Canopy development, CO₂ exchange and carbon balance of a modeled agroforestry tree

PEKKA NYGREN, PASI KIEMA and SILVIA REBOTTARO

Summary  We developed a whole-canopy CO₂ exchange simulation model to study effects of pruning on the carbon balance of trees. Model inputs include global short-wave radiation, photosynthetic photon flux density (PFD), air temperature, time series of the development of canopy diameter, height and total leaf area during the simulation period and local geographical and atmospheric parameters. Canopy structure is derived stochastically from the time series of canopy development and growth functions of individual phytoelements. The PFD incident on a phytoelement is computed from the average gap frequency of the canopy and the binary random probability of sunflecks on the phytoelement. Instantaneous CO₂ assimilation rate of each phytoelement is computed from PFD and phytoelement age. Assimilation rates are integrated over space and time to estimate whole-canopy CO₂ assimilation. The model was used to study carbon balance in five sources of the leguminous agroforestry tree Erythrina poeppigiana (Walpers) O.F. Cook during two 6-month pruning intervals. The canopy description appeared to be realistic. According to the simulations, cumulative assimilation did not provide enough carbon for tree growth until two months after pruning, indicating dependence of tree growth on reserve carbohydrates. The two most productive sources, which had the most open canopies, were the most dependent on reserve carbohydrates after pruning.

Keywords: allocation, biomass production, canopy photosynthesis, Erythrina poeppigiana, pruning, radiation regime, simulation.

Introduction

Agroforestry is a production system in which annual or perennial food or fodder crops are grown in biological interaction with trees growing on the same plot (Somarriba 1992). The trees are included in the system to diversify production or to improve the crop microenvironment (Beer 1987). In many agroforestry systems, the trees are subject to periodic pruning, e.g., to produce fuelwood (Russo 1993), forage (Catchpoole and Blair 1990) or green manure (Beer 1988, Duguma et al. 1988). Understanding the effects of pruning on tree carbon balance and growth is important for both the management of agroforestry systems and the selection of tree species and clones for agroforestry. The estimation of CO₂ assimilation by the whole canopy is the first step in the construction of the whole-plant or crop carbon balance.

The introduction of portable CO₂ exchange measuring systems has enabled in situ determination of leaf CO₂ assimilation rate parameters with reasonable accuracy (Long and Hällgren 1993); however, direct measurement of whole-canopy gas exchange of a tree is still a laborious task (Goulden and Field 1994). Simulation models based on foliage distribution, radiative transfer within the canopy and leaf photosynthesis have been used to estimate canopy CO₂ exchange in forest stands (e.g., Baldocchi and Hutchison 1986, Grace et al. 1987, Oker-Blom et al. 1989, Wang and Jarvis 1990) and fruit orchards (Cohen et al. 1987). Many forest-stand models are based on CO₂ exchange of individual trees that is directly integrated over the whole stand (e.g., Grace et al. 1987, Oker-Blom et al. 1989, Wang and Jarvis 1990). There have been few attempts to develop individual-tree models (Myneni and Impens 1985b, Rauscher et al. 1990, Wu 1993), although such models may have application in agroforestry, especially in widely spaced or hedgerow systems.

Rauscher et al. (1990) presented a process model for the growth of juvenile poplars (Populus spp.), the basic unit of which is an individual leaf. The model includes a detailed three-dimensional description of the canopy, and no simplifying assumptions of canopy architecture are needed, because the exact position of each leaf is known. However, direct application of the approach to fast-growing, periodically pruned agroforestry trees is practically impossible because of the need for repeated, exhaustive structural measurements. We have developed an alternative approach that maintains the calculation of gas exchange at the individual leaf level, but derives the canopy structure stochastically from repeated sim-
ple field measurements of canopy and leaf structure. The radiative flux incident on a leaf is estimated on the basis of the average gap frequency of the canopy and the binary random probability of sunflecks striking the leaf (Nilson 1992). A Monte Carlo type technique (e.g., Oker-Blom 1986) is applied to estimate average whole-canopy CO$_2$ exchange under given conditions.

We applied this approach to develop a simulation model, CANEX (CANopy Carbon EXchange), to estimate whole-canopy CO$_2$ exchange of an isolated agroforestry tree (Erythrina poