Time vs light: A potentially useable light sum hybrid model to represent the
juvenile growth of Douglas-fir subject to varying levels of competition

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Abstract

Substitution of potential useable light sum for time in a commonly used mensurational
equation resulted in a better fit to data from a complex vegetation management
experiment. The experiment involved Douglas fir as a crop species and a variety of
competing weed species. Site occupancy by weeds varied with time as control operations
were intermittently either included or excluded from treatments over a period of four
years. There were four randomized complete blocks of 8 weed control treatments.
Potentially useable light sum was estimated using measurements of radiation from a
meteorological station that were modified by coefficients representing the ability of the
crop plants to use light with varying soil water, vapour pressure deficit, and temperature.
Light sums were further reduced by estimated competition for light from weeds. Fits of
the model to individual plots within the experiment yielded coefficients that did not differ
significantly weed control treatments, suggesting that the model accounted for significant
variations in growth resource availability between treatments. Potentially useable light
Introduction

Forest scientists have long been aware of the importance of light (Zon, 1917), and many studies have explored the direct interception of light by competing vegetation (Cannell and Grace, 1993; Comeau et al., 1993; Yunusa et al., 1995; Richardson et al., 1996; Seo et al., 1997; Comeau et al., 1998; Richardson et al., 1999; Kimberley and Richardson, 2001; Watt et al., 2003a). Weeds also affect local growth resource availability, particularly soil water and nutrient supply (Mead et al., 1993; Richardson, 1993; Richardson et al., 1993; Yunusa et al., 1995; Richardson et al., 1996; Richardson et al., 1997; Kirongo et al., 2002; Richardson et al., 2002; Watt et al., 2003c; Watt et al., 2003a; Watt et al., 2003b; Watt et al., 2004).

Local microclimatic conditions modify crop growth by mediating light use. Net primary productivity (NPP) of a plant canopy has been found to be directly proportional to light interception (Monteith, 1977), and local microclimate affects the slope of the relationship between intercepted light and NPP. The 3-PG model explicitly represents this principle for forest crops by calculating soil water, vapour pressure deficit, temperature and fertility modifiers on use of intercepted photosynthetically active radiation (Landsberg and Waring, 1997). The 3-PG model can be expressed as:
\[
NPP = \varepsilon \sum_{t=1}^{T} \min\{f_\theta, f_D\} f_T f_F f_S
\]

Where NPP=net primary productivity, \(t=\) time interval (month), APAR=absorbed photosynthetically active radiation, \(\varepsilon=\)maximum quantum efficiency for a species, \(f_\theta=\)soil water modifier (0-1), \(f_D=\)vapor pressure deficit modifier (0-1), \(f_T=\)temperature modifier (0-1), \(f_F=\)frost modifier (0-1), \(f_S=\)senescence modifier (0-1). The model maintains a soil water balance using soil depth, soil type, rainfall, temperature, LAI and the Penman-Monteith equation for calculating evapotranspiration to calculate the soil water modifier. Most modifiers are calculated using generally understood processes, such as the logarithmic decline of stomatal conductance with increasing vapour pressure deficit. The fertility modifier is simply a number chosen by the user.

Once NPP has been estimated for a given month, the amount of photosynthate used for respiration is calculated using a constant supplied by the user, and the rest is allocated to foliage, stems or roots. Allocation coefficients are estimated from measurements of allometry, assuming that lower fertility results in increased allocation to roots. The actual proportions allocated to these pools depend on coefficients supplied by the user that make allocation vary with tree diameter at breast height.

The 3-PG model has attracted plenty of interest, but it has a few characteristics that forest mensurationists usually try to avoid. It is not path invariant (Clutter, 1963; Clutter et al., 1983), and it has many estimated parameters so that it might be fitted to the same dataset in a variety of ways and users need to fit parameters locally to sub-models so that the
model will represent any given species in a particular location. Carbon allocation is
derived from allometry, which may lead to slight biases in allocation, and estimating leaf
area index can be problematic. The senescence modifier is ad hoc, and reflects the fact
that senescence is poorly understood. In addition, it is highly recursive, so that errors
may propagate when dependent variables from one month’s simulation are used as
independent variables during the next month.

