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Yield Response of Indeterminate Potato (*Solanum tuberosum* L.) to Simulated Insect Defoliation

Jesse R. Ziems, Benjamin J. Zechmann, W. Wyatt Hoback,* John C. Wallace, Rod A. Madsen, Thomas E. Hunt, and Leon G. Higley

ABSTRACT

Yield response to insect defoliation is primarily a function of light interception. A series of leaf removal experiments were conducted on an indeterminate chipping variety of Irish potato, *Solanum tuberosum* L., to simulate late-season insect defoliation injuries. Leaf removal was conducted following a computer simulation model for growing insect populations. Across 2 yr, 50 to 75% of the canopy leaf area was removed during a 10-d period. In 2001, 75% leaf removal resulted in a 14% yield loss (in total potato weight) while in 2002, 50% defoliation resulted in 15% yield loss and 75% leaf removal resulted in 22% yield loss. In addition to yield differences, high defoliation reduced number and weight of large (65–100 mm diam.) tubers and increased the number of small tubers (47–64 mm diam.). Yield loss was significant when defoliated canopies remained below a leaf area index (LAI) of 4.0. Percentage light interception was a better predictor of potato yield than was percentage defoliation. These data are consistent with the light interception hypothesis and show that remaining leaf area is a better predictor of yield potential than percentage defoliation. Thus, treatment decisions based on light interception and LAIs rather than estimates of percentage defoliation should be applicable to indeterminate varieties of potato.

Yield loss caused by defoliating insect pests is most frequently correlated with the amount of leaf tissue removed (Peterson and Higley, 2001). Some studies indicate that low levels of defoliation may lead to an increased rate of photosynthesis because of improved water, nutrient, and light availability to remaining leaves after defoliation (Ostlie, 1984; Pedigo, 1989; Welter, 1989; Higley, 1992; Peterson et al., 1992; Peterson and Higley, 1996; Trumble et al., 1993). Thus, the remaining leaf area may have a higher photosynthetic rate compared with leaves on undefoliated plants (Higley, 1992; Peterson et al., 1992). In addition, it is possible that regrowth can occur following defoliation, improving net photosynthesis (Ostlie, 1984; Pedigo, 1989; Welter, 1989; Trumble et al., 1993; Peterson and Higley, 1996).

J.R. Ziems, B.J. Zechmann, and W.W. Hoback, Dep. of Biol., Univ. of Nebraska, Kearney, NE 68849; J.C. Wallace, CSS Farms, 2016 32 Road, Minden, NE 68959; and R.A. Madsen, T.E. Hunt, and L.G. Higley, Dep. of Entomol., Univ. of Nebraska–Lincoln, Lincoln, NE 68583-0816. Support for this project was provided through the Nebraska Potato Development Board, UNK Research Services Council, the Agricultural Research Division of the University of Nebraska–Lincoln, University of Nebraska Agricultural Experiment Station Projects 17-068, 17-080 and 17-086, and CSS Farms. This is paper no. 14528 of the Journal Series of the University of Nebraska Agricultural Research Division. Received 24 Aug. 2005. *Corresponding author (hobackww@unl.edu).

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For defoliated plant canopies, a reduction in light interception is most likely the primary cause for yield reduction (Higley, 1992; Peterson and Higley, 2001). This observation has led to the development of the defoliation–light interception hypothesis, which states that defoliation reducing canopy light interception below approximately 90% results in a linear relationship between reduced canopy light interception and reduced yield (Johnson, 1987; Waggoner and Berger, 1987; Higley, 1992). Over the past 15 yr, research in soybean [*Glycine max* (L.) Merr.] has established that yield loss from defoliating pests supports the light interception hypothesis (Higley, 1992; Hunt et al., 1994; Haile et al., 1998a, 1998b; Hammond et al., 2000; Peterson and Higley, 2001). Thus, in soybean and other crops, yield loss curves based on reductions in leaf area have proven to be effective in determining economic injury levels (EILs) from defoliating pests (Higley, 2001).

