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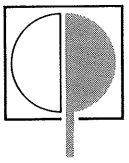

Effect of beet yellowing viruses on light interception and light use efficiency of the sugarbeet crop

K. J. de Koeijer and W. van der Werf*

Wageningen Agricultural University, Department of Theoretical Production Ecology, P.O. Box 430, 6700 AK Wageningen, The Netherlands

We monitored the development of ground cover by green and yellow leaves in healthy sugarbeet and in sugarbeet infected with beet mild yellowing virus (BMYV) and beet yellows virus (BYV). Infection with BMYV reduced light interception by green foliage by up to 40%, due to leaf yellowing. Infection with BYV reduced light interception by green leaves by up to 55%, due to 50% cover by yellow leaves and decreased total (green + yellow) ground cover. Dry matter accumulation was regressed against cumulative light interception by green foliage to estimate light use efficiency of the visually unaffected foliage. Healthy and BMYV infected sugarbeet had similar light use efficiencies, indicating that yield loss can be entirely attributed to interception of solar energy by yellow, unproductive foliage. Infection with BYV decreased light use efficiency. The results show that yield losses caused by yellowing viruses can be assessed by monitoring the disease-induced reduction in ground cover by green leaves.

Keywords: beet yellows virus; closterovirus; beet mild yellowing virus; luteovirus; damage assessment; yield loss model; ground cover

Yellowing viruses affect sugarbeet crops worldwide. In Europe, two taxonomically distinct viruses are responsible for the disease: beet yellows virus (BYV), belonging to the closterovirus group, and beet mild yellowing virus (BMYV), belonging to the luteovirus group. BYV causes reductions in sugar production up to 60% when all plants are infected in the seedling stage (Smith and Hallsworth, 1990). BMYV causes reductions in sugar production up to 35%. Both viruses are transmitted by aphids, predominantly the green peach aphid, *Myzus persicae*. Epidemics are often localized on a regional scale and depend upon conditions favouring early and widespread primary crop infection and/or extensive secondary spread (Jepson and Green, 1983; Harrington, Dewar and George, 1989; Dewar and Reed, 1991; van der Werf *et al.* 1992).

BYV and BMYV are transmitted in the semi-persistent and persistent manner, respectively (Duffus, 1973). In sugar beet, the virus is transported from the inoculated leaf within a few days. Symptoms develop in all leaves that grow and are sinks after the virus becomes systemic. Leaves do not show yellowing symptoms until they reach maturity. From old to young, three categories of leaves occur on infected beet plants: (1) old leaves that are healthy and green, because they were full grown before the virus became systemic; (2) leaves of intermediate age that have acquired the virus through the vascular system and show symptoms; (3) young leaves that are systemically infected but have not developed symptoms (van der Werf, Bonnier and Peters, 1989). Young leaves on infected plants have similar rates of photosynthesis as young leaves on healthy plants (de Koeijer, unpublished results), while the photosynthetic capacity in infected leaves diminishes as symptoms develop (van der Werf, 1988). Healthy old leaves on infected plants have unaffected rates of photosynthesis, but they will often be covered by younger leaves, and hence receive little light.

Crop loss assessment is an important component of plant disease management (Zadoks and Schein, 1979). An assessment method estimates final (expected) reduction in quantity or quality of harvested product on the basis of variables that can be observed before harvest. The crucial element of any assessment method is a mathematical model that relates observed variables to yield loss. Such a mathematical model can be a descriptive regression model or a more or less complex dynamic model, integrating crop physiological processes.

One approach to crop loss assessment is based on the more or less linear relationship that is often found between cumulative radiation interception by field crops and dry matter production (Monteith, 1977; Steven *et al.*, 1986):

$$Y = \int_{t_s}^{t_h} E f I \, dt.$$

Here, Y is total dry matter at harvest (g m^{-2}), I is the daily incoming photosynthetically active radiation (PAR) m^2 (ground surface) per day (MJ m^{-2} day^{-1}), f is the fraction of incoming PAR intercepted by leaf canopy, E is crop light use efficiency (g MJ^{-1}), t_s is

*Author to whom correspondence should be addressed.