Mensurational models are precisely estimated from growth data obtained from permanent
sample plots and often represent growth and yield very efficiently, but they are highly
abstract, and therefore they are not sensitive to changes in factors affecting growth such
as climate. Some models have been built that include effects of environmental factors
and management activities on juvenile crops (Mason and Whyte, 1997; Mason, 2001)
that have more desirable properties from a mensurationist’s point of view. The
abstraction of these approaches limits their capability to represent a highly dynamic
system with changing weed and microclimatic influences. The equation used to represent
yield of juvenile tree crops is often (Belli and Ek, 1988; Mason and Whyte, 1997; Mason,
2001; McKay and Mason, 2001):

\[ Y_T = Y_0 + \alpha T^\beta \]  

(2)

Where \( Y_T \) = estimate of variable \( Y \) at time \( T \), \( T = \)time in years, and \( \alpha \) and \( \beta \) are estimated
parameters. Estimated parameters are sometimes linearly related to site, vegetation
management, site preparation, and seedling quality effects. Equation (2) allows for a
decline in relative growth rate that occurs as juvenile trees grow (Britt et al., 1991; South, 1991; Mason and Whyte, 1997; Mason, 2001; Kirongo and Mason, 2003).

The idea explored in this paper is that a synthesis of mensurational models and physiological approaches like 3-PG can be built by directly substituting potentially used radiation sum for time in mensurational equations such as equation (2). With such a synthesis no attempt is made to directly measure APAR, nor is carbon allocation explicitly represented. Yield equations used for juvenile trees and sigmoid equations used for older crops implicitly represent effects of APAR and allocation on relative growth rate. Using modifiers such as those in the 3-PG model to assess what proportion of incoming light could potentially be used by plants if it were intercepted makes these hybrid equations sensitive to changes in growth resource availability that may be influenced by weeds, changing sites, or varying weather patterns from year to year.

The hypothesis formally tested during this study was that parameters of a potentially useable light sum model fitted to the range of treatments in a powerful, complex weed control experiment would not differ significantly between treatments. This test compared estimates of growth resource availability in the fitted model with “class” level effects of weed control treatments. Moreover, it was postulated that, as a contrast, a time-based model fitted to individual plots within the same experiment would yield estimated coefficients that differed significantly between weed control treatments.

Methods
Overview

The following model was fitted to ground-line diameter (GLD) measurements from a weed control experiment in Oregon:

\[ Y_T = Y_0 + \alpha R_T^\beta \]

\[ R_T = \sum_{t=1}^{T} R_t \min\{f_\theta, f_D\} f_T f_{CI} \]  \hspace{1cm} (3)

Where \( Y_T \)=GLD at time \( T \), \( \alpha \) and \( \beta \) are parameters estimated from the dataset,

\( R_t \)=radiation in month \( t \), \( R_T \)=potentially useable light sum, \( f_\theta \)=soil water modifier (0-1),

\( f_D \)=vapor pressure deficit modifier (0-1), \( f_T \)=temperature modifier (0-1), and \( f_{CI} \)=light competition modifier. This model is a blend of key sub-models from model 3-PG and a commonly used mensurational equation that avoids the need to directly estimate absorbed photosynthetically active radiation, does not require estimates of carbon allocation, and can be both fitted and used without recursion.

A Critical Period Threshold (CPT) experiment in Oregon was selected for the study. CPT studies have been used in forestry for evaluation of vegetation management schedules (Wagner et al., 1999), and they implicitly represent two-sided competition between crop trees and weeds with extreme variations in timing of weed and tree interactions. Modeling growth in such a study using traditional mensurational techniques would be difficult because mensurational methods do not explicitly represent effects of changing resource availability when they vary from year to year within plots.
The selected experiment was at latitude 44°37' N and longitude 123°35' W in the Oregon coast mountain range, on an Apt clay soil at an elevation of 250 m, and was a species by competition factorial design with four randomized complete blocks (Rosner and Rose, 2006). The site was located on gentle slopes with two blocks on each of two aspects. Container-grown stock of four tree species were planted on the site, but only plots containing *Pseudotsuga menzeisii* were used for the study described here. Competition treatments included a range of annual weed control operations through five years:

<table>
<thead>
<tr>
<th>Year</th>
<th>Treatment</th>
</tr>
</thead>
<tbody>
<tr>
<td>2000</td>
<td>OOOOO</td>
</tr>
<tr>
<td>2001</td>
<td>OOTTT</td>
</tr>
<tr>
<td>2002</td>
<td>OTTTT</td>
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<td>2005</td>
<td>TTTOO</td>
</tr>
<tr>
<td>2006</td>
<td>TTTTO</td>
</tr>
<tr>
<td>2007</td>
<td>TTTTT</td>
</tr>
</tbody>
</table>

Where each letter represents a year, O=no weed control and T=weed control. Trees were planted at 3.1 x 3.1 m in late January of 2000, and each square plot contained 64 trees. The middle 36 trees were measured in each plot.

The ground-line diameter (GLD) and height of each tree was measured after planting, and each October thereafter. Weed species and % cover within 1 m of each tree were estimated every July by placing a frame around each tree that was divided into quadrants and ocularly estimating the % cover.
A soil pit was dug on the site during the winter of 2005/2006 following several days of rain, and the depth of roots was measured. Soil cores were extracted using a 101.29 cm³ soil corer at six depths separated by 15 cm and beginning at 7.5 cm from the soil surface. Gravimetric moisture content, dry bulk density and wet bulk density of each core were measured in a laboratory. Dry bulk density ranged from 0.98 in the top sample to 1.14 at 82 cm below the soil surface. Gravimetric moisture content at field capacity was found to be 0.4, and approximately 95% of roots were within 45 cm of the soil surface. Given that the soil was clay, gravimetric moisture content at zero plant available water was assumed to be 0.2, and this yielded a maximum available soil water (ASW) estimate of 180 mm and a minimum ASW of 90 mm.

Weed cover

The weed cover in each treatment varied in accordance with prescriptions until year three, when a followup vegetation management operation was not conducted (Figure 1). The missing followup operation did not detract from the study reported here, as the measured % cover of weeds, not the nominal treatment schedule, was used to run the water balance model.

Leaf area index (LAI) was needed for both trees and weeds in each month in order to run a water balance model. LAI of trees within 3.14 m² circles at each measurement time was calculated from GLD²*height using an equation fitted to destructively sampled juvenile Douglas fir trees (Shainsky and Radosevich, 1992). Weed LAI was calculated in two ways: (1) by assuming that the 100% weed cover for the predominant grass and forbs on
the site was at an LAI of 3.5, and directly scaling LAI to % cover estimates; and (2) by assuming that individual weed species would reach maximum LAI values as those reported in the literature (Breuer et al., 2003) when they reached 100% cover and maximum reported heights for the species (Breuer et al., 2003). Heights were estimated for each competing life form and for each time since treatment by the person who conducted the weed surveys. The first of these methods would be more accessible to forest managers, while the second might be more accurate. LAI estimates for intervening months were estimated by multiplying the difference in LAI between two measurement dates by the following equation:

\[ \text{LAI}_x = \text{LAI}_p + (\text{LAI}_N - \text{LAI}_p) \int_{x_p}^{x} \sin(x / 6 \pi + 1) / 12 \]

(4)

Where \(x\)=month number (January=1, February=2, etc.) with negative numbers -1 and -2 for November or December, \(X_p\)= the previous October, and a shift in \(x\) of minus three to get periodicity of change in line with seasons. LAI\(_P\) and LAI\(_N\) were LAIs estimated from measurements in the previous and next October, respectively. This implied that little growth in LAI would occur over the winter months, and that most change would occur in the spring and early summer. Where vegetation management treatments had been applied the same equation allowed for a gradual change in weed LAI during early spring prior to the new weed % cover estimate in July. Resulting estimates of monthly leaf area index in each treatment are shown in Figure 7b.

Weather data

A tipping bucket rain gauge was established on the site during June 2000, as well as an electronic air temperature gauge (the instruments were supplied by Onset Computer Co.,
Bourne, Massachusetts, USA). Temperature was measured every hour from that point on. The temperature record contained a few small gaps, and these plus rainfall estimates between January and June 2000 were filled with measurements from a meteorological station 50 km away at Corvallis run by the Oregon Climate Service, Department of Oceanic and Atmospheric Sciences, Oregon State University. The Corvallis station was at 90 m elevation. The study called for the use of monthly summaries of weather data, and so the filling of gaps with data from a close meteorological station was deemed reasonable. Comparisons of on-site weather measurements with those at the Corvallis station during periods when both had data showed that monthly estimates were very similar at both sites. Mean daily maximum, minimum and mean temperatures were calculated for each month, as well as total monthly precipitation.