There is limited research on potato defoliation and treatment thresholds. Only two species-specific economic thresholds have been published in potato: Colorado potato beetle (*Leptinotarsa decemlineata*) and variegated cutworm (*Peridroma saucia*) (Peterson, 1997). Researchers on potato defoliation have historically attempted to relate insect densities or percentage defoliation to yield. In addition, there is substantial inconsistency regarding the accuracy of experimentally determined yield loss from defoliation in potato (e.g., Zehnder and Evanylo, 1989; Senanayake and Holliday, 1990; Senanayake et al., 1993; Shields and Wyman, 1984; Zehnder et al., 1995; Nault and Kennedy, 1998). Most defoliation research on potato has used single-day simulated defoliation. Work in other systems (e.g., soybean) strongly indicates that single-day defoliation does not accurately simulate the effects of insect defoliation (e.g., Ostlie, 1984; Hunt et al., 1994) but that sequential defoliation methods can be designed to adequately model insect defoliation.

In Nebraska, this uncertainty has been the main reason for growers to use a conservative threshold of 10% defoliation. There is a wide range of determinacy among potato cultivars, and the responses to defoliations and corresponding thresholds may be different for different determinacy groups and may be affected differently by defoliation timing within determinacy groups. In the research reported here, we used a series of sequential leaf-removal field experiments to determine yield losses from defoliation. We used a computer model to guide defoliation to simulate injury (consumption) from a larval lepidopteran population during the most injurious larval stages. We imposed defoliation levels so that potato will have remaining LAIs of 2.5 and 1.5, during

Abbreviations: EILs, economic injury levels; LAI, leaf area index; PAR, photosynthetically active radiation.

three growth stages. The objectives of these experiments are to validate the light interception hypothesis to potato defoliation and to provide producers with accurate and practical EILs for defoliating insects.

MATERIALS AND METHODS

Experimental field trials took place in two different locations in Kearney County, Nebraska. Field soils in 2001 were classified as Valentine ELS loamy fine sand, 0 to 9% slope. Soils in 2002 and 2003 were classified as Simeon sandy loam, 0 to 3% slope. The field in 2001 was an irrigated center-pivot quarter, and the field for 2002 and 2003 was an irrigated linear-move pivot. The planting dates were 7 May 2001, 17 May 2002, and 1 May 2003. Water, nutrient, herbicide, insecticide, and fungicide applications were consistent with the commercial production practices.

The potato cultivar used was a Frito Lay proprietary chipping potato 'FL1879', an indeterminate variety, resulting from a cross between 'Snowden' and 'FL1207'. This cultivar produces a very lush canopy with almost continuous vegetative growth that replaces senesced leaflets throughout the growing season. FL1879 rarely flowers but produces high yields of large tubers.

Experimental design for all studies was a randomized complete block with four replications. Plots were four rows by 3 m with the center two rows receiving treatments and the outer rows acting as border rows. A 1-m buffer area was placed between all treatments.

In 2001, manual defoliation was conducted at late season (plant maturity). In 2002, defoliations occurred at early, mid, and late seasons (corresponding to tuber initiation, full bloom, and plant maturity, respectively). In 2003, manual defoliation was conducted at early and midseasons. Specific defoliation levels varied among years based on differences in pretreatment canopy leaf areas. Defoliation treatments were chosen to provide final LAIs below 3.5 (the critical LAI), specifically between 1.0 and 2.0 (high defoliation) and between 2.0 and 3.0 (low defoliation). Late-season treatment levels in 2001 were untreated check and 50 and 75% defoliations (Table 1). In 2002, early-season treatments consisted of an untreated check and 30 and 50% defoliation, midseason treatments consisted of an untreated check and 15 and 30% defoliations, and late-season treatments were the same as 2001 (untreated check and 50 and 75% defoliation) (Table 1). In 2003, additional defoliation treatments were imposed to determine more accurate EILs across seasons for defoliating insects. These treatments were untreated check and 50, 65, and 80% defoliations for the early-season defoliation period and an untreated check and 50, 55, and 70% for the midseason defoliation period (Table 1).