sowing date (day of the year) and t_h is harvesting date (day of the year). Crop light use efficiency, E, is in the order of 3.0 g (dry matter) MJ^{-1} (PAR) for well managed crops. Spitters (1990) used the acronym LINTUL to characterize the class of descriptive crop growth models based on the above equation, from Light INTerception and UtiLization. The fraction PAR intercepted by leaves, f, can be described as a function of leaf area index, but it can also be determined directly in the field by estimating ground cover. Methods for quantifying ground cover include direct visual assessment and measurement of infra-red reflectance (Burstall and Harris 1983; Haverkort *et al.*, 1991). LINTUL models have been successfully used to describe yield loss due to fungal leaf diseases which kill portions of the leaves, e.g. peanut leaf spot, caused by *Cercosporidium personatum* and by *Cercospora arachidicola* (Waggoner and Berger, 1987) and potato late blight, caused by *Phytophthora infestans* (Haverkort and Bicamumpaka, 1986). These diseases reduce the fraction interception f as a result of the necrosis of infected leaf tissue. Crop light use efficiency is unaffected.

Yield reduction by yellowing viruses could be estimated with a LINTUL model that disregards radiation interception on yellow leaf area if photosynthetic assimilate production and assimilate demands of such leaves are negligible (although not zero). BYV and BMYV-infected leaves with clear symptoms have indeed very low or even negative rates of photosynthesis (van der Werf, 1988; van der Werf, unpublished results). Using a crop physiological model to investigate the importance of injury mechanisms, it was concluded that three factors account for 90% of the yield loss caused by BYV: (1) reduced LAI, resulting in lowered radiation interception; (2) reduced absorptivity of yellow leaves, increasing the scatter of radiation to sky and soil; (3) severe reduction (up to 100%) of photosynthesis in yellow leaves (Rossing *et al.*, 1992). The last factor was by far the most influential. In theory, these three factors can be accounted for in a LINTUL model in which the radiation intercepted by green foliage is accumulated. The purpose of the work described in this paper is to investigate the applicability of this approach for the assessment of yield losses caused by BYV and BMYV in sugarbeet.

Materials and methods

Field experiments were carried out at two locations in 2 years. In the first experiment, carried out in Voorthuizen (NL) in 1989, light interception and dry matter production were monitored in healthy sugarbeet and in sugarbeet infected with either BYV or BMYV. The results of this experiment were used to estimate crop light use efficiency for the three categories of sugarbeet. If the LINTUL-based crop loss assessment model is valid, the three treatments would yield similar estimates of crop light use efficiency. In the second experiment, carried out in Wageningen in 1993, radiation interception by green leaf canopy and dry matter accumulation were monitored in healthy sugarbeet and in sugarbeet infected with BMYV. The results of this experiment were used to validate the LINTUL model parametrized with the 1989 data.

Experiment 1: Parameter estimation

The experiment in Voorthuizen was carried out in a sugarbeet crop cv. Univers on sandy soil, sown on 24 May 1989 at a row distance of 50 cm to a stand of 100,000 plants ha^{-1}. The sowing date was exceptionally late because the original experimental field had to be abandoned because of herbicide damage. Treatments consisted of (A) control, (B) inadvertent infection mainly with BMYV, (C) inoculation with BMYV on 8 June 1989 (cotyledon stage), (D) inoculation with BYV on 9 June 1989 (cotyledon stage) and (E) inoculation with BYV on 27 June 1989 (six–seven leaf stage).

Some plants in the control plots became infected (mostly with BMYV), due to natural spread. These plots were included in the monitoring and analysis (treatment B). On 15 August substitute control plots (treatment A) were laid down within the same field just outside the original experimental area. It is assumed that the substitute plots had the same canopy development before 15 August as the original control plots. Other cross infections were negligible. Treatments were replicated in five plots (but one plot of treatment C was discarded after the first harvest). The main plots were 7.5 m long and 5 m wide across the rows. Subplots of 2 m row length across six rows were harvested periodically.

Inoculations. Viruliferous *Myzus persicae* were reared on virus-infected sugarbeet in the glasshouse. BYV and BMYV were maintained in sugarbeet in separate glasshouses. Inoculations were made by transferring three to five viruliferous *M. persicae* to each plant in a plot, using a paint-brush. Four days after inoculation, the field was sprayed with the aphicide pirimicarb (0.5 kg ha^{-1}).

Assessment of ground cover. The percentage cover by green leaves, yellow leaves and bare soil were determined twice a week in each plot. We used a 1 × 0.5 m frame, subdivided by wires in two hundred square cells of 5 × 5 cm, to obtain reproducible visual assessments of the percentages cover. For the one or two *least* prevalent categories of cover, we counted the number of squares occupied. Scattered patches, too small to cover an entire grid cell, were added together. The final cumulative number of wholly occupied grid cells out of two hundred on the whole frame yields the percentage cover for a given category. Percentage cover by the most prevalent category (e.g. bare soil in early season or green leaf area in a well developed canopy), was estimated by subtraction from 100. (Sometimes it was estimated independently for checking purposes.) Leaf cover was classified as yellow when symptoms were clearly visible from *ca* 1 m viewing distance. Thus the yellow leaf category included intermediate shades between green and yellow. In a few pilot studies, we found that observer bias and estimation error were acceptable (rarely greater than 5%), despite the arbitrary classifications that are necessary when leaf tissue is in a transition from green to yellow. Often, especially later in the season, only a minority of leaf tissue is in such a transition. The percentage cover estimated in this way was equated with proportion radiation interception. Treatment differences were

analysed with analysis of variance, applying a variance stabilizing log transformation when appropriate, and using the multiple range test of Ryan *et al.* for multiple comparisons. These analyses were done with procedure GLM of Statistical Analysis System (SAS), version 6, for VAX (SAS Institute Inc., 1989).

Cumulative light interception, dry matter production and crop light use efficiency. Daily global radiation data were obtained from the Wageningen Agricultural University meteorological station, located 30 km from the experiment. Incoming PAR was calculated as 0.5 × global radiation (Monteith, 1977). Cumulative intercepted PAR was calculated by summing up daily products of incoming PAR and interpolated green cover fraction. Harvests were made on 17 July and on 5 and 25 September. Crop light use efficiency, E, was determined in two ways. First, by calculating the ratio between final dry matter production and PAR intercepted on green leaves for each plot. Second, by regressing total dry matter against cumulative light interception by green foliage, using SAS procedure REG, option NOINT. We forced the regression line through the origin, because theoretically dry matter accumulation and leaf canopy growth start at the same time. Because no ground cover data were taken in treatment A before 15 August, these plots were omitted when calculating the regression coefficients.

Experiment 2: Model validation

The validation experiment was carried out in a sugarbeet crop cv. Univers on river clay soil near Wageningen, sown on 30 March 1993 at a row distance of 50 cm to a stand of 120,000 plants ha^{-1}. Treatments were made in four repetitions: (A) healthy control, (B) inoculation with BMYV on 15 June 1993 (25–30 leaf stage; canopy closed) and (C) inoculation with BYV on 16 June 1993.

Periodic harvests were made on 2 and 30 August and on 27 September. Proportions ground cover and intercepted PAR were determined as in Experiment 1.

Results

Experiment 1: Parameter estimation

Fifty per cent emergence was on 4 June (day 155). Ground cover remained below 10% during June in all treatments. Ground cover in the control (*Figure 1A*) increased to 90% at the end of July, reaching values close to 100% from 10 August onwards. Total ground cover (green + yellow) in the inadvertently-infected plots (*Figure 1B*) and in the BMYV-inoculated plots (*Figure 1C*) was very similar to that in the control treatment. Total ground cover was slightly delayed in the two BYV treatments (*Figures 1 D, E*) which showed similar courses of green, yellow and total ground cover. Total ground cover in the treatments A, B and C stabilized around 98%, while in the BYV treatments D and E, total cover stabilized at a significantly lower value of ±94%. Averaged over the period 15 August–20 September, total ground cover (± standard error of the mean) amounted to 98.7 ± 0.14, 98.2 ± 0.05, 98.6 ± 0.17, 93.2 ± 0.85 and 94.7 ± 0.86 in the treatments A–E, respectively. Significant differences at the 5% level exist between the groups (A, B, C) and (D, E) but not within these groups, according to Ryan *et al.* multiple range test, using the logarithm of the fraction bare soil as dependent variable in the analysis.

In the BYV treatments (D, E) ground cover by yellow leaves developed from mid July, slightly earlier and/or in larger proportions than in treatments B and C. Throughout the season, BYV-infected plots had about 11% more ground covered by yellow leaves than the BMYV treatment (C). The proportion ground cover by yellow leaves stabilized around 50% in both BYV treatments and just below 40% in treatment C. The overall effect of all treatments on the integral of light intercepted by green leaf area was large. Cumulative interception of light by green foliage in the respective treatments A–E was 950 ± 16 (n = 5), 860 ± 19 (4), 840 ± 22 (5), 630 ± 50 (5) and 670 ± 22 (5) MJ (PAR) m^{-2}. Yellow ground cover in the five treatments in the period 1 August–20 September averaged 0, 18.8 ± 2.8, 19.0 ± 2.0, 31.8 ± 1.6 and 32.3 ± 0.7%. Significant differences at the 5% level exist between the groups (A), (B, C) and (D, E) but not within these groups, according to Ryan *et al.* multiple range test.

At final harvest the control plots yielded 1.6 ± 0.04 kg (dry matter) m^{-2} of which 0.78 ± 0.02 kg was storage root. In the treatments B–E, the total yields were respectively 1.4 ± 0.05, 1.4 ± 0.05, 1.0 ± 0.05 and 0.9 ± kg (dry matter) m^{-2}. The relative reductions in the B, C, D and E treatments were 14, 13, 44 and 40%, respectively for total biomass and 21, 23, 55 and 56% for root biomass.

Average values per treatment for the ratio of total dry matter production to total PAR intercepted on green leaves were 3.27 ± 0.13, 3.35 ± 0.12, 2.87 ± 0.10 and 2.88 ± 0.04g MJ^{-1} in treatments B, C, D and E, respectively. Significant differences exist between the groups (B, C) and (D, E) but not within these groups. Linear regression of dry matter against intercepted PAR for all observations during the season of the combined treatments B and C (n = 28) and the combined treatments D and E (n = 30) yield crop light use efficiencies of 3.34 ± 0.054 g MJ^{-1} and 2.85 ± 0.027 g MJ^{-1}, respectively. The relationship between yield and light interception in control treatment A (open circles in *Figure 2*) conforms to the regression line for the BMYV-infected plots B and C. These results indicate that healthy and BMYV infected sugarbeet have the same crop light use efficiency, while the efficiency is about 15% lower in BYV infected sugarbeet.

Experiment 2: Model validation

The BYV inoculation was not successful, rendering this treatment unsuitable for analysis. Date of 50% emergence was 24 April (day 114). Ground cover reached 10% by mid May and 90% by mid June (*Figure 3*). Total (green + yellow) ground cover had a plateau of about 95%. In the BMYV-infected plots, ground cover by yellow leaves started to develop in late June and increased gradually until it reached 39% at the end of September. The reduction of cumulative intercepted PAR was less than 1% on 2 August, 7% on 30 August and 11% at 27 September. The corresponding reduc-

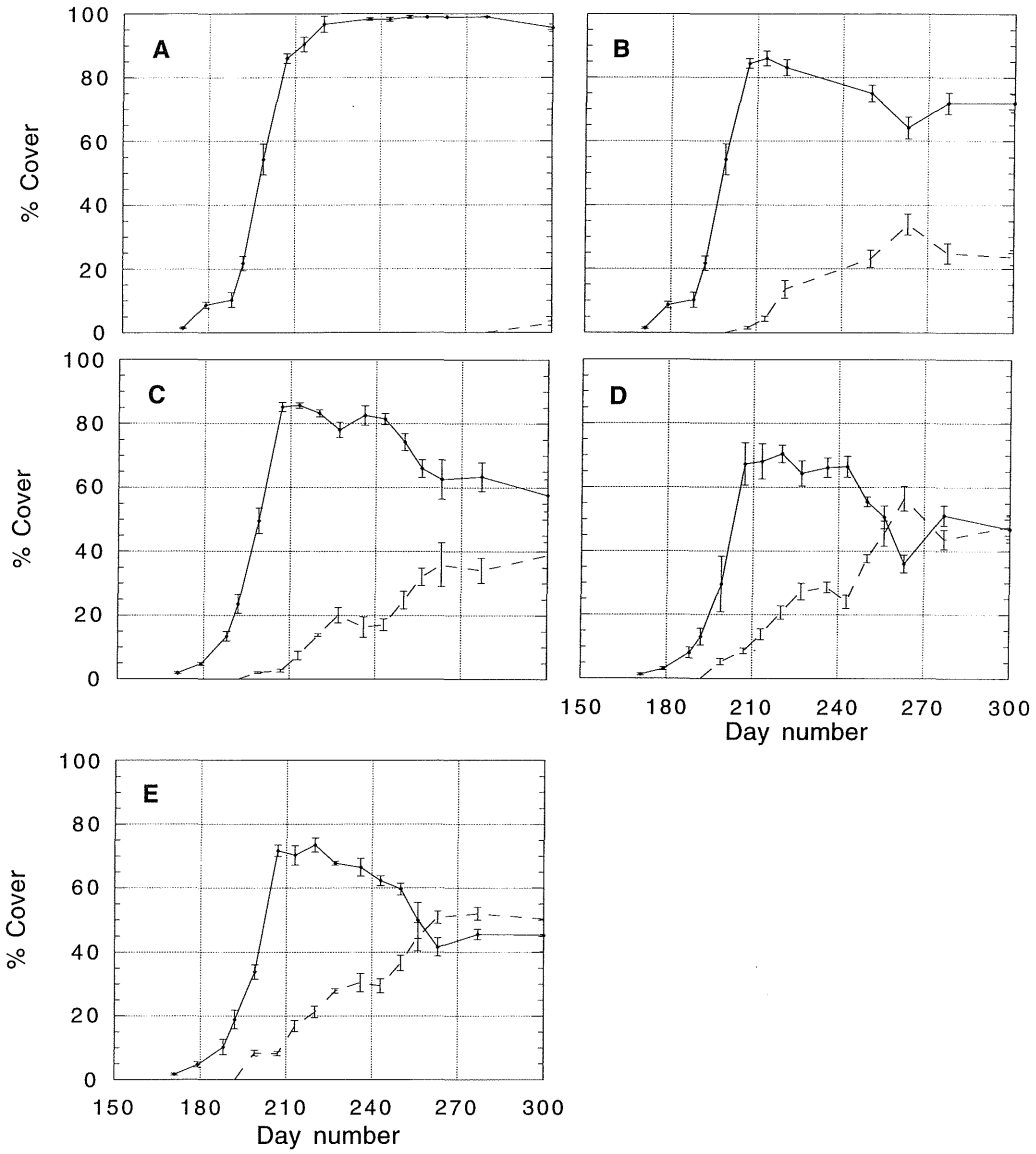

Figure 1. Seasonal course of sugarbeet ground cover with green leaves (——) ± standard error of the mean (SEM) and with yellow leaves (– – – –) ± SEM, in five treatments in Experiment 1. Treatments: (A) control; (B) inadvertent infection with BMYV (beet mild yellowing virus); (C) inoculation with BMYV on 8 June; (D) inoculation with BYV (beet yellows virus) on 9 June; (E) inoculation with BYV on 27 June. The time axis is divided in 30 day periods that broadly correspond to the months of June (day number 152–181), July (182–212), August (213–243), September (244–273) and October (274–304).

tions of total biomass on these dates were 0, 10% and 27% (*Figure 4*). The data points of Experiment 2 conform to the regression line (E = 3.34 g MJ^{-1}) for the control and BMYV treatments determined in Experiment (*Figure 4*) except for the final yield in the BMYV inoculated plots, which deviated significantly. Part of this deviation may be explained by rapid leaf senescence, possibly as a result of wet weather in combination with secondary parasites, such as *Alternaria* spp. (Russell, 1964), which are common on BMYV infected leaves. During September, leaf biomass in the BMYV infected plots decreased from 0.29 ± 0.046 kg m^{-2} to 0.22 ± 0.015 kg m^{-2}.

Discussion

The assessment of yield losses due to yellowing viruses in sugar beet has a history of at least 50 years. The first quantitative work was done by Watson, Watson and Hull (1946) in England. Their method was formally described and advocated by Heathcote, Russell and van Steijvoort (1973). It uses the concept of infected plant weeks (IPWs). These are defined as the integral of the proportion of plants showing symptoms over time during the growing season. For instance, one IPW is accumulated when all the plants of a crop show *symptoms* during 1 week, or when 50% of the crop show symptoms during 2 weeks. Estimates of yield loss per IPW are about 1.5% for BMYV, 1.5–3% for BYV, and about 3–4.5% when the viruses occur together in plants (Heathcote *et al.*, 1973; Heijbroek, 1988).

