

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

E. G. Mason, R. W. Rose, and L. S. Rosner

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 (*Pseudotsuga menzeisii* (Mirb.) Franco) as a crop species and a variety of competing species. Site occupancy by competing vegetation varied with time because control operations were intermittently either included or excluded from treatments over a period of 4 years. There were four randomized complete blocks of eight competition 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 competing vegetation. Fits of the model to individual plots within the experiment yielded coefficients that did not differ significantly between competition control treatments, suggesting that the model accounted for significant variations in growth resource availability between treatments. Potentially useable light sum equations provide an integrated link between traditional mensurational modeling and ecophysiological modeling.

Résumé : La substitution du temps par la lumière potentiellement utilisable cumulée dans une équation dendrométrique courante a produit un meilleur ajustement aux données issues d'une expérience complexe d'aménagement de la végétation. L'expérience a mis en relation le douglas vert (*Pseudotsuga menzeisii* (Mirb.) Franco) comme espèce d'avenir et une variété d'espèces compétitrices. L'occupation de la station par la végétation compétitrice a varié en fonction du temps puisque les opérations de maîtrise de la végétation ont été incluses ou exclues des traitements de façon intermittente pendant une période de 4 ans. Le plan expérimental comprenait huit traitements de maîtrise de la végétation compétitrice répétés dans quatre blocs aléatoires complets. La lumière potentiellement utilisable cumulée a été estimée à partir de mesures du rayonnement provenant d'une station météorologique. Ces mesures ont été modifiées par des coefficients représentant la capacité des plants d'avenir à utiliser la lumière sous des conditions variées d'humidité du sol, de déficit de pression de vapeur et de température. La lumière cumulée a ensuite été réduite en fonction d'une valeur estimée de la compétition pour la lumière de chaque type de végétation compétitrice. L'ajustement du modèle aux parcelles individuelles du dispositif expérimental a produit des coefficients qui n'étaient pas significativement différents entre les traitements de maîtrise de la compétition, ce qui indique que le modèle a tenu compte d'une variation significative de la disponibilité des ressources pour la croissance entre les traitements. Les équations de lumière potentiellement utilisable cumulée fournissent un lien intégré entre la traditionnelle modélisation dendrométrique et la modélisation écophysologique.

[Traduit par la Rédaction]

Introduction

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 princi-

ple 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

$$[1] \quad \text{NPP} = \varepsilon \sum_{m=1}^M \text{APAR}_m \min\{f_{\theta}/f_D\} f_T f_F f_S$$

where m is the time interval (months), APAR is absorbed photosynthetically active radiation, ε is the maximum quantum efficiency for a species, f_{θ} is the soil water modifier (0–1), f_D is the vapour pressure deficit modifier (0–1), f_T is the temperature modifier (0–1), f_F is the frost modifier (0–1), f_S is the senescence modifier (0–1). The model maintains a soil water balance using soil depth, soil type, rainfall, temperature, leaf area index (LAI), and the Penman–Monteith equation for calculating evapotranspiration to cal-

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culate the soil water modifier. Most modifiers are calculated using models that represent underlying 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), it has many estimated parameters so that it might be fitted to the same data set in a variety of ways, and users need to fit parameters locally to submodels 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; therefore they are not sensitive to changes in factors affecting growth such as climate. Some models that have been built to include effects of environmental factors and management activities on juvenile crops (Mason and Whyte 1997; Mason 2001) 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 competing vegetation and microclimatic influences. The equation used to represent yield of juvenile tree crops is often the following (Belli and Ek 1988; Mason and Whyte 1997; Mason 2001; McKay and Mason 2001):

$$[2] \quad Y_t = Y_0 + \alpha t^\beta$$

where Y_0 is the initial yield, Y_t is the estimate of Y at time t , t is the time in years, and α and β 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; 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 eq. 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 equa-

Table 1. Table of competition control treatments in the experiment.

Treatment label	Year 1	Year 2	Year 3	Year 4	Year 5
OOOOO					
OOTTT			X*	X	X
OTTTT		X	X	X	X
TOOOO	X				
TTOOO	X	X			
TTTOO	X	X	X		
TTTTO	X	X	X	X	
TTTTT	X	X	X	X	X

*Year of implementation of weed control.

tions 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 competing vegetation, 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 competition 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 competition 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 control treatments.