Defoliations used in these studies were similar to previous studies conducted in alfalfa (*Medicago sativa* L.) and soybean (e.g., Haile et al., 1998a, 1998b; Hammond et al., 2000; Madsen et al., 2004; Peterson and Higley, 2001). Initial leaf area was determined by completely defoliating all leaves from four plants and measuring leaf area using a leaf area meter (Model LI-3100, LI-COR, Lincoln, NE). Defoliation rates were based on feeding by lepidopteran larvae such as armyworm (*Pseudaletia unipuncta*) or celery looper (*Anagrapha falcifera*) and were modeled for the amount of leaf removal per day over a 10-d period. Although larval development of lepidopterans may last for several weeks, greater than 90% leaf consumption occurs at the last one to two larval stages, which typically last about 10 d (Haile et al., 1998a). We used a computer model, DEFOL (Higley, unpublished, 1988), to determine appropriate levels of defoliation to simulate a developing lepidopteron pest population over a 10-d period of maximum injury. For each day of the experiment, an increasing amount of leaf area, based on DEFOL, was removed from each plot, and leaflet area from each treatment was measured using LI-3100.

Insect defoliation was simulated by manually severing individual leaflets at the axil. In late-season 2001 and all seasons in 2002, defoliation was imposed by removing 50 to 75% of the targeted defoliation level from the upper and midportions of the canopy in the early stages of each defoliation event and all portions of the canopy by the end of the 10-d experimental period. In 2003, defoliation was conducted on all portions of the canopy randomly throughout the experimental period. Check plots had no leaf area removed but received similar foot trampling both years.

One day before the beginning of defoliation, LAI was measured with a plant canopy analyzer (LI-COR Model LAI-2000). Measurements consisted of one reading above the canopy and three readings below the canopy for each plot. In 2001 and 2002, LAI was measured approximately every 7 d throughout the 10-d defoliation period and postdefoliation. In 2003, LAI measurements were taken to assure defoliation accuracy in the same manner as the two previous years, but postdefoliation measurements were not recorded.

In 2001 and 2002, photosynthetically active radiation (PAR) was measured using a 1-m line quantum sensor (LI-COR Model LI-191 SA0) connected to a data logger (LI-COR Model LI-1000). In 2001, PAR was measured by taking one reading above the canopy and three measurements below the canopy in the center furrow by placing the line quantum sensor between and parallel to the center two rows. In 2002, measurements were taken in the same way as 2001 with the addition of a measurement conducted by placing the line quantum sensor perpendicular to and in the center of the furrow between the center treatment rows. Percentage light interception was determined based on above- and below-canopy readings. Light measurements were taken between 1200 and 1300 h on clear days with light intensities above 1500 μmol photon m^{-2} s^{-1}. The PAR was measured approximately weekly. In 2003, no measurements of PAR were taken.

Potato was harvested manually after the kill date and plant senescence, approximately 40 d after late-season defoliation. Potato yield and quality were determined based on count, size, and yield by size, internal defects, external defects, solids, and chip-frying quality. Because of size-grading differences between years, tubers were graded through hexagon sizing screens, and results were tabulated by using total yield and only three size classes: large (65 to >102 mm in diameter), small (<47 to 65 mm in diameter), and marketable (51–102 mm in diameter). Specific gravity was measured using an SFA potato hydrometer (Snack Food Association, Alexandria, VA).

Size and yield data were analyzed using Sigma Stat's two-way ANOVA, with defoliation phenology (early or late) as one factor and defoliation level (0, low, medium, and high) as the other factor. Treatment means were separated by protected LSD. All other data were analyzed using a one-way ANOVA by growth stage.

Table 1. Achieved defoliation levels for all years, seasons, and treatments.

		Defoliation treatments			
Year	Growth stage	Check	Low	Mid	High
2001	Plant maturity	0	50	–	75
2002	Tuber initiation	0	30	–	50
	Full bloom	0	15	–	30
	Plant maturity	0	50	–	75
2003	Tuber initiation	0	50	65	80
	Full bloom	0	50	55	70

RESULTS

For all years, the target of LAI at the end of the 10-d defoliation period was achieved within 3%. All defoliation treatments substantially reduced light interception below that of the check. The relationship between LAI and percentage intercepted light was linear, with 90% light interception occurring above LAIs of 4 (Fig. 1).

The LAI for low- and high-defoliation treatments increased postdefoliation for both 2001 and 2002, indicating significant regrowth (Fig. 2). High levels of regrowth were observed visually in 2003 as well. In 2001, the LAI for the check plots after plant maturity showed a slight steady decline representing leaf senescence. In 2001, LAIs were similar among treatments at about 34 d postdefoliation. In 2002, the LAI for the control began with a similar steady decline, and at about 15 d postdefoliation, a rapid decline in LAI was observed. At 24 d postdefoliation, both defoliated treatments stopped regrowth and declined rapidly. The control declined much faster. As a result, LAI for the high-defoliation treatment was greater than the control treatment LAI 30 d postdefoliation (Fig. 2). In 2003, the check plots were also observed to senesce earlier than defoliated treatment plots.

