A Model of Competition between Trees and Grass for Radiation, Water and Nutrients

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ABSTRACT

Conditions for the coexistence of trees and grass are explored using a mathematical model describing plant competition for radiation, water and nutrients. The model describes growth of both species in terms of key physiological processes (radiation interception, photosynthesis, respiration, grazing, litterfall, assimilate partitioning, nutrient uptake and water use) and is used to analyse how species compete by depriving each other of resources essential for growth. Changes of growth parameters are shown to lead to shifts in species composition (e.g. through replacement of one species by another).

Key words: Competition model, vegetation competition, grass-tree competition, carbon budgets, photosynthesis, assimilate partitioning.

INTRODUCTION

Plants often compete by depleting resources required by neighbours. Harper (1977) considers that the resources for which this competition is most important are radiation, water and nitrates. Yet models of interspecific vegetation competition (Horn, 1975a, b, 1976; Agren and Fagerstrom, 1980; Hastings, 1980; Shugart and West, 1980 and references therein, and de Wit, 1960, 1966) seldom explicitly consider how resource accumulation by one species promotes its own growth at the expense of other species by depriving them of vital resources. Exceptions are Gates (1980a, b) and Walker et al., (1981).

In this paper plant growth is described in terms of a limited number of key processes: radiation interception, photosynthesis, respiration, grazing, litterfall, assimilate partitioning, nutrient uptake and water use, and we examine the way the growth and coexistence of trees and grass are influenced by interspecific competition for radiation, water and nutrients. Competition for radiation is modelled explicitly in terms of interception by the tree canopy and the consequent reduction of radiation reaching the grass layer. Competition for nutrients and water is modelled qualitatively by expressing the photosynthetic rate and partitioning coefficients of both species as functions of the dry weights of the two interacting species.

The model consists of a pair of ordinary differential equations describing the production and loss of foliage dry weight of trees and above-ground grass dry weight. According to the model, and depending upon parameter values, competition can lead to a pure population of either trees or grass or a mixture of grass and trees or a system where neither species survives. These outcomes are represented by stable equilibrium points to which the model solutions evolve. Graphical analysis of the differential equations reveals that, depending upon parameter values, the model possesses either one or two stable equilibria. Cashes of either the grass or tree population occur when vegetation switches from one stable equilibrium to another or when equilibria shift in state-variable space.
Conditions for coexistence of competitors can be explored through the model and related to vegetation patterns in nature. Harper (1977), has compiled a list of factors which can promote the coexistence of competitors. (See also Agren and Fagerstrom, 1980).

The model of radiation competition is presented in the next section, followed by the model of competition for water and nutrients. The final section discusses the potential for making the model more realistic (e.g. through the introduction of spatially patchy vegetation distributions) and its potential role in explaining patterns of species composition, in predicting the productivity of agricultural mixtures of trees and pastures, in assessing the causes of dieback disease of eucalypts in rural Australia and in guiding decision making in forest management (e.g. will a species regenerate naturally after clear-felling?).

COMPETITION FOR RADIATION

Growth model for a forest canopy

The present model of competition between two plant canopies is based upon the forest growth model of McMurtrie and Wolf (1983). Consider a forest stand of foliage dry weight $L(t)$, root dry weight $R(t)$ and stem plus branch dry weight $S(t)$, where $t$ is the time variable. (All weights are in units of $t \text{ ha}^{-1}$).

The net-photosynthetic sub-model calculates gross photosynthesis from the amount of radiation intercepted and reduces this by the amount of substrate consumed in leaf respiration. According to Beer's law, the fraction of incident radiant energy intercepted by the canopy is, ignoring losses through reflection (usually less than 10 per cent of photosynthetically active radiation), 

\[
[1 - \exp(-k_L \text{ LAI})]
\]

where LAI represents the canopy leaf area index and $k_L$ is a canopy extinction coefficient. The relationship between leaf area index and leaf weight is

\[
\text{LAI} = S_{aL} L,
\]  

where $S_{aL}$ is the specific leaf area of trees. The gross rate of photosynthetic production is

\[
P_{gL} = P_{oL}[1 - \exp(-k_L S_{aL} L)],
\]  