Methods

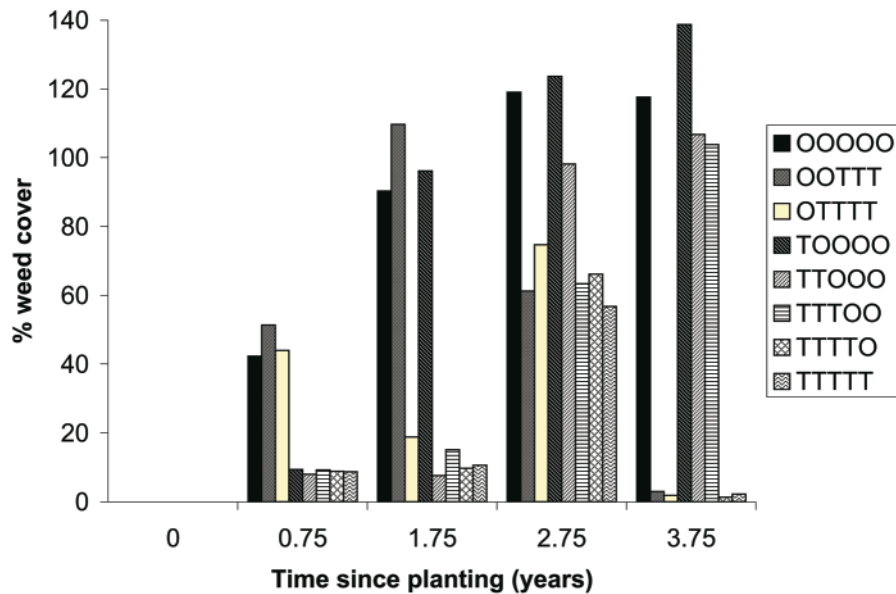
Experimental layout

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 competing vegetation with extreme variations in timing of competing vegetation 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 44°37'N, 123°35'W in the Oregon coast mountain range, on an Apt clay soil at an elevation of 250 m, and was a species × 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 Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) were used for the study described here. Competition treatments included a range of annual competition control operations through 5 years (Table 1).

Trees were planted at 3.1 m × 3.1 m in late January of

Fig. 1. Percent weed cover by year and treatment. When weed species overtopped each other, then cover could exceed 100%. See Table 1 for treatments.



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. Competing vegetation species and percent 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 percent 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 and minimum available soil water estimates of 180 mm and 90 mm, respectively.

Competing vegetation cover

The competing vegetation cover in each treatment varied in accordance with prescriptions until year 3, when a followup vegetation management operation was not conducted (Fig. 1). The missing followup operation did not detract from the study reported here, as the measured percent cover of competing vegetation, not the nominal treatment schedule, was used to run the water balance model.

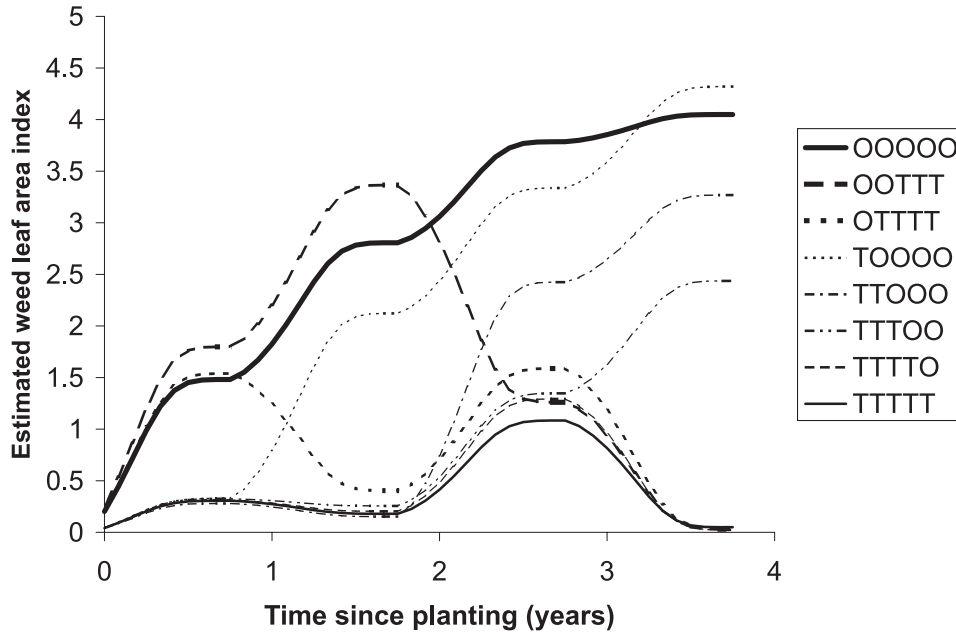
LAI was needed for both trees and competing vegetation in each month to run a water balance model. LAI of trees within 3.14 m² circles at each measurement time was calculated from GLD² × height using an equation fitted to destructively sampled juvenile Douglas-fir trees (Shainsky and