Percentage light interception for 2001 also showed a similar trend as LAI from canopy regrowth (Fig. 3). At 20 d postdefoliation, the percentage light interception for high-defoliation treatments exceeded the percentage light interception of low-defoliation treatment.

Tuber Initiation Defoliation Results

In 2002, no significant differences were observed from any defoliation treatment relative to the control for total yield, marketable yield, small-size yield, or large-size yield (Table 2). However, in 2003, there were significant differences in total yield in all size classes. The high-defoliation treatment (80% defoliation) resulted in total yield significantly lower than other treatments. The mid-level (65% defoliation) had a significantly greater total yield than the high, but this was significantly lower than the control total yield (Table 2). The high-defoliation treatment in 2003 was significantly lower than all other treatment levels for marketable yield and large-size yield (Tables 2 and 3). With a decrease in large-size tubers, the small-size yield for the high-defoliation treat-

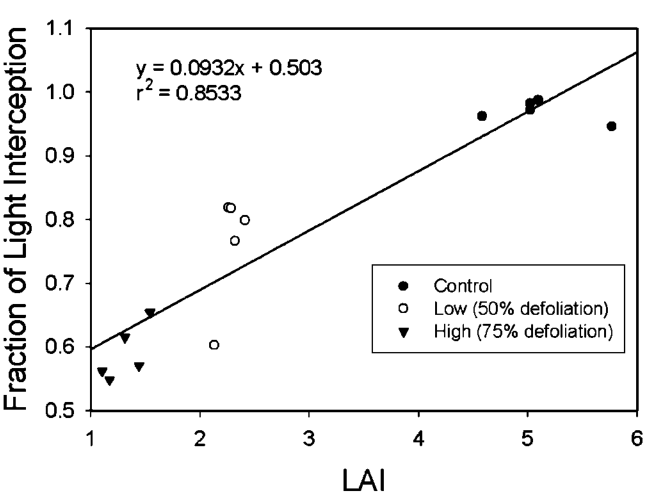

Fig. 1. Relationship between leaf area index (LAI) and fraction of light interception for 'FL 1879' potato. Data are combined for 2001 and 2002.

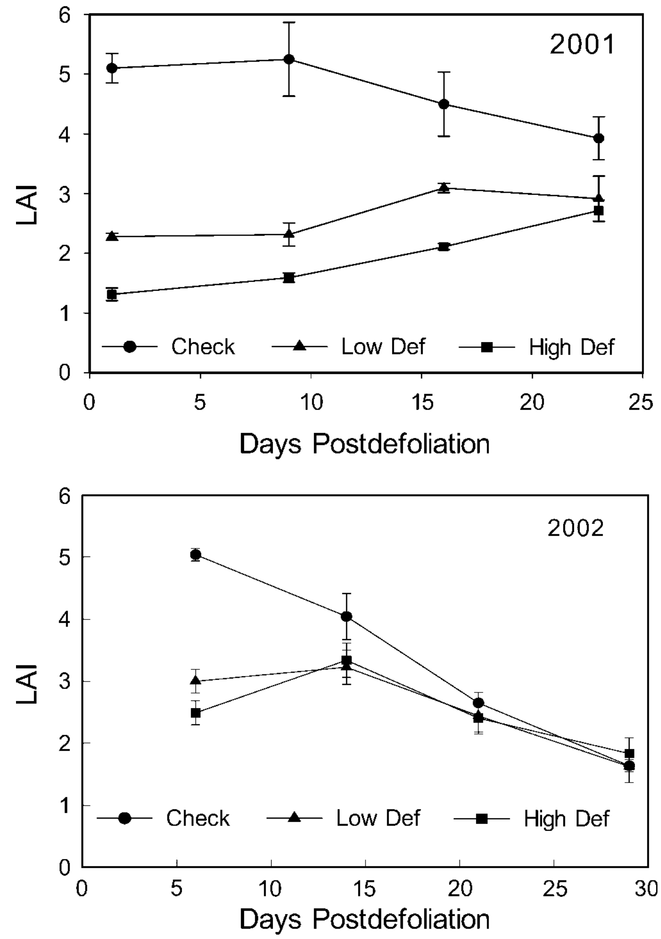

Fig. 2. Mean (standard error) leaf area index (LAI) for 'FL1879' potato defoliated for low (50%) and high (75%) leaf removal in 2001 and 2002.

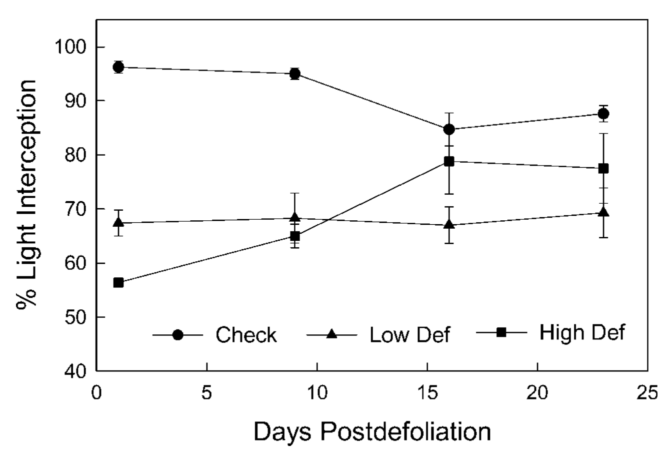

Fig. 3. Light interception data from 2001 for 'FL1879' potato defoliated for low (50%) and high (75%) leaf removal. Increasing slopes indicate regrowth while decreasing slopes represent senescence.

Table 2. Yield data and standard error (SE) for total yield and marketable yield for all treatments and seasons (p = 0.05).

Year	Growth stage	Total yield				Marketable yield (51–102 mm)			
		Check	Low	Mid	High	Check	Low	Mid	High
		Mg ha^{-1}							
2001	Plant maturity	48.9a ± 0.9	47.7ab ± 2.5	–	42.6b ± 0.7	46.6a ± 0.7	44.8a ± 2.8	–	38.4b ± 1.4
2002	Tuber initiation	55.4a ± 3.1	52.4a ± 3.2	–	52.9a ± 4.8	51.9a ± 3.5	49.4a ± 3.2	–	49.2a ± 4.7
	Full bloom	55.4a ± 3.1	53.3a ± 1.5	–	63.1a ± 3.4	51.9a ± 3.5	49.8a ± 1.6	–	59.9a ± 3.1
	Plant maturity	55.4a ± 3.1	46.8b ± 1.8	–	43.7b ± 2.5	51.9a ± 3.5	44.0ab ± 1.7	–	39.3b ± 2.9
2003	Tuber initiation	63.7a ± 1.4	59.9ab ± 2.1	55.8b ± 2.3	41.7c ± 3.0	61.4a ± 1.8	58.1a ± 2.3	54.2a ± 2.3	38.3b ± 3.2
	Full bloom	63.7a ± 1.4	61.0a ± 3.2	61.3a ± 1.2	59.1a ± 1.2	61.4a ± 1.8	58.7a ± 3.2	58.6a ± 1.1	56.7a ± 1.6

ment was significantly higher than all other treatment levels (Table 3).

Full-Bloom Defoliation Results

In 2002, there were no significant yield reductions observed at any treatment level (0, 15, or 30%) for total yield, marketable yield, or small yield. In the large-size class, the yield of the high-defoliation treatment was significantly lower than that of the control treatment and the low-treatment levels. In 2003, no significant yield reductions were observed at any treatment level (0, 50, 55, or 70%) for total yield, marketable yield, small-size yield, or large-size yield.

Plant Maturity Defoliation Results

The high-defoliation treatment in 2001 had a significantly lower marketable yield than the low-defoliation and control treatments (Table 2). In 2001, there were no significant yield reductions observed at any treatment level (0, 50, or 75%) for small-size yield or large-size yield. In 2002, for total yield and marketable yield, the high-treatment yields were significantly lower than the control and low-treatment levels (Table 2). In 2002, the low-treatment-level small-size yield was significantly lower than the control or high-treatment levels. All treatment levels were significantly different from each other in the large-size yield category in 2002 with the control treatment having the highest yield and the high treatment having the lowest yield (Table 3).