where $P_{oL}$ represents the rate when all energy is intercepted. Typically, $P_{oL}$ increases linearly with incident radiation until light-saturation, after which photosynthesis is limited by the rate of diffusion of CO$_2$ into the leaves (Thornley, 1976; Harper, 1977; Charles Edwards and Fisher, 1980; Net photosynthetic production is estimated as

\[
P_{nL} = P_{gL} - r_L L,
\]  

where $r_L$ is the rate of leaf dark respiration [weight of CO$_2$ (dry weight of foliage)$^{-1}$ year$^{-1}$]. Here $P_{gL}$, $P_{nL}$ and $r_L$ are expressed in terms of mass of CO$_2$. Estimates of foliar respiration rates are provided for various tree species by Agren et al. (1980), Grier and Logan (1977), Larcher (1980), Linder and Axelsson (1982), Linder and Lohammar (1981), Sollins, Harris and Edwards (1976), Tranquillini (1979) and Woodwell and Botkin (1970).

The model treats growth as a process which occurs when available photosynthate is surplus to tissue maintenance requirement. If a fraction $\eta_L$ of assimilate is partitioned to leaves the rate of production of new foliage by trees is

\[
\text{Prod}_L = Y_L \eta_L P_{nL},
\]
where \( Y_L \) is a conversion efficiency parameter, and if the rate of foliage loss by litterfall and grazing is given by \( \gamma_L \), the rate of change of leaf dry weight is

\[
\frac{dL}{dt} = Y_L \eta_L P_{nL} - \gamma_L L. \tag{5}
\]

The analysis which follows assumes that all model parameters are constant through time.

**Growth model for grass**

It is straightforward to construct a corresponding differential equation for the dynamics of the above-ground grass dry weight \( G(t) \). Consider a spatially uniform distribution of grasses with a spatially uniform over-storey of trees. The intensity of light reaching the grass is reduced by interception and reflection by the tree canopy. Interception of incident radiation is assumed to obey Beer's law according to which the fraction of full daylight penetrating both the tree and grass canopies is \( \exp(-k_L S_{aL} L - k_G S_{aG} G) \). The fraction intercepted by foliage is \( [1 - \exp(-k_L S_{aL} L)] \) (Eqn (2)). The remainder of incident radiation is intercepted by grass, \( \exp(-k_G S_{aG} G) [1 - \exp(-k_G S_{aG} G)] \). The total rate of gross photosynthesis by grass is given by

\[
P_{BG} = P_{OG} \exp(-k_L S_{aL} L) [1 - \exp(-k_G S_{aG} G)], \tag{6}
\]

where grass-parameters with subscript \( G \) correspond to tree parameters with subscript \( L \). The rate of net photosynthesis for grass is

\[
P_{nG} = P_{BG} - r_G \tag{7}
\]

where \( r_G \) represents the rate of dark respiration for the grass (weight of CO\(_2\) per dry weight of grass year\(^{-1}\)). The rate of new grass production is

\[
Prod_G = Y_G \eta_G P_{nG} \tag{8}
\]

and the rate of increase of grass dry weight, taking account of mortality and litterfall, is

\[
\frac{dG}{dt} = Y_G \eta_G P_{nG} - \gamma_G G. \tag{9}
\]

As discussed by McMurtrie and Wolf (1983), tree growth is only possible if

\[
P_{oL} k_L S_{aL} > r_L + \gamma_L / (\eta_L Y_L) \tag{10}
\]

which is the condition that \( dL/dt > 0 \) in (5) in the limit \( L \to 0 \). Similarly, in the absence of competition from trees, grass growth is only possible if

\[
P_{oG} k_G S_{aG} > r_G + \gamma_G / (\eta_G Y_G). \tag{11}
\]

The analysis which follows assumes that both inequalities hold.