Heijbroek (1988) criticized the IPW concept, observing that yield loss per IPW decreases with later infection in field trials. The most likely explanation for this phenomenon is that later infected plants show symptoms on a smaller proportion of their total leaf area and hence incur smaller reductions in their growth

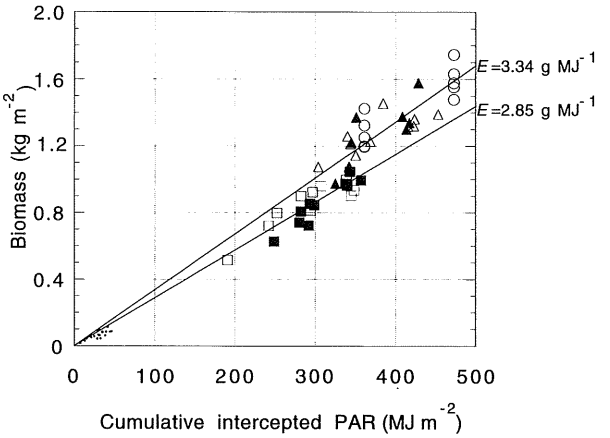

Figure 2. Relationship between total biomass and cumulative intercepted photosynthetically active radiation (PAR) by green leaves up till three consecutive harvest dates in five treatments in Experiment 1. Treatments: A (circle): control; B (open triangles): inadvertent BMYV infection; C (solid triangles): BMYV inoculation on 8 June; D (open squares): BYV inoculation on 9 June; E (solid squares): BYV inoculation on 27 June. Yields at first harvest are indicated as dots, near the origin. The two lines represent the linear regressions forced through the origin of treatment B, C (upper line) and treatment D, E (lower line). Points for control treatment A correspond to the regression line for treatments B and C.

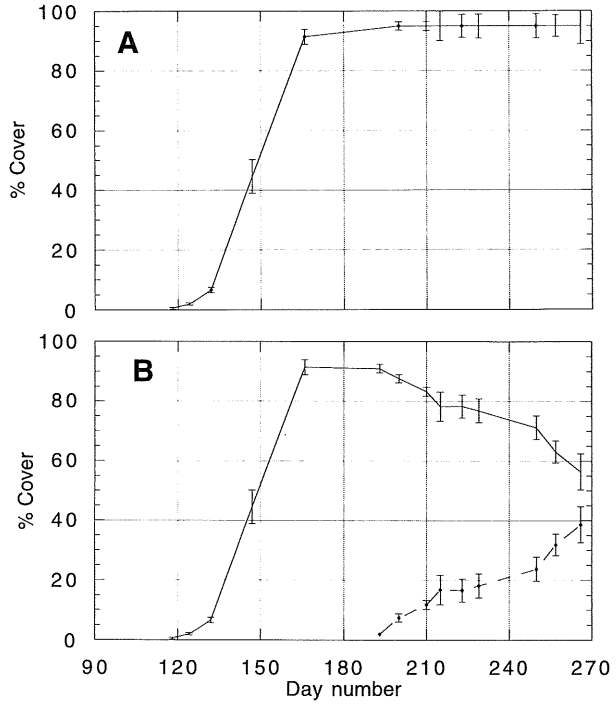

Figure 3. Seasonal course of ground cover of sugarbeets with green leaves (——) ± SEM and with yellow leaves (– – – – –) ± SEM in Experiment 2. Treatments: (A) control; (B) inoculation with beet mild yellowing virus on 15 June.

rate than earlier infected plants (van der Werf, Kempenaar and Peters, 1989). Heijbroek (1988) advocated the use of curvilinear relationships between infection date and yield loss for crop loss assessment. Unfortunately, these relationships are difficult to apply in practice because infections occur over an extended period in farmers fields and these dates are difficult to determine retrospectively (van der Werf *et al.*, 1989a).