Defoliation and subsequent regrowth caused shifts in the distribution of photosynthate between new leaf tissue and tuber bulking. Although the potential exists to affect tuber attributes, no significant differences were found in solids or defects for any year, nor were significant differences in fry quality observed between treatments in any year or season.

Total potato yields declined in association with decreases in light interception below approximately 90% in 2001 and 2002 (Fig. 4) although details of this relationship were obscured by experimental noise. Yields of large-sized potato (suitable for chipping) were more strongly affected by reductions in light interception than total potato weight (Fig. 5). These data indicate interactions between defoliation and production of smaller potato tubers.

DISCUSSION

Conditions in 2001 were more conducive for potato tuber growth than in 2002, probably because greater rainfall occurred in 2001. In 2002, day and nighttime temperatures were above average with minimal irrigation. The amount of leaf area removed was about the same in both years (2001 and 2002). Leaf area index likely declined more rapidly in 2002 than 2001 because of relatively smaller initial canopy size as a result of hotter and drier conditions during the middle and late growing season in 2002. Additionally, greater leaf area recovery was observed in the high-defoliation treatment in 2001 than in 2002 (Fig. 4). These differences in environmental conditions most likely led to fewer large-sized tubers and more small-sized tubers in 2002 (Table 3). In contrast, the 2003 growing season had nearly optimal conditions with early-season rainfall, low insect pressure, low fungal disease pressure, and few irrigation problems.

In soybean, yield losses from defoliation do not occur unless LAIs are reduced below 3.5 by the beginning of reproductive stages, where canopy light interception decreases to less than 90% (Higley, 1992; Haile et al., 1988a, 1998b). Typically, potato crops achieve a LAI of 5 to 6 (Allen and Scott, 2001), and maximum light interception (>90%) is achieved at LAIs of about 4. Early development of maximum light interception directly relates to yield potential (Allen and Scott, 2001). If the

Table 3. Yield data and standard error (SE) for all small-size class and large-size class for all treatments and seasons (p = 0.05).

Year	Growth stage	Small (<47–65 mm) yield				Large (>65–102 mm) yield			
		Check	Low	Mid	High	Check	Low	Mid	High
		Mg ha^{-1}							
2001	Plant maturity	16.2a ± 2.5	19.4a ± 2.9	–	17.7a ± 2.5	32.7a ± 2.0	28.6a ± 3.3	–	24.7a ± 3.0
2002	Tuber initiation	24.4a ± 1.2	22.5a ± 2.1	–	26.4a ± 3.7	31.1a ± 2.1	29.9a ± 2.6	–	26.5a ± 2.9
	Full bloom	24.4a ± 1.2	53.3a ± 1.5	–	63.1a ± 3.4	31.1a ± 2.1	28.6a ± 0.9	–	38.2b ± 2.6
	Plant maturity	24.4ab ± 1.2	46.8b ± 1.8	–	43.7b ± 2.5	31.1a ± 2.1	24.6b ± 1.7	–	16.4c ± 1.7
2003	Tuber initiation	10.1a ± 0.6	8.6a ± 0.8	9.2a ± 0.6	14.9b ± 0.8	53.6a ± 1.6	51.3a ± 2.6	46.6a ± 2.8	26.8b ± 3.4
	Full bloom	10.1a ± 0.6	9.2a ± 0.2	12.2a ± 0.8	11.4a ± 1.4	53.6a ± 1.6	51.7a ± 3.3	49.1a ± 1.3	47.7a ± 2.3