**Graphical analysis of model behaviour**

The pair of ordinary differential Eqns (5) and (9) represents a self-consistent model of the growth of a system of grass and trees in competition for incident radiation. The dynamic behaviour of the model can be explored qualitatively using graphs of the relationships between \( G \) and \( L \), satisfying \( dL/dt = 0 \) (the tree zero-isocline) and \( dG/dt = 0 \) (the grass zero-isocline). The \( L \) zero-isocline consists of two straight lines, the zero equilibrium \( L = 0 \) and the non-trivial equilibrium solution of (5) \( L = L^* \), which are plotted in Fig. 1. The \( G \) zero-isocline includes the trivial equilibrium \( G = 0 \) and a curve...
representing the non-trivial equilibrium solution of (9) as in Fig. 1. The shape of the latter curve reflects the fact that trees outcompete grass for radiation with an increased foliage weight implying a reduced amount of radiation available to grass. There is no analogous change in the \( L \) zero-isocline because the model (5, 9) does not admit competitive effects of grass upon trees. Possible equilibrium point solutions exist wherever the pair of zero-isoclines intersect. As illustrated in Fig. 1, two qualitatively different zero-isocline configurations are possible, depending upon whether or not the pair of non-trivial zero-isoclines intersect.

\[ L_0 = 0 \text{ and } L = L^* \]

Solution trajectories, marked by arrows in the state-variable space of Fig. 1, provide a graphical means to identify those equilibria which are locally stable. The pattern of the trajectories indicates that the vegetation will move towards a mixture of grass and trees for the configuration of Fig. 1B whereas a monoculture of trees results for Fig. 1A. The distinction between these two possibilities is best understood in terms of whether sufficient radiation penetrates the equilibrium tree canopy to allow growth, which is impossible if the light intensity under the tree canopy falls below the compensation point at which grass photosynthesis is balanced by respiration.

The stable species mixture of Fig. 1B occurs if \( dG/dt > 0 \) in the limit \( G \to 0 \) when \( L = L^* \) or alternatively if \( dL/dt < 0 \) in the limit \( G \to 0 \) when \( G/dt = 0 \). The latter criterion for a species mixture to occur can be expressed algebraically.

\[
Y_L \eta_L P_{ol} < \frac{Y_L \eta_L P_{ol} (r_G + r_G Y_G \eta_G)}{k_{ol} \eta_G Y_G} + \frac{r_L \eta_L Y_L + \gamma_L}{k_L S_{al}} \ln \left( \frac{P_{og} k_G S_{ag} \eta_G Y_G}{\gamma_G + r_G Y_G \eta_G} \right).
\]

The present model could be extended along the lines of Charles-Edwards (1981), Charles-Edwards and Fisher (1980) and McMurtrie and Wolf (1983) to provide a comprehensive picture of the growth of other biomass components. However, the additional insights which may be gained are offset by the increased complexity. Moreover, McMurtrie and Wolf (1983) indicate in general terms how allocation to other plant components can be estimated from a knowledge of equilibrium \( L \) and \( G \) dry weights.

**COMPETITION FOR SOIL NUTRIENTS AND WATER**

The model

The above model does not consider the competitive effects of grass upon tree growth. Interference by grass could arise as competition for soil nutrients or water or, in the early
stages of tree growth, as competition for radiation. This paper considers only competition for nutrients or water. In terms of the processes considered in the model competitive interference from grass is likely to influence the partitioning coefficient \( \eta_L \) or the photosynthetic rate of trees.

Changes in the partitioning of assimilate to above and below ground organs often occur in response to fertilization and irrigation (Miller and Miller, 1976; Keyes and Grier, 1981; Linder and Axelsson, 1982) and are likely to be key factors governing the response of trees to grass competition. Increased root competition for soil water or nutrients is likely to cause an increase in the allocation of carbon to fine root production by trees, at the expense of above-ground growth, probably including foliage production (Legg, 1981; Drew, 1982; Reynolds and Thornley, 1982). The graphical analysis in Fig. 1 shows that the consequent decline of \( \eta_L \) implies a reduced equilibrium value \( L^* \) (see McMurtrie and Wolf, 1983 for a qualitative insight) and hence a shift of the non-trivial \( L \) zero-isocline to the left. According to Fig. 1B such a shift would move the intersection point to an equilibrium with more grass and less tree foliage. The effect of a shift of the \( L \) zero-isocline of Fig. 1A can be similarly interpreted.