Monthly radiation estimates were obtained from the University of Oregon’s Solar Radiation Monitoring Laboratory on-line from http://solardat.uoregon.edu/. The Eugene radiation station used was at latitude 44.05 N, longitude 123.07 W and at an elevation of 150 m.

Monthly weather and LAI estimates were assembled as related tables in a database, and then a water balance model was run over the first four years of measurements in each plot, using a monthly time step.

Monthly rainfall, mean temperature and mean daily radiation are shown in Figure 2. As can be seen, the site was characterised by wet, cold winters and warm dry summers, with
extremes in radiation due to clouds and low sun angles during winter followed by clear 
skies and high sun angles during summer.

Modeling soil water

The water balance model was identical to that used in 3-PG (Landsberg and Waring, 
1997) except that parameters required for the Penman Montieth equation were weighted 
averages, with LAI estimates of weeds and trees used as weights. Individual parameter 
estimates used are shown in Table 1. The water balance modifier used for light sums 
was also identical to that used in the 3-PG model.

Vapour pressure deficit was estimated from mean daily maximum and minimum 
temperatures by assuming that vapour pressure deficit was 0.5 times the saturated vapour 
pressure at the maximum temperature minus saturated vapour pressure at the minimum 
temperature.

A VPD modifier was used that is identical to that used in the current version of the 3-PG 
model. It was represented as:

\[ f_D = \exp(-0.05 \times \text{vpd}) \]  \hspace{1cm} (5)

Where vpd=vapor pressure deficit. This modifier was also used to calculate stomatal 
conductance from maximum stomatal conductance in the water balance model.
A temperature modifier, also identical to that used in the 3-PG model was based on the minimum, optimum and maximum temperatures for photosynthesis as:

\[
f_T(T_a) = \left( \frac{T_a - T_{\text{min}}}{T_{\text{opt}} - T_{\text{min}}} \right) \left( \frac{T_{\text{max}} - T_a}{T_{\text{max}} - T_{\text{opt}}} \right)^{(T_{\text{max}} - T_{\text{opt}})/(T_{\text{opt}} - T_{\text{min}})}
\]  

(6)

where \( f_T = 0 \) if \( T_a \leq T_{\text{min}} \) or \( T_{\text{max}} \leq T_a \), and \( T_{\text{min}}, T_{\text{opt}} \) and \( T_{\text{max}} \) were the minimum, optimum and maximum temperatures for net photosynthetic production.

Competition for light

Competition for light was estimated using the ratio of squares of weed and crop mean heights times the % cover of weeds as a competition index and the following equation to estimate light transmission to crop plants (Richardson et al., 1999):

\[
CI = \frac{H_{\text{weeds}}^2}{H_{\text{crop}}^2} C
\]

\[
f_{CI} = 1 - (1 - \exp(-0.76 \times CI))^{1.289}
\]  

(7)

Where \( f_{CI} = \)light competition modifier, \( CI = \)competition index, \( H = \)heights of weeds or crops as noted, and \( C = \)percentage cover of weeds.

Fitting the potentially useable light sum model

Potentially useable light sums (see equation 3) were then calculated for each month in each plot. Those sums that corresponded to times of tree measurement were extracted
from the table using a SAS (SAS-Institute-Inc., 2000) DATA step, and then model (3) was fitted to measurements of GLD. PROC NLIN was used to fit the model to each plot, and then the fitted coefficients, $\alpha$ and $\beta$, were subjected to analysis of variance using the formal experimental design so that and significant differences between them could be identified. The same within plot NLIN fitting procedure and subsequent analysis of variance test was applied to model (2), using time as the principal independent variable, to determine whether or not the experiment would yield significant differences between coefficients when effects of weeds on growth resource availability were not explicitly accounted for.