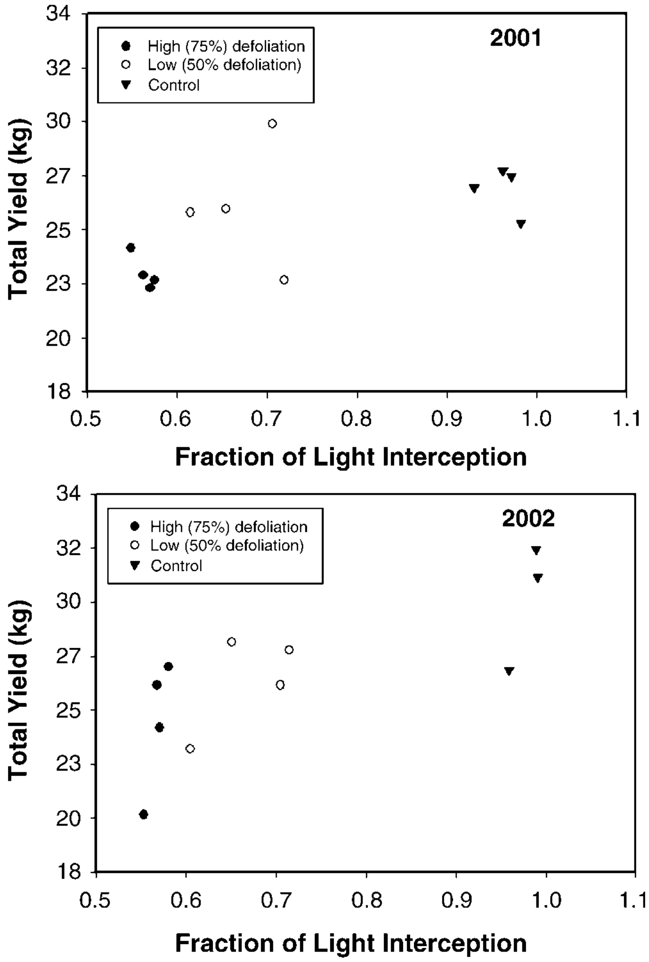

Fig. 4. Relationship between lowest fraction of light interception observed and total yield for 2001 and 2002.

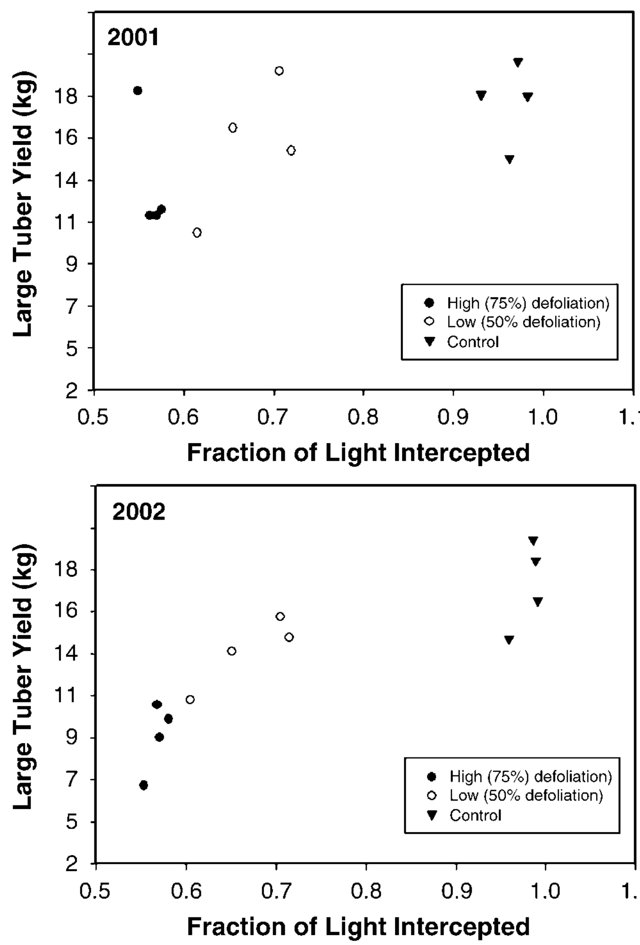

Fig. 5. Relationship between lowest fraction of light interception observed and yield of large tubers for 2001 and 2002.

physiological basis for yield loss from defoliation is reduction in light interception, as our data indicate, then potato could tolerate much more defoliation than current thresholds suggest.

Other factors including type of injury, timing of injury, and location of injury, all influence yield loss of commercial vegetable crops (Pedigo et al., 1986; Peterson and Higley, 2001). In potato, Shields and Wyman (1984) found plants to be more sensitive to simulated insect injury beginning at the top of the canopy and progressing down through the canopy (e.g., as with Colorado potato beetle) than from injury beginning at the bottom of the canopy and progressing upward [e.g., as with variegated cutworm (Shields et al., 1985)]. Colorado potato beetle larvae feed for about 2 to 3 wk and, in early stages of development, preferentially eat young tender buds and leaves. Older larvae and adults feed on older leaves. Most cutworm larval feeding occurs on lower portions of the plant canopy at night (Shields et al., 1985). In contrast, celery looper (*Syngrapha falcifera*) and cabbage looper (*Trichoplusia ni*) larvae usually do most of their damage to upper and midportions of the canopy during their fourth and fifth larval stages.