The effect of grass competition upon photosynthesis could arise either directly, through declined photosynthetic efficiency, or indirectly through a reduction of the growing period. In either case the effect can be modelled by introducing functions which modify the photosynthetic rates as follows

\[
\frac{dL}{dt} = \eta_L Y_L [P_L f_L(L, G) - r_L L] - \gamma_L L,
\]

\[
\frac{dG}{dt} = \eta_G Y_G [P_G f_G(L, G) - r_G G] - \gamma_G G.
\]

The functions \( f_L \) and \( f_G \) may be assigned values in the range 0 to 1, depending upon the intensity of competition. The competition-free case, \( f_L = f_G = 1 \), is illustrated in Fig. 1. Competition between trees and grass for the available soil moisture and nutrients will tend to reduce the values of \( f_L \) and \( f_G \).

**Graphical analysis of the model**

This competitive interaction can be analysed qualitatively through its effect upon the shapes of the zero-isoclines of Fig. 1. Assume initially that the competitive effect of trees upon grasses is negligible, \( f_G = 1 \). The function \( f_L \) describes how the intensity of grass competition varies as a function of \( G \) and \( L \). Provided the value of \( f_L \) declines to zero at high \( G \) values the \( L \) zero-isocline will bend to the left and cross the \( G \)-axis at a grass density corresponding to the dry weight beyond which tree growth is impossible. If the \( L \) zero-isocline is monotonic, as illustrated in Fig. 2, reshaping the \( L \) zero-isocline in this way introduces many possible outcomes to the interaction. In each of Fig. 1A and B bending the \( L \) zero-isocline introduces three qualitatively different possibilities, depending upon the number of points of intersection between the two non-trivial zero-isoclines. Where there is no intersection, the vegetation moves towards a monoculture of trees (Figs 1A, 2A), but when the \( L \) zero-isocline is shifted as in Fig. 2B, the zero-isoclines can intersect, and a monoculture of either grass or forest can result, depending upon initial conditions. Coexistence is not possible since the equilibrium corresponding to the intersection of the zero-isoclines is unstable as indicated by the pattern of solution trajectories.

Figure 2 B, where either of two outcomes is possible, merits closer attention. Here, the entire grass-tree state variable space can be divided into two portions, each possessing a single stable equilibrium, the tree-only equilibrium or the grass-only equilibrium. These
equilibria are circled in Fig. 2B, with arrows representing the path of solutions. From anywhere within one portion the solution will evolve towards its stable point. The two portions are divided by a line called the separatrix. A third possible outcome with a pair of intersections and with stable equilibria corresponding to either a tree monoculture or coexisting trees and grass is illustrated in Fig. 2E.

Figure 1B, where the non-trivial zero-isoclines intersect, possesses a single equilibrium corresponding to a stable mixture of trees and grass. The relatively slight incline of Fig. 2C preserves the equilibrium intact, but shifting the \( L \) zero-isocline to the left (e.g. under conditions of more intense competition from grass) eliminates the intersection altogether, giving rise to a grass-only system (Fig. 2D). A third possibility, with two non-trivial intersections representing mixed species equilibria as well as the tree-only and grass-only equilibria, is feasible depending upon the detailed form of the function \( f_L \) (Fig. 2F). The trajectories plotted in Fig. 2F indicate that the higher of these two possible mixed species equilibria is stable in addition to the grass-only system. That these six are not the only possible configurations of the zero-isoclines is illustrated by the competition model of Walker et al. (1981).

Assume that the photosynthetic rates of both species are reduced through competition for water and nutrients (\( f_L < 1 \) and \( f_G < 1 \)). This causes an increase in the inclination of the grass zero-isocline in Fig. 2, but, provided the \( G \) zero-isocline remains a monotonic function of \( L \), the zero-isocline pattern necessarily conforms with one of the possibilities of Fig. 2. No qualitatively new behaviour emerges.