Radosevich 1992). This way of estimating tree LAI did not account for the dependency of LAI on site conditions. Had we been estimating absorbed photosynthetically active radiation then this would have been a serious issue, but it was thought that these estimates were adequate for estimates of rainfall interception and evapotranspiration. Competing vegetation LAI was calculated in two ways: (i) by assuming that the 100% competing vegetation cover for the predominant grass and forbs on the site was at an LAI of 3.5, and directly scaling LAI to percent cover estimates and (ii) by assuming that individual competing vegetation species would reach maximum LAI values similar to 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 vegetation species and for each time since treatment by the person who conducted the competing vegetation surveys. The first of these methods would be more accessible to forest managers, whereas 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:

$$[3] \quad LAI_x = LAI_p + (LAI_N - LAI_p) \int_{X_p}^x \frac{\sin(x/6\pi) + 1}{12dx}$$

where *x* is the month number (January = 1, February = 2, ..., October = 10, and numbers -1 and 0 for November or December), *X_p* is the the previous October, and a shift in *x* of -3 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 competing vegetation LAI during early spring

Fig. 2. Leaf area index by treatment. See Table 1 for treatments.



prior to the new competing vegetation percent cover estimate in July. Resulting estimates of monthly LAI in each treatment are shown in Fig. 2.

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). 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 in 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. These measurements were obtained on-line from <http://www.ocs.oregonstate.edu/index.htm>. 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://solarat.uoregon.edu/>. The Eugene radiation station used was at 44°05'N, 123°07'W and at an elevation of 150 m. Comparisons of monthly estimates of temperature and rainfall at Eugene and at the experimental site showed that conditions were very similar and, therefore, that radiation estimates at Eugene were a reasonable surrogate for on-site radiation measurements.

Monthly rainfall, mean temperature, and mean daily radiation are shown in Fig. 3. As can be seen, the site was char-

acterized 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 approach

The following model was fitted to GLD measurements from the competition control experiment:

$$[4] \quad \text{GLD}_m = \text{GLD}_0 + \alpha \left(\frac{R_m}{1000} \right)^\beta$$

$$R_M = \sum_{m=1}^M R_m \min[f_0/f_D] f_T f_{CI}$$

where GLD_m is the GLD in month m , α and β are parameters estimated from the data set, R_m is the radiation in month m , R_M is the potentially useable light sum, f_{CI} is the light competition modifier, and the other variables are as previously defined. This model is a blend of key submodels from model 3-PG and a commonly used mensurational equation that avoids the need to directly estimate APAR, does not require estimates of carbon allocation, and can be both fitted and used without recursion.

Modeling soil water and effects of temperature and vapour pressure deficit

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 means, with LAI estimates of competing vegetation and trees used as weights. Individual parameter estimates used are shown in Table 2. The soil water modifier used for light sums was also identical to that used in the 3-PG model. Monthly weather and LAI estimates were assembled as related tables in a database, and then a water balance model

Fig. 3. Monthly rainfall, radiation, and mean temperature during the period of the study.