An overall model (3) was also fitted to all plots simultaneously. In this latter model estimates of $\alpha$ and $\beta$ were identical for all plots, unlike former implementations of equation (2) (Mason, 1992; Mason and Whyte, 1997; Mason, 2001).

Residuals were graphed, and the normality of residuals was tested using PROC UNIVARIATE in SAS using the “plot normal” options. This included a Shapiro Wilkes test for deviation from normality.

**Results**

*Overview*

Figure 3 shows graphs of ground line diameter for all plot averages with either time or potentially useable light sum on the x-axis. Ground line diameter was much more
correlated with potentially useable light sum than with time. Figure 3 shows the plot
against a light sum calculated using weed LAI values estimated from the second, more
complicated technique, however, results were similar for both methods of LAI
calculation.

Observed and modeled GLD development

Mean observed GLD development in the treatments reflected the highly variable
applications of vegetation management treatments (Figure 4). Treatments subjected to
early vegetation management and later weed infestation generally exhibited higher initial
growth trajectories but then lagged behind other treatments where vegetation
management was applied for more years. In some cases trajectories crossed each other.

Residuals from model (6) applied to all data simultaneously, and using the complex
measure of weed LAI, were within + or – 10, had a root mean square error of 30.1, and
exhibited very little heteroscedasticity (Figure 5). Residuals from this model were only
slightly skewed, and had a Shapiro-Wilkes W statistic of 0.966, which indicated that
residuals deviated slightly from a normal distribution (P<0.0027). They exhibited very
little bias, however (Figure 5). Plots of mean treatment trajectories from the model are
shown in Figure 6. Using simple estimates of weed LAI (with 100% weed cover equal to
an LAI of 3.5) resulted in a small increase in the root mean square error to 30.4.

Removing the light competition modifier meant that the root mean square error of the
more complex LAI estimation model increased to 30.9, indicating that light competition
was relatively minor compared to competition for water. The final yield equation for
model (3) using values of computed potentially useable light was:

$$GLD_T = GLD_0 + 1.0298\left(\frac{R_T}{1000}\right)^{1.6475}$$  

(8)

Standard errors estimated coefficients (α and β of model (3)) were 0.0826 and 0.0377
respectively.

Comparison of overall fit with individual plot fits

Results of the analyses of variance of the coefficients of the PULSE model (3) fitted to
each plot showed that neither the α nor the β coefficients differed significantly between
weed control treatments (P<0.54 and P<0.25). By contrast the time-based model (2)
yielded coefficients for each plot that were significantly different between weed control
treatments (P<0.0003 and P<0.0001).

Discussion

A potentially useable light sum equation (PULSE) model accounted for very dynamic
changes in growth patterns in the experiment described here with a very simple
mensurational equation. Increasing plant size, access to site resources, and changing
carbon allocation were implicit in the equation, and so estimates of absorbed
photosynthetically active radiation, carbon allocation, and a recursive model structure
were not required. As coefficients for this model did not differ significantly between
weed control treatments, we can assume that the model accounted for critical differences
in growth resource availability brought about by the treatments. The result was a model
form that forest managers could reasonably access, understand and use. Weather inputs
for management use are now readily available on the internet (e.g.: see
http://www.daymet.org), and if LAI can be effectively estimated from simple measures of
plants, such as stem measurements or % plant cover, then using these techniques for
mensurational models will be easy. The analysis presented here showed that simple
measures were almost as effective as more complicated LAI estimation procedures based
on reported LAI maxima for individual weed species. If meteorological data are
provided as web services in the format of SOAP or Microsoft’s .NET, then required
model inputs will be seamlessly integrated with model software. GIS layers might be
used to provide estimates of soils type as well as maximum and minimum ASW required
for the water balance model.

Leaf area indices are required for a water balance model. New optical tools such as the
LAI2000 (Licor Ltd.) make LAI measurement much less costly, and managers should
consider measuring LAI routinely in permanent sample plots so that models of LAI
development for particular species and stand structures can be created.

Fitting a standard statistical model to the development of GLD with time in this
experiment would have been difficult. High levels of variation in weed site occupancy
and changing site influences with time within the same plots would a necessitate an
analysis of change in GLD from year to year, and the resulting model would not reflect site influences to the degree that model (6) did. Moreover, a purely statistical model would have been excessively local, and would not have provided much insight into the processes involved. For example, Figure 7a shows available soil water deficit plotted by treatment against time.