Simulations of the model (13) with

\[
f_L = \exp (-\beta G) \quad \text{and} \quad f_G = 1,
\]

(14)
FIG. 3. Simulations of the model (13, 14) of competition between trees and grass for radiation, water and nutrients. ——, $L$; —, $G$. Parameter values are $\eta_L = 0.2$, $\eta_G = 0.5$, $Y_L = 0.6$, $Y_G = 0.6$, $P_{aL} = 50\, \text{ha}^{-1}\, \text{year}^{-1}$, $P_{aG} = 80\, \text{ha}^{-1}\, \text{year}^{-1}$, $\gamma_G = 2\, \text{year}^{-1}$, $S_{aL} = 3.5\, \text{m}^2\, \text{kg}^{-1}$, $r_L = 0.5\, \text{year}^{-1}$, $r_G = 0.5\, \text{year}^{-1}$. Initial conditions are $L = 1\, \text{ha}^{-1}$ and $G = 1\, \text{ha}^{-1}$. A, $k_L = 0.6$, $k_G = 0.6$, $S_{aG} = 3.5\, \text{m}^2\, \text{kg}^{-1}$, $\beta = 0.1\, \text{ha}^{-1}$, $\gamma_L = 0.25\, \text{year}^{-1}$. B, as in A but with $\gamma_L = 0.5\, \text{year}^{-1}$. C, as in B but with initial conditions $L = 0.4\, \text{ha}^{-1}$ and $G = 1\, \text{ha}^{-1}$. The initial conditions B and C are on opposite sides of the separatrix. D, as in A but with $k_L = 0.3$, $k_G = 0.9$, $S_{aG} = 8\, \text{m}^2\, \text{kg}^{-1}$, $\beta = 0.05\, \text{ha}^{-1}$. E, as in D but with $\gamma_L = 0.35\, \text{year}^{-1}$. The zero-isoclines corresponding to the simulations of A, B, C, D and E are depicted in Fig. 2A, B, B, C, and D respectively.

are presented in Fig. 3. The monoculture of trees reached in Fig. 3A matches the equilibrium circled in Fig. 2A. The transition from the monoculture of trees (Figs 2A, 3A) to the monoculture of either species (Figs 2B, 3B, C) is achieved by increasing a single parameter $\gamma_L$ (reflecting perhaps increased insect grazing or increased litterfall). The pair of solutions depicted in Fig. 3B and C differ only in their initial conditions, which lie on opposite sides of the separatrix of Fig. 2B. In Fig. 3B initial conditions $L = 1\, \text{ha}^{-1}$, $G = 1\, \text{ha}^{-1}$ give rise to a monoculture of trees whereas in Fig. 3C, where initially $L = 0.4\, \text{t} \, \text{ha}^{-1}$ and $G = 1\, \text{t}\, \text{ha}^{-1}$, a monoculture of grass results. The respective outcomes of Fig. 3B and C match the alternative equilibria circled in Fig. 2B. The transition from stable coexistence (Figs 2C, 3D) to the grass-only outcome (Figs 2D, 3E) is also achieved by altering the single parameter $\gamma_L$.

The rate at which vegetation approaches its stable equilibrium point can be derived from eigenvalue analysis of the model (13, 14) linearized about the appropriate equilibrium. (See for example May, 1973) Fig. 3 illustrates that this rate can vary markedly with parameter values.

**DISCUSSION**

It is interesting to speculate on whether changes in vegetation patterns in perturbed natural ecosystems can be explained in terms of switches between stable equilibria. If the situation illustrated in Fig. 2B applies, management practice (e.g. a clear-fell or other less extreme treatment) might force the vegetation across the separatrix and thus
 inadvertently switch the system from a stable tree-only system to a stable grass-only system. Similar possibilities exist for Fig. 2E and F. When the system crosses the separatrix rapid crashes of either \( G \) or \( L \) could result.

A further possibility is that equilibrium grass and foliage weights can vary as zero-isoclines shift in response to variations of parameter values. An increase of \( \gamma_L \), reflecting perhaps increased attack by defoliating insects, can shift the zero-isocline pattern either from Fig. 1A (tree monoculture) to Fig. 1B (grass or tree monoculture) or from Fig. 1C (mixed species) to Fig. 1D (grass monoculture). This shift occurs as the \( L \) zero-isocline descends with increasing \( \gamma_L \) until the intersection pattern alters. Analogous shifts of the relative positions of the \( L \) and \( G \) zero-isoclines can be effected by altering any of the model parameters. When the zero-isocline intersections are altered in this way rapid population changes can occur.

