Letter to the Editor

Defoliation, Disease, and Growth: A Reply

Kenneth B. Johnson

Department of Plant Pathology, University of Minnesota, St. Paul 55108.

In their recent letter, Waggoner and Berger (19) proposed methods to analyze disease-induced crop yield losses using the integrals of healthy leaf area duration (HAD) and of the related variable, healthy leaf area absorption of solar radiation (HAA). Their examples demonstrate the usefulness of this approach to understand crop yield. The recent work of Haverkort and Bicamumpaka (6) in Africa on potato late blight (*Phytophthora infestans* (Mont.) de Bary) is another excellent example of the relationship between HAA and yield.

The purpose of this letter is not to disagree with the findings of Waggoner and Berger, but to build on and unify concepts presented both by these authors and others who have been interested in the mechanistic basis of pest- and disease-induced crop loss. Implications of radiation interception and efficiency of its use are discussed in relation to crop productivity, damage functions caused by pests, and the problem of understanding the effects of multiple pests on crop yield.

Crop productivity. Solar radiation interception (RI) (megajoules per square meter) by green leaf area, i. e., the variable integrated to give HAA (19), and radiation use efficiency (RUE) (grams per megajoule) were by used Monteith (15) as factors in equation for analyzing crop productivity in Great Britain. Crop productivity (grams per square meter) was the product of RI · RUE.

As illustrated by Waggoner and Berger, RI generally is a function of leaf area index (LAI, i.e., square meters of leaf tissue per square meter of land) that follows Beer's law (Fig. 1). The effect of this relationship on crop productivity is twofold. First, for crops with known LAI growing at a relatively constant RUE, total dry matter production can be estimated by integrating the LAI-RI relationship over a season. Second, and important to plant pathologists interested in disease effects on yield, as crop LAI increases, portions of leaf area may be lost without greatly affecting RI. If we use Figure 1 as an example, a crop with an LAI of 3 will intercept about 92% of the radiation of a crop with an LAI of 4. At higher LAIs, differences in radiation interception diminish even further.

RUE is the second factor regulating productivity. For many crops, including apples, beets, potatoes, and barley, the value of this efficiency factor in well-watered and unstressed situations is approximately 1.4 g of dry matter per megajoule of total radiation intercepted (15), or approximately 2.8–3.2 g/MJ of photosynthetically active radiation (PAR) (12). (These values represent solar energy conversion efficiencies of 2.4–2.9% [15,22].) Temperature, CO_2 concentration, water stress, nutrition, tissue age, biotic diseases, and air pollutants are all variables that may influence RUE. Combined effects of the above variables on RUE may be additive, multiplicative, or governed by Liebig's Law of the minimum (20). Examples of how these variables are combined are given in many crop growth simulators (2,9,10,14,17).

HAA, HAD, and yield. For the diseases and crops they chose, Waggoner and Berger (19) successfully demonstrated use of HAD and HAA to estimate harvested yield. HAA gave linear relationships with yield and HAD curvilinear because of the Beer's law relationship between RI and LAI. It should be noted that in contrast to HAA, HAD cannot discern between high LAI for short duration and low LAI for long duration.

An impression left by the Waggoner and Berger letter was that knowledge of the amount of solar radiation intercepted by the green portion of a crop canopy is all that is needed to predict crop loss. For many pests and diseases, this may be so, but, as discussed below, for some it may not. Their letter singles out logic faults in the area under the disease progress curve (AUDPC) variable, but simple models based on HAA may also have similar faults. Used over an entire season, HAA yield loss models may not account for different tissue partitioning ratios or source-sink relationships at different stages of crop growth. Consequently, restriction of HAA models only to the period when the harvested portion is rapidly developing may be necessary (3,7).

Although very precise relationships have been obtained between the integral of RI and total dry matter production (1,12,15,18,22), relationships between RI and the amount of dry matter in the grain or tuber are usually less refined (1,12,18). Varying harvest indexes (i.e., proportion of total dry matter harvested), crop growth strategies, and interactions between growth and development are factors that affect RI relationships with harvested yield (4,5,18). Relationships between HAA and yield should probably be studied in conjunction with more traditional analyses of disease effects on components of yield (3–5).

RI, RUE, and pest damage. Boote et al (2), in a widely cited paper, categorized pest effects on plant growth into seven groups: tissue consumers, leaf senescence accelerators, stand reducers, light stealers, photosynthetic rate reducers, assimilate sappers, and turgor reducers. They did this to develop strategies for coupling pest effects to detailed crop growth simulators. However, if their categories are examined closely, an argument can be made for grouping the pest effects into two larger groups representing major effects on RI (the first four) and major effects on RUE (the last three). (Of course, some pests affect both RI and RUE.)

Given these two general effects of pests on crop growth, it may be possible to develop concepts that are useful to crop loss assessment and pest management. For example, in Figure 2 are two damage functions developed from experimentation with a simple potato growth model (9,10). This model uses an RI · RUE approach and is driven by solar radiation and temperature (9). The upper curve (Fig. 2A) represents percent loss of final tuber yield from defoliation of older leaf tissue at midseason. The effect on the potato crop is a reduction in RI and is not dissimilar to diseases causing premature leaf senescence such as early blight caused by *Alternaria solani* (Ell. & Mart.) Jones & Grout. Again, because of the Beer's law relationship between LAI and RI, the initial yield reduction is small at low to moderate levels of defoliation. At higher levels of defoliation, the yield loss response is greater.

The second curve (Fig. 2B) is the damage function that results from feeding of the potato leafhopper, *Empoasca fabae* (Harris) at midseason. While feeding, the potato leafhopper injects a toxic substance into leaf tissue that greatly reduces net photosynthesis (13,21). For a period of time the leaves remain green and symptomless, but after prolonged feeding (usually, several weeks), a marginal necrosis of leaves termed "hopperburn" occurs. The

major effect of potato leafhopper feeding is reduction of RUE in photosynthetically active tissues (10). The yield loss response with increasing potato leafhopper populations is greatest at low densities and the rate of response diminishes at higher insect densities.
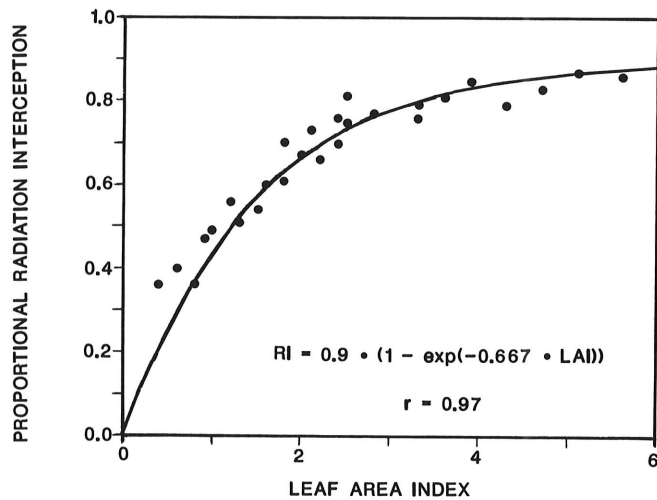

Fig. 1. The relationship between leaf area index and proportion of solar radiation intercepted in potato. Data are from Allen and Scott (1). The equation was fit by the author.
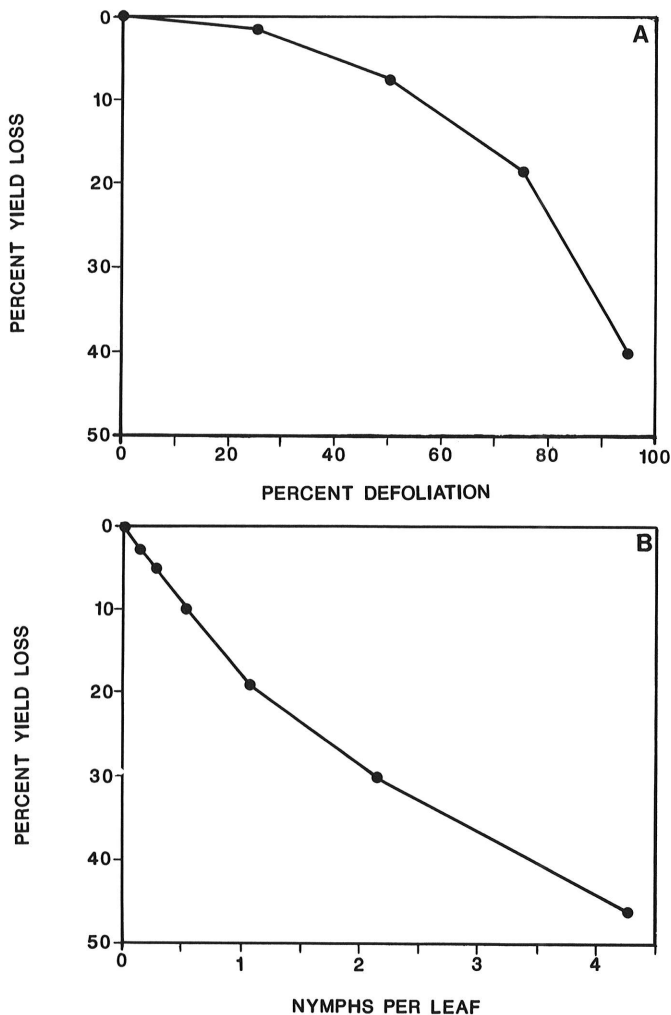

Fig. 2. Percent loss of final tuber yield resulting from two kinds of injury in a simulated potato crop (9). **A,** One-time defoliation of older leaf tissue at midseason (8). **B,** Feeding of potato leafhopper nymphs over a period of approximately 1 mo at midseason (10).

The shapes of the damage curves in Figure 2 have been termed type I (Fig. 2B) and type II (Fig. 2A) (16). The amount of damage at low pest or disease densities distinguishes the two curves; thus, on a relative scale, economic thresholds for the two types of damage curves are distinctly different (16). In general, for pests affecting foliage of crops attaining moderate to high LAIs, those influencing RI probably will show type II damage functions. Conversely, those pests influencing primarily RUE will have damage functions more like the type I curve.

RI, RUE, and multiple pests. In demonstrating the usefulness of HAA and HAD, Waggoner and Berger (19) used a portion of the results of an analysis made to relate disease and defoliation ratings to yield of potato (11). The study was a factorial experiment with multiple levels of early blight, potato leafhopper, and Verticillium wilt caused by *Verticillium dahliae* Kleb. The variable correlated with yield was area under the proportion of green leaf area remaining curve (AUGLAC), which was defined as the integral of [(1 − defoliation)·(1 − [early blight + hopperburn])]. As Waggoner and Berger reported, AUGLAC was correlated with yield ($r = 0.8$); but, this was not the complete conclusion.

When the relationship between yield and AUGLAC was analyzed separately for each pest, significant correlations still existed, but the slopes of regressions of yield on AUGLAC were dependent on the specific pest (Fig. 3). Early blight and Verticillium wilt, both of which reduce RI by prematurely senescencing older leaf tissues, had similar slopes. In contrast, the average slope obtained from regressing yield on AUGLAC across potato leafhopper treatments was approximately three times greater because of reduction of RUE by the potato leafhopper in green leaf tissues. Without hopperburn and some premature senescence causing a reduction in AUGLAC at high leafhopper populations, the slope of the relationship between yield and AUGLAC across potato leafhopper treatments would have been vertical or undefined.

Conclusion. Crop productivity defined as the product of RI · RUE provides a framework for understanding pest- and disease-
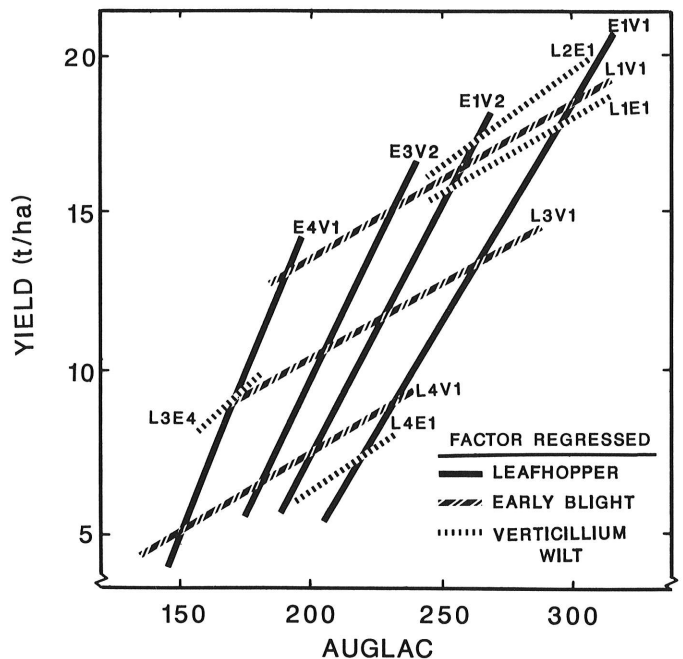

Fig. 3. Results of regression of total yield on area under the proportion of green leaf area remaining curve (AUGLAC) for Russet Burbank potato in a factorial experiment involving multiple infestations of early blight (E), Verticillium wilt (V), and potato leafhopper (L). Regressions were done separately on subsets of each pest factor. A subset was defined as all plots of a particular pest factor that were related by having similar infestations of the other two pests. Labels in the figure indicate the relative infestation levels of the other two pests for each subset. Low pest infestation levels = 1. Data are from Johnson et al (11).

induced reductions in yield. Pest and disease effects on crop growth can be categorized into effects on RI and effects on RUE. Integrals such as HAA are very useful but may be best understood in conjunction with conventional analyses of pest and disease effects on components of yield. Analyzing pest-induced yield loss in terms of RI and RUE provides a conceptual basis for understanding damage functions and may lead to testable and valid models for the effects of multiple pests on crop growth and yield.

LITERATURE CITED

1. Allen, E. J., and Scott, R. K. 1980. An analysis of growth of the potato crop. J. Agric. Sci. Camb. 94:583-606.
2. Boote, K. J., Jones, J. W., Mishoe, J. W., and Berger, R. D. 1983. Coupling pests to crop growth simulators to predict yield reductions. Phytopathology 73:1581-1587.
3. Carver, T. L. W., and Griffiths, E. 1981. Relationship between powdery mildew infection, green leaf area, and grain yield of barley. Ann. Appl. Biol. 99:255-266.
4. Gaunt, R. E. 1980. Physiological basis of yield loss. Pages 98-111 in: Crop Loss Assessment, Proceedings of the E. C. Stakman Commemorative Symposium. P. S. Teng, and S. V. Krupa, eds. Univ. Minn. Agric. Exp. Stn. Misc. Publ. 7.
5. Gaunt, R. E. 1987. A mechanistic approach to yield loss assessment based on crop physiology. Pages 150-159 in: Crop Loss Assessment and Pest Management, P. S., Teng, ed. The American Phytopathological Society, St. Paul, MN.
6. Haverkort, A. J., and Bicamumpaka, M. 1986. Correlation between intercepted radiation and yield of potato crops infested by *Phytophthora infestans* in central Africa. Neth. J. Plant Pathol. 92:239-247.
7. Hooker, A. L. 1979. Estimating disease losses based on the amount of healthy leaf tissue during the plant reproductive period. Genetika 11:181-192.
8. Johnson, K. B., Conlon, R. L., Adams, S. S., Nelson, D. C., Rouse, D. I., and Teng, P. S. 1987. Validation of a simple potato growth model in the north central United States. Am. Pot. J. (in press).
9. Johnson, K. B., Johnson, S. B., and Teng, P. S. 1986. Development of a simple potato growth model for use in crop-pest management. Agric. Sys. 19:189-209.
10. Johnson, K. B., Teng, P. S., and Radcliffe, E. B. 1987. Coupling feeding effects of potato leafhopper, *Empoasca fabae*, nymphs to a model of potato growth. Environ. Entomol. 16:250-258.
11. Johnson, K. B., Teng, P. S., and Radcliffe, E. B. 1987. Analysis of potato foliage losses caused by interacting infestations of early blight, Verticillium wilt, and potato leafhopper; and the relationship to yield. Z. Pflanzenkr. Pflanzenschutz. 94:22-33.
12. Khurana, S. C., and McLaren, J. S. 1982. The influence of leaf area, light interception, and season on potato growth and yield. Potato Res. 25:329-342.
13. Ladd, T. L., and Rawlins, W. A. 1965. The effects of the feeding of the potato leafhopper on photosynthesis and respiration in the potato plant. J. Econ. Entomol. 58:623-628.
14. Loomis, R. S., and Adams, S. S. 1983. Integrative analyses of host-pathogen relations. Annu. Rev. Phytopathol. 21:341-362.
15. Monteith, J. L. 1977. Climate and the efficiency of crop production in Britain. Philos. Trans. R. Soc. London 281:277-294.
16. Mumford, J. D., and Norton, G. A. 1987. Economics of integrated pest control. Pages 191-200 in: Crop Loss Assessment and Pest Management. P. S. Teng, ed. The American Phytopathological Society, St. Paul, MN.
17. Ng, E., and Loomis, R. S. 1984. A simulation of growth and yield of the potato crop. Simulation Series Monographs, PUDOC, Wageningen, The Netherlands.
18. Shibles, R. M., and Weber, C. R. 1966. Interception of radiation and dry matter production by various soybean planting patterns. Crop Sci. 6:55-59.
19. Waggoner, P. E., and Berger, R. D. 1987. Defoliation, disease, and growth. Phytopathology 77:393-398.
20. Waggoner, P. E., Norvell, W. A., and Royle, D. J. 1980. The law of the minimum and the relation between pathogen, weather, and disease. Phytopathology 70:59-64.
21. Walgenbach, J. F., and Wyman, J. A. 1985. Potato leafhopper feeding damage at various potato growth stages. J. Econ. Entomol. 78:671-675.
22. Williams, W. A., Loomis, R. S., and Lepley, C. P. 1965. Vegetative growth of corn as affected by population density. I. Productivity in relation to interception of solar radiation. Crop Sci. 5:211-215.