Yield losses also may vary with potato cultivar, which may be related to time of defoliation. For example, relatively severe early- or late-season feeding by Colorado potato beetle had little effect on potato yield (cv. 'Katahdin') in Manitoba while moderate defoliation in midseason resulted in considerable (>35%) yield reduction (Hare, 1980). When defoliated early in the season, plants of many cultivars recovered completely, regrowing to LAIs above 4, if defoliation did not exceed 10 to 33% of the plant's leaf area (Cranshaw and Radcliffe, 1980). Mechanical defoliation simulating short-term damage provided similar results (Cranshaw and Radcliffe, 1980; Shields and Wyman, 1984). Senanayake and Holliday (1990) in Manitoba found that season-long defoliation by low numbers of Colorado potato beetles resulted in significant loss and much lower EILs based on larval density at first bloom although information on LAIs and light interception was not reported.

Timing of injury (tuber initiation, full bloom, and plant maturity) has been shown to play a large role in the amount of defoliation plants can withstand before yield loss occurs (Sparks and Woodbury, 1967; Hare, 1980; Cranshaw and Radcliffe, 1980; Wellik et al., 1981; Ferro et al., 1983; Shields and Wyman, 1984; Zehnder and Evanylo, 1989; Dripps and Smilowitz, 1989; Senanayake and Holliday, 1990; Senanayake et al., 1993). All previous studies indicate that potato plants are able to withstand higher amounts of defoliation during tuber initiation and maturity than at full bloom, but economically significant amounts of injury differ greatly among locations and climates.

In this study, relationships between canopy leaf area (LAI) and light interception (Fig. 1) generally follow previous studies on potato (Allen and Scott, 2001). However, our data show maximum light interception occurs at an LAI of 5 while previous data suggest maximum light interception is achieved at an LAI of 4 (Allen and Scott, 2001). These differences might reflect experimental variability or may reflect true underlying differences, such as variety or cultural practices. After defoliation, light interception followed leaf area, and some recovery was observed in high-defoliation treatments when postdefoliation leaf regrowth occurred (Fig. 2).

Yield, leaf area, and light interception data broadly supported the hypothesis that yield losses from defoliation in potato are associated with reductions in canopy light interception. The specifics of these relationships were obscured by experimental variability; however, the trends in yield reduction and light interception were consistent across both years. Additionally, yield effects from defoliation were greater with larger tubers than other sizes (Table 3; Fig. 4 and 5). Defoliation at plant maturity occurred during maximal movement of photosynthate and stored carbohydrate from leaves to tubers (Allen and Scott, 2001). Under circumstances of reduced source availability, plants appear to fill across tuber sizes, rather than increasing size of only larger tubers (Allen and Scott, 2001). Proportion of grades is of economic importance because oversized and undersized tubers may not be usable for commercial chipping. Defoliation acts by reducing light interception, affects total yield, and modifies the proportion of marketable tubers and hence economic yield. The fact remains, however, that indeterminate potato can withstand higher levels of defoliation than previously shown in the literature.

These data demonstrate that indeterminate varieties of potato may experience significant yield loss from late-season defoliation, which is consistent with the results of other research (Cranshaw and Radcliffe, 1980; Nault and Kennedy, 1998). Our findings indicate that the current economic threshold used in central Nebraska of 10% defoliation is excessively conservative because yield loss did not occur until defoliation levels reached 75% of the control LAI. However, at defoliation levels near 70%, quality is likely to be as significant a consideration as yield weight because glycoalkaloid levels in potato tubers have been shown to double with this much defoliation (Hlywka et al., 1994). Also, because canopy size and regrowth potential will differ among varieties and at different points in the growing season, these factors must be considered in developing comprehensive guidelines for potato defoliators. Consequently, appropriate economic thresholds for potato defoliators will need to be based on considerations of factors influencing canopy size, defoliation–yield loss relationships, and defoliation–glycoalkaloid levels. As a practical starting point, results in this study suggest that setting an insect defoliation threshold based on insect densities sufficient to cause 30 to 40% would help reduce unnecessary insecticide use while providing an ample cushion against yield or quality loss.

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