The model (13) is a mathematical statement of a set of hypotheses which are open to experimental testing. As such the model could be integrated with laboratory and field experiments to improve understanding of vegetation competition. Harper (1977) describes several experiments where the outcome of competition between two crop species is determined by the ability of one species to deprive the other of light, water or nutrients. Often the competition manifests itself as an interaction between various growth limiting processes. The present model, which synthesises the key growth processes into a pair of equations, is suited to the analysis of such experiments. The approach also lends itself to the analysis of experiments on the productivity of species mixtures versus monocultures (Trenbath, 1978; Gates, 1980a, b).

Elimination or reduced growth of eucalypt species through dieback in rural Australia has been attributed to a range of factors including pasture improvement, increased insect grazing, impaired uptake by roots and increased pasture grazing by domestic animals (Old, Kile and Ohmart, 1981). Since the model (13) embodies many of the processes which have been associated with the incidence of eucalypt dieback, it could provide a useful analytic tool to identify factors which are instrumental and to test hypotheses on the dieback problem.

The model embodied in Eqn (13) is unlikely, as it stands, to be useful as a forest yield predictor. McMurtrie and Wolf (1983) discuss in general terms how the model could be extended to suit this purpose.

One of the weaknesses of the model is the assumption of spatial homogeneity. Gaps in the canopy mean that a considerable fraction of incident radiation is not intercepted by foliage and that the distribution of light reaching the forest floor is patchy. This feature could be incorporated by modifying the radiation interception model (2) along the lines of Jackson and Palmer (1979) or by dividing the area into sub-units each of which obeys dynamics of the form (13). It is quite possible that grass and trees could coexist by virtue of the spatial patchiness of the light environment.

After rigorous testing, the model could also be used to assess the impact of forest management practices. Here the objective might be to determine how management practices affect the ability of a particular species to regenerate naturally after a management practice such as clear-felling. Isocline graphs such as Fig. 2 could provide a useful framework for guiding impact assessments and for devising strategy to restore disturbed ecosystems.

There is no reason to restrict the above model formalism to interactions between trees and grass. The competitive interaction between any pair of plant species could be cast in the present framework and the model could be extended to an arbitrary number of species. Of course the complexity of possible model behaviours would be compounded in the process – the rich diversity of dynamic behaviour exhibited by the simple model (13) provides a warning of pitfalls which could be inherent in constructing highly complex models of ecological competition and succession.
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DEFINITIONS OF SYMBOLS

<table>
<thead>
<tr>
<th>Symbol</th>
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<tbody>
<tr>
<td>$\beta$</td>
<td>Intensity of competitive interference of grass on trees</td>
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<tr>
<td>$f_G$</td>
<td>Reduction of grass photosynthetic rate through water and nutrient competition from trees</td>
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<tr>
<td>$f_L$</td>
<td>Reduction of tree photosynthetic rate through water and nutrient competition from grass</td>
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<td>$G$</td>
<td>Grass dry weight</td>
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<td>$\gamma_G$</td>
<td>Rate of litterfall of grass</td>
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<td>$\gamma_L$</td>
<td>Rate of litterfall of tree foliage</td>
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<tr>
<td>$k_G$</td>
<td>Radiation extinction coefficient for grass canopy</td>
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<td>$k_L$</td>
<td>Radiation extinction coefficient for tree canopy</td>
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<td>$L$</td>
<td>Dry weight of tree foliage</td>
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<td>LAI</td>
<td>Leaf area index</td>
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<td>$\eta_G$</td>
<td>Partitioning coefficient for above-ground grass production</td>
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<td>$\eta_L$</td>
<td>Partitioning coefficient for tree foliage</td>
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<td>$P_{OG}$</td>
<td>Gross photosynthetic rate of grass assuming complete interception</td>
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<td>$P_{OL}$</td>
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<td>$Y_L$</td>
<td>Conversion efficiency of substrate into dry weight for trees</td>
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LITERATURE CITED


