (1986). This more erect habit of quackgrass in mixtures late in the season would allow for more efficient PAR interception by the quackgrass in mixture with wheat and, in turn, greater reproductive effort. Rhizome development in quackgrass primarily occurs during the crop ripening phase (Cussans, 1968; Rauber and Bottger, 1984; Skutterud, 1984).

LUE values based on TSHT showed a significant trend that as quackgrass proportion in mixture increased LUE value increased (Table 24). This increasing LUE can be explained by comparing the spreading habits of the two species. Wheat is a determinate, erect plant
that produces tillers close to its primary shoot. In contrast quackgrass is an invasive, indeterminate plant that produces tillers adjacent to the primary shoot as well as in daughter plants far from the main shoot. Thus the naturally greater tillering potential of quackgrass, due to greater dispersion ability, provided larger LUE values based on TSHT. LUE values based on TSHT also increased as total stand density increased. At higher plant densities plants filled the smaller interplant spaces more rapidly and with less shoots than at lower stand densities. There were no density by mixture interactions for LUE values based on TSHT.

LUE values based on TFEC were positively correlated with increases in wheat proportion. The quackgrass monoculture was much less efficient in irradiance utilization in terms of TFEC than any of the mixtures or the wheat monocultures. This lowered LUE is more a reflection of the fecundity values for wheat being much larger than those from quackgrass, rather than a true reflection of a trend due to treatment effects. For example, over the two years the average quackgrass monoculture produced 3083 rhizome nodes m$^{-2}$ and the average wheat monoculture produced 11,090 kernels m$^{-2}$ (Wilcox - unpublished).

LUE of mixtures, particularly mixtures with high proportions of quackgrass, were usually greater than LUE values calculated for monocultures (Table 24) and PAR transmittance values for mixtures were usually intermediate to monocultures (Figures 14 and 15). This treatment response difference between LUE and PAR transmittance for wheat-quackgrass mixtures suggests that the greater LUE of mixtures was not due to increased PAR interception. Instead, improved PAR utilization efficiency, perhaps through improved quackgrass leaf positioning last half of the growing season, was responsible for greater LUE.
of mixtures. In the wheat-quackgrass mixtures it was observed that wheat shoots often supported the quackgrass in an upright habit which would allow more of the quackgrass plant to receive irradiance than when in a more prostrate habit. Quantitative assessment of quackgrass leaf positioning in the additive series was not conducted. Alternatively, late season shifts in radiation spectral quality and radiation quantity could also contribute or be responsible for the greater LUE of mixtures (Allen et al., 1975; Norman and Arkebano, 1991). Greater LUE for mixtures relative to monocultures has also been reported by Willey (1979) in intercrops.

Competition for light in the wheat-quackgrass mixtures was variable and temporally dependent. Wheat was superior to quackgrass in irradiance interception in the first half of the growing season and underwent progressive senescence in the latter half of the growing season. Losses induced in quackgrass by wheat PAR interception in the first half of the growing season were possibly offset by more efficient quackgrass leaf positioning in the latter half. Unlike annual species, early shading is not likely to be effective against quackgrass as the majority of its light requirements for rhizome production occurs after crop growth ceases (Cussans, 1968; Rauber and Bottger, 1984; Skutterud, 1984). From a practical standpoint these results indicate that depending only on competition for light from wheat to suppress quackgrass can be unsuccessful over the long run. Successful quackgrass management in wheat will require the integration of wheat competition for light with other control measures.