Model coefficients presented here are not intended to be applied generally to young stands of Douglas fir. This is a methods paper, and more intensive measurements of site and plant parameters would be required in order to fit a more generalisable model. The ease with which light competition was accommodated in the model represents a clear advantage of this hybrid modeling approach.

Nutritional fertility of soil is not included in the model, nor is it properly accounted for in 3-PG. Identification of fertility modifiers for different soils, and research that reveals why these fertility modifiers apply in specific situations is an urgent need.

Explicit estimation of absorbed photosynthetically active radiation (APAR) would be an improvement over this technique in circumstances where maximum LAI is influenced by management factors such as fertilization (Amateis et al., 2000; Ducey and Allen, 2001; Allen et al., 2002; Albaugh et al., 2003; Westfall et al., 2004). It the study described here, however, discontinuous tree canopies made estimations of APAR difficult. If forest managers begin routinely estimating LAI by using either handheld optical devices or
remote sensing then mensurational models that employ used light sums will become feasible.

The idea that time is equivalent to potentially useable or used radiation sums might be applied to growth and yield modeling with difference equations. Having separate light sums for primary and secondary growth in order to account for their different phenologies may offer flexible models that account for differences in tree form caused by seasonal differences in climate. This topic will be addressed in a future paper.

The methodology described here offers researchers and managers a synthesis between mensurational and physiological modeling techniques that will facilitate the inclusion of research findings into operational models, and may provide managers with more site-specific estimates of the effects of management activities in forests. Specifically representing growth resource limitations in models clarifies how these limitations might be reduced and growth rates thereby increased.

Conclusions

A potentially useable light sum model of ground line diameter development for four years after planting was fitted to individual plots within a complex weed control experiment. The fits yielded coefficients that did not differ significantly between weed control treatments. A time-based model fitted to the same data yielded parameter estimates that did vary significantly between treatments.
An overall model fitted to the experiment (equation 3) had 95% of residuals between +4 and -4 mm.

References


Acknowledgements

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Table 1 – Parameter used in modifier models

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<th>Parameter</th>
<th>Value</th>
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<th>Reference</th>
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<td>Water balance</td>
<td>Max stomatal conductance - trees</td>
<td>0.018</td>
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<td></td>
<td>Max stomatal conductance - weeds</td>
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<td>m/sec</td>
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*Estimates for simple LAI estimation only. Estimates of these parameters varied as LAIs of different species varied within plots (Breuer et al., 2003) for the second LAI estimation procedure.
Figure captions

Figure 1 – Percent weed cover by year and treatment. When weed species overtopped each other, then cover could exceed 100%.

Figure 2 – Monthly rainfall, radiation and mean temperature during the period of the study

Figure 3 – Plots of plot mean ground line diameter against time (top) and potentially useable light sum (bottom)

Figure 4 – Ground line diameter by vegetation management treatment

Figure 5 – Residual vs predicted ground line diameter for the potentially useable light sum model

Figure 6 – Monthly plot of modelled ground line diameter by treatment using the PULSE approach

Figure 7 – Monthly available soil water deficit (top), and LAI by treatment (bottom)
Figure 1

% weed cover vs. Time since planting (years)

Legend:
- OOOOO
- OOTTTE
- OTTTTT
- TOOOOO
- TTOOO
- TTTOO
- TTTTO
- TTTTT

0 0.75 1.75 2.75 3.75

Time since planting (years)
Figure 2

- Rain
- Radiation
- Mean Temperature

Rainfall (mm/month) vs. Temperature (°C) & Radiation (MJ/day)
Figure 3

1. Chart 1: Ground line diameter (mm) vs. Time since planting (years)

2. Chart 2: Ground line diameter (mm) vs. Potentially useable light sum (Megajoules/sq m)
Figure 4

Time since planting (years)

GLD (mm)
Figure 5

Predicted GLD (mm)

Residual (mm)
Figure 6

![Graph showing the ground line diameter (mm) over time since planting (years).](image-url)
Figure 7

Soil water deficit (mm)

Time since planting (years)

Estimated weed leaf area index

Time since planting (years)