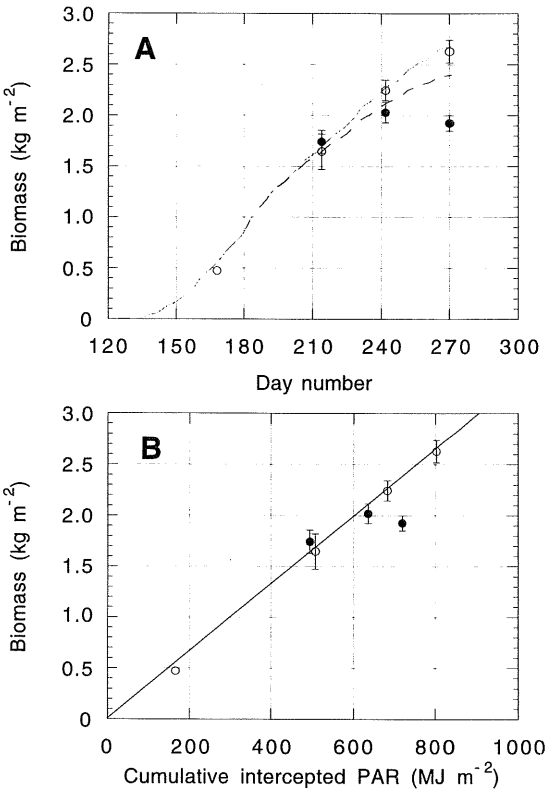

Figure 4. Growth of total biomass in two treatments in Experiment 2 as a function of time (A) and as a function of cumulative photosynthetically active radiation (PAR) intercepted by green leaves (B). Treatments are: control (open circles) and inoculation on 15 June with BMYV (solid circles). Lines (control: ——; BMYV: – – – – –) are calculated with the LINTUL model, using a crop light use efficiency of E = 3.34 g (total dry matter) MJ^{-1} (PAR intercepted on green cover). The value of E was estimated independently in Experiment 1.

Another complicating factor is that the relationship between infection date and yield loss depends on crop development stage and sugarbeet variety (Smith and Hallsworth, 1990).

Scott and Jaggard (1985) used a LINTUL model to assess yield reduction by yellowing viruses. They observed that crop light use efficiency was reduced by about 20% in sugarbeet infected with yellowing viruses. In the calculation of light interception, they included all the leaves, green and yellow. Our results indicate that the size of the reduction of E depends on the earliness of the infection when light interception is measured in this way, because later infected plants develop symptoms on a smaller proportion of their leaf area.

The method described in this paper has a number of advantages over the older methods. (1) Unlike the IPW method, it does *not* overestimate damage due to late infections, because the relatively small extent of yellowing symptoms on late-infected plants is accounted for by using green cover as an input to the model. (2) Unlike the approaches advocated by Heijbroek (1988) and Scott and Jaggard (1985), it avoids the difficult, tedious and time-consuming estimation of infection dates (3). It may be capable of taking account of the influence of environmental conditions and the genotypes of sugar beet and virus on the severity of symptoms. It has been observed (Björling, 1961, 1963; Smith and Hallsworth, 1990) that yield loss and severity of symptoms are correlated. The present green leaf

based LINTUL model predicts that beet variety–virus strain interactions that have a small effect on green leaf cover, will have little effect on yield. This prediction can be tested. Some requirements of the new method can also be mentioned. (1) It requires monitoring of green leaf cover over the whole of the growing season. When early observations are missing, damage estimates will become less reliable. (2) It requires skillful (although fairly easy to learn) assessments of leaf cover, using a grid or other instrument to enable consistent and reproducible estimates.

The LINTUL model may provide a useful tool for damage assessments at the field or regional level. To estimate yield loss in a given field, data collection must start as early as possible and a spatial sampling plan must be worked out to cover the crop in a representative manner, taking account of the patchy distribution of virus-infected plants. A logical procedure would be stratified sampling in which proportions of crop area covered with yellow patches is estimated and the percentage of green ground cover in and outside patches. When taking ground cover measurements, it is very important to use the right spatial resolution. At large spatial scales, as on aerial photographs, infected plots look like entirely yellow patches, but at a finer resolution green soil cover in these patches may still appear to be as high as 50%. The present LINTUL model has been developed and tested for the finer spatial resolution and cannot without appropriate adjustments be applied to data obtained at an other levels of spatial detail.

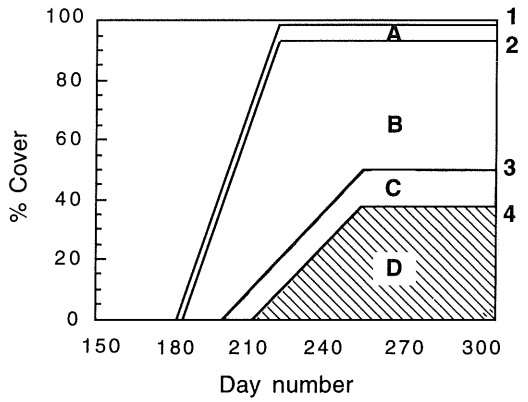

Figure 5. Summary view of the effects of beet yellows virus (BYV) and beet mild yellowing virus (BMYV) on ground cover in sugarbeet. Four lines are drawn: (1) Total ground cover of a healthy or BMYV infected crop; (2) Total ground cover of a crop with an early BYV infection; (3) Ground cover by yellow foliage in a crop with an early BYV infection; (4) Ground cover by yellow foliage in a crop with an early BMYV infection. The area A indicates the reduction in intercepted light energy due to reduced total ground cover in BYV infected sugarbeet. The area D indicates the reduction in intercepted light energy due to ground cover with yellow leaves in BMYV infected sugarbeet. The area C indicates the greater loss of light energy on yellow leaves that occurs in sugarbeet infected with BYV, compared to the loss occurring in sugarbeet infected with BMYV. Cumulative intercepted PAR is proportional to area B in the case of a BYV infection and to the sum of the areas A, B and C in the case of a BMYV infection. The greater yield loss caused by BYV is due to smaller total cover, greater cover by yellow leaves, and to a lower ratio of production to the amount of light intercepted on green foliage (light use efficiency).

Summarizing the effect of yellowing viruses on crop growth

Our observations can be summarized in a simple (and somewhat speculative) graphical model (*Figure 5*). This summary is based on the ground covers observed in Experiment 1. First, during most of the season, there was a more or less constant difference in ground cover by yellow leaves between BMYV and BYV infected plots of 11%. Second, during most of the season, there was a difference in total (green + yellow) over between BYYV and BYV infected plots of 6%. Both differences are accounted for in *Figure 5*, which shows the differences in total soil cover between BYV and BMYV infected sugarbeet during the season. In this figure, the upper line (1) indicates green cover in healthy sugarbeet. Dry matter production is proportional to the area under this line. (It is, of course, also proportional to incoming radiation, which has a seasonal course with a maximum on the longest day, 20 June.) BMYV infected sugarbeet follow also line 1 for total cover, but BYV infected sugarbeet follow line 2. Expressed verbally, BYV infected crops loose more solar energy to the soil. Lines 3 and 4 represent ground cover by yellow leaves in BYV and BMYV infected sugarbeet, respectively. BYV infected beet have a greater proportion of cover with yellow leaves. Hence, they loose more energy to this category of leaves than BMYV infected sugarbeet. Overall, production in BYV infected sugarbeet is proportional to the area B, while production in BMYV infected sugarbeet is proportional to the sum of the areas A, B and C.

Conclusions

Dry matter accumulation in healthy and BMYV infected crops is characterized by a common crop light use efficiency, $E = 3.34 \pm 0.05$ g (total dry matter) MJ^{-1} (PAR intercepted by green foliage). This implies that the light interception and utilization model satisfactorily describes the effect of infection with BMYV on dry mater production in sugarbeet.

In the 1989 experiment dry matter accumulation in BYV infected plots was characterized by a lower light use efficiency than was calculated for healthy and BMYV infected plots, so yield loss caused by BYV in sugarbeet can not be entirely attributed to a reduction of soil cover by green leaves. This conclusion is tentative because of lack of repetition over years. Further research is needed to substantiate and explain the lower crop light use efficiency observed in BYV infected plots.

The LINTUL model provides scope for retrospective assessment of damage in farmers fields. It may be made usable for prediction or tactical crop protection decision making (*sensu* Rabbinge, Rossing and van der Werf, 1993) if it is extended with a model that makes forecasts of the future development of green ground cover.

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