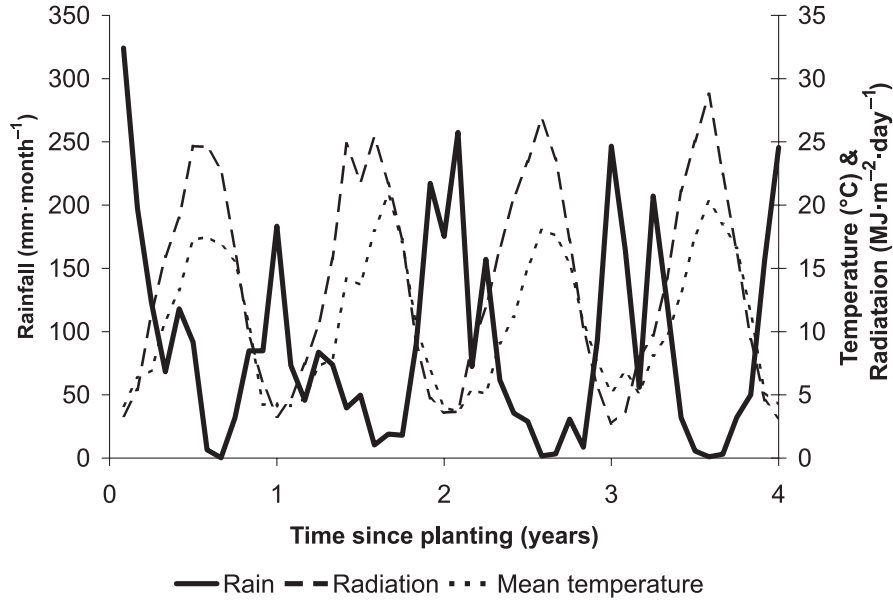


Table 2. Parameter used in modifier models.

Modifier	Parameter	Value	Units	Reference
Water balance	Maximum stomatal conductance of trees	0.018	m·s ⁻¹	Coops and Waring 2001
	Maximum stomatal conductance of weeds	0.018	m·s ⁻¹	E.G. Mason, estimate*
	LAI for maximum canopy conductance	3.33		J.J. Landsberg, personal communication
	Boundary layer conductance of trees	0.2	m·s ⁻¹	Landsberg and Waring 1997
	Boundary layer conductance of weeds	0.25	m·s ⁻¹	E.G. Mason, estimate
	Intercept of net radiation relation for trees	-90	W·m ⁻²	J.J. Landsberg, personal communication
	Slope of net radiation relation for trees	0.8		J.J. Landsberg, personal communication
	Intercept of net radiation relation for weeds	-90	W·m ⁻²	J.J. Landsberg, personal communication
	Slope of net radiation relation for weeds	0.65		Inferred from relative albedos of forest and grassland (McNaughton and Jarvis 1983)
		Maximum available soil water	180	mm
	Minimum available soil water	90	mm	This study
	LAI for maximum rainfall interception	4		J.J. Landsberg, personal communication
Temperature	Maximum temperature for photosynthesis	40	°C	Lewis et al. 1999
	Optimum temperature for photosynthesis	20	°C	Lewis et al. 1999
	Minimum temperature for photosynthesis	-2	°C	Lewis et al. 1999
Vapour pressure deficit	Exponential decay parameter	-0.5		Landsberg and Waring 1997
Light competition	M ₁	-0.760		Richardson et al. 1999
	M ₂	1.289		Richardson et al. 1999

*The estimates are 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.

was run over the first 4 years of measurements in each plot, using a monthly time step.

Vapour pressure deficit (VPD) was estimated from mean daily maximum and minimum temperatures by assuming that vapour pressure deficit was one-half 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

$$[5] \quad f_D = e^{-0.05(\text{VPD})}$$

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

$$[6] \quad f_T(\bar{T}) = \left(\frac{\bar{T} - T_{\min}}{T_{\text{opt}} - T_{\min}} \right) \left(\frac{T_{\max} - \bar{T}}{T_{\max} - T_{\text{opt}}} \right)^{(T_{\max} - T_{\text{opt}})/(T_{\text{opt}} - T_{\min})}$$

where $f_T = 0$ if $\bar{T} \leq T_{\min}$ or $T_{\max} \leq \bar{T}$; T_{\min} , T_{opt} and T_{\max} were the minimum, optimum, and maximum temperatures for net photosynthetic production; and \bar{T} was the mean temperature for each month.

Competition for light

Competition for light was estimated using the ratio of squares of competing vegetation and crop mean heights

times the percent cover of competing vegetation as a competition index and the following equations to estimate light transmission to crop plants (Richardson et al. 1999):

$$[7] \quad CI = \frac{H_{\text{weeds}}^2}{H_{\text{crop}}^2} C$$

$$[8] \quad f_{CI} = 1 - (1 - e^{M_1 \times CI})^{M_2}$$

where f_{CI} is the light competition modifier, CI is the competition index, H is the height of competing vegetation or crops as noted, C is the percent cover of competing vegetation, and M1 and M2 were parameters estimated in competition experiments (Richardson et al. 1999), with values given in Table 2.

Fitting the potentially useable light sum model

Potentially useable light sums (see eq. 4) were then calculated from time of planting 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 eq. 4 was fitted to measurements of GLD. The NLIN procedure was used to fit the model to each plot, and then the estimated coefficients, α and β , were subjected to analysis of variance using the formal experimental design so that significant differences between them could be identified. The same within-plot NLIN fitting procedure and subsequent analysis of variance test was applied to eq. 2, using time as the principal independent variable, to determine whether or not the experiment would yield significant differences between coefficients when effects of competition on growth resource availability were not explicitly accounted for.

An overall eq. 4 was also fitted to all plots simultaneously. In this latter model, estimates of α and β were identical for all plots, which contrasts with time-based applications of the same basic eq. 2 (Mason 1992; Mason and Whyte 1997; Mason 2001) where the parameters had to vary with site quality and site management treatment.

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

Results

Figure 4 shows graphs of GLD for all plot means with either time or potentially useable light sum on the x axis. GLD was much more correlated with potentially useable light sum than with time. Figure 4 shows a plot of modeled GLD against a light sum calculated using competing vegetation LAI values estimated from the second, more complicated technique; however, results were similar for both methods of LAI calculation.

Mean observed GLD development in the treatments reflected the highly variable applications of vegetation management treatments (Fig. 5). Treatments subjected to early vegetation management and later competing vegetation 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 eq. 4 applied to all data simultaneously, and using the complex measure of competing vegetation LAI, were (with one exception) within ± 10 mm, had a root mean square error of 2.69 mm, and exhibited very little heteroscedasticity (Fig. 6). 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 ($P = 0.0027$). However, they exhibited very little bias (Fig. 6). Plots of modeled mean treatment trajectories are shown in Fig. 7. Using simple estimates of competing vegetation LAI (with 100% competing vegetation cover equal to an LAI of 3.5) resulted in a small increase in the root mean square error to 2.71 mm. Removing f_{CI} meant that the root mean square error of the more complex LAI estimation model increased to 2.75 mm, indicating either that light competition was relatively minor compared with competition for water or that a better formulation of light competition was required. Estimated values of coefficients for the final yield equation for eq. 4 were $\alpha = 1.0298$ and $\beta = 1.6475$. Standard errors of the coefficients were 0.0826 and 0.0377, respectively.

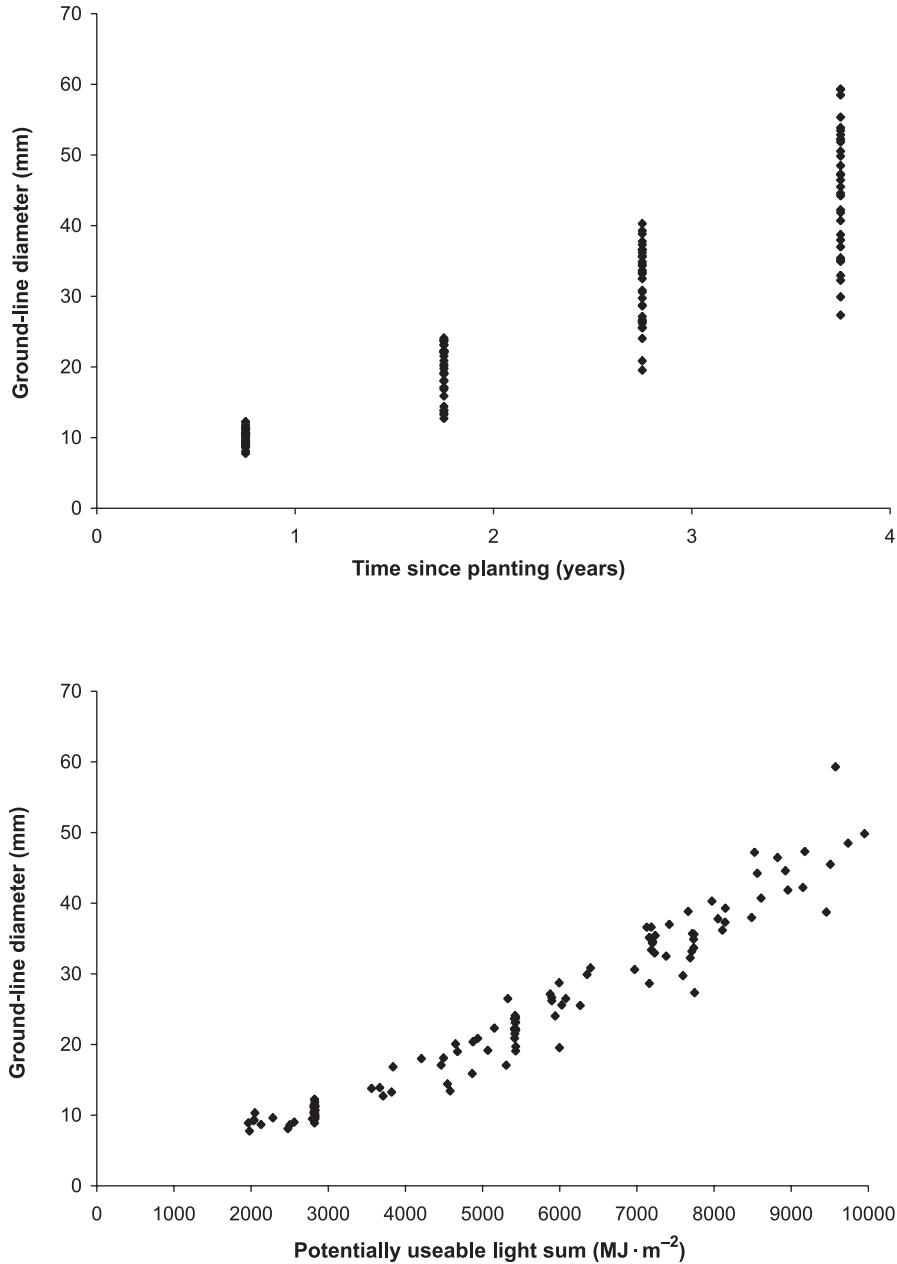
Results of the analyses of variance of the coefficients of the potentially useable light sum equation (PULSE, eq. 4) fitted to each plot showed that neither the α nor the β coefficients differed significantly between competition control treatments ($P = 0.54$ and $P = 0.25$, respectively). In contrast, the time-based eq. 2 yielded coefficients for each plot that were significantly different between competition control treatments ($P = 0.0003$ for α and $P = 0.0001$ for β).

Discussion

Growth and yield modelling methods developed many decades ago (Clutter 1963) are highly abstract and fitted to local measurements of forest growth, and they are still routinely used by forest managers. Inevitably they are geographically local, and they will be biased if climates change. A similar modeling problem arises from site management: changes to microsites through such treatments as control of competing vegetation require models that are sensitive to, and to some extent represent the processes involved in, crop responses to these changes. Complex physiological models of forest growth that might be used to represent these processes (McMurtrie and Wolf 1983) generally require that users specify many coefficients and provide local measurements of variables that may be difficult or expensive to obtain. In addition, their recursive structures may lead to compounded errors. The overcomplexity of many physiological models and the inadequacy of traditional mensurational models when representing effects of climate change and site management (Mason et al. 1997; Mason 2004) have led to the development of "hybrid" models.

The PULSE method used in the study described here provides a coherent integration between mensurational methods and physiological modeling. Some hybrid models have been devised that run mensurational growth and yield models and physiological models in parallel (Snowdon et al. 1998). The "parallel model" approach resulted in better fits where water deficits limited forest growth, but it lacked model co-

Fig. 4. Plots of plot mean ground-line diameter against time (top) and potentially useable light sum (bottom).



herence and resulted in the use of indices derived from simulations of stands that were often somewhat different from mensurationally modeled stands.

Hybrids that are coherent and that represent a full carbon balance are exemplified by the 3-PG model (Landsberg and Waring 1997) described previously. Such models require that carbon allocation is known, and processes regulating changes in allocation in response to varying sites and stand management are not well enough understood to be quantified routinely. In addition, these models require recursion, thereby risking compounded errors. The PULSE approach does not require that carbon allocation be quantified, and it can be applied in a nonrecursive, path-invariant manner.

Hybrid models that rely heavily on allometric relationships (Valentine and Mäkelä 2005) could in theory be fitted to mensurational data. An approach using light sums might

be married to such a model so that the model depended on potentially useable light rather than time. This is a topic for future research.

A PULSE model with a very simple mensurational equation accounted for very dynamic changes in growth patterns in the experiment described here. Increasing plant size, access to site resources, and changing carbon allocation were implicit in the equation, and so estimates of APAR, carbon allocation, and a recursive model structure were not required. Because coefficients for this model did not differ significantly between competition control treatments, we can assume that the model represented differences in growth resource availability brought about by the treatments better than did a time-based model. The result was a model form that forest managers could reasonably access, understand, and use. Weather inputs for management use are now read-

Fig. 5. Ground-line diameter by vegetation management treatment. See Table 1 for treatments.

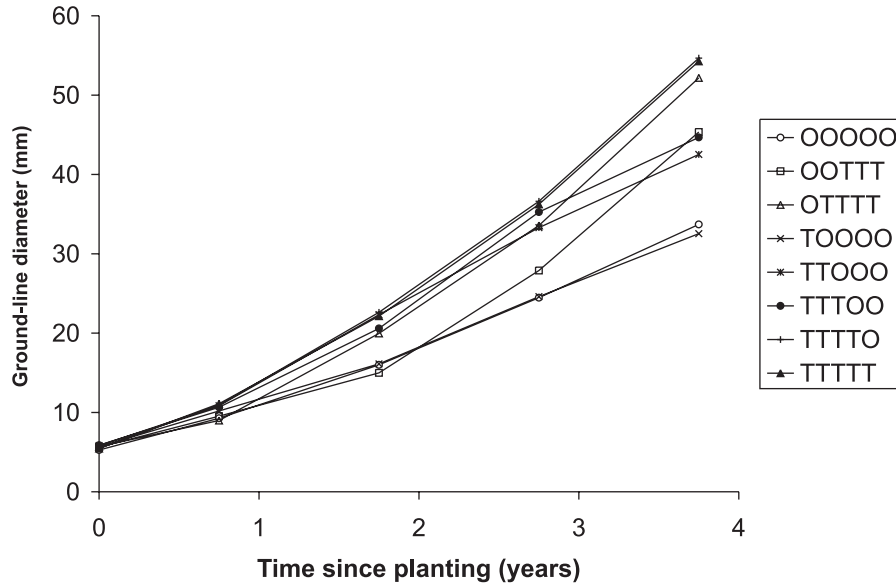
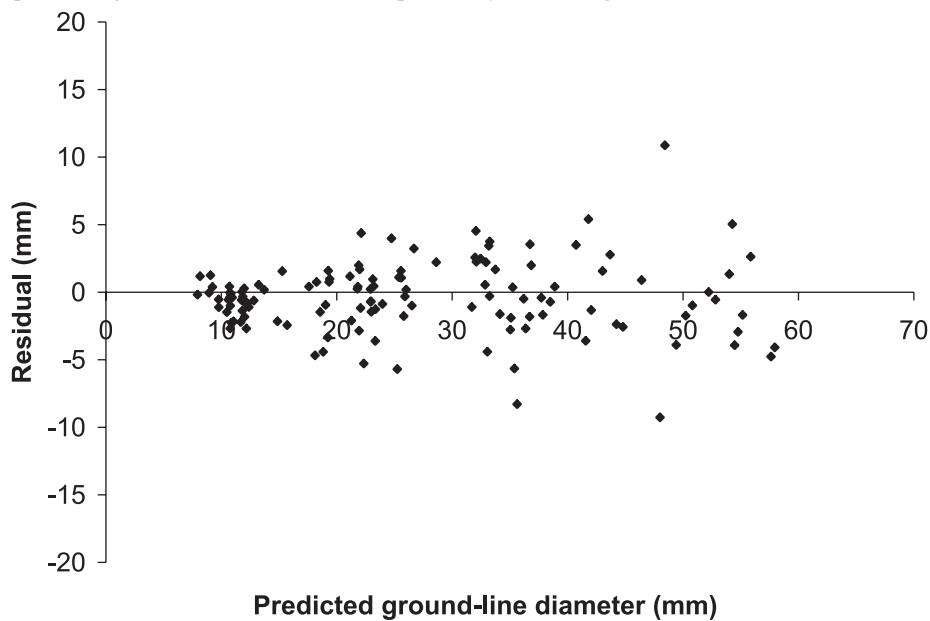


Fig. 6. Residual versus predicted ground-line diameter for the potentially useable light sum model.



ily available on the internet (e.g., see <http://www.daymet.org>); if LAI can be effectively estimated from simple measures of plants, such as stem measurements or percent 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 competing vegetation 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 soil type as well as maximum and minimum available soil water 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., Lincoln,

Neb.) 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 traditional mensurational yield model that included time as an independent variable to the development of GLD in this experiment resulted in an inferior fit when compared with eq. 4. High levels of variation in competing vegetation site occupancy and changing site influences with time within the same plots required an explicit representation of the effects of these influences. Moreover, eq. 2 provided less insight into the processes involved. For example, Fig. 8 shows available soil water deficit from the water balance used in eq. 6 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

Fig. 7. Monthly plot of modelled ground-line diameter by treatment using the PULSE approach. See Table 1 for treatments.

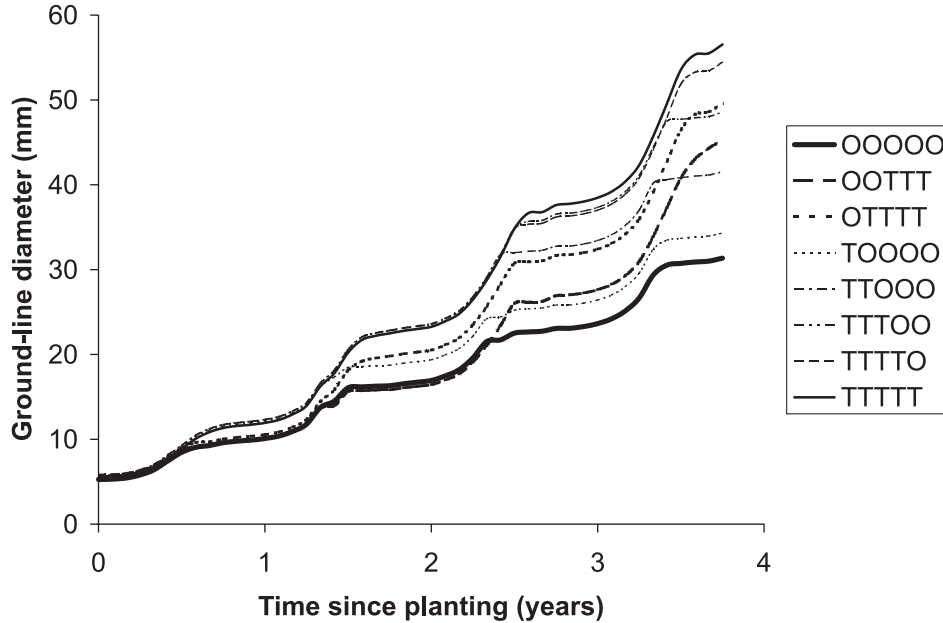
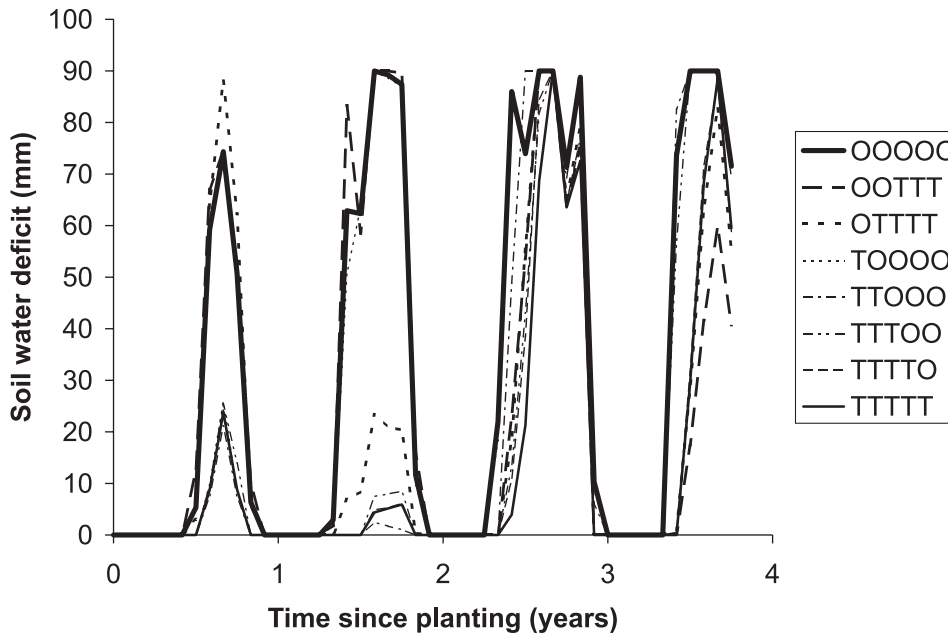


Fig. 8. Monthly available soil water deficit. See Table 1 for treatments.



methods paper, and more intensive measurements of site and plant parameters would be required to fit a more generalizable model. For instance, the ease with which light competition (f_{CI}) was accommodated in the model is an 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 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). However, in the study described here, 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 to account for their different phenologies may offer flexible models that account for differences in tree form caused by seasonal differences in climate. In addition, the ability to interpolate intra-annual dynamics (Fig. 6) is a useful feature where scheduling of

operations like pruning need to be made at monthly resolutions. 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 4 years after planting was fitted to individual plots within a complex competition control experiment. The fits yielded coefficients that did not differ significantly between competition 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 (eq. 4 had more than 99% of residuals within ± 10 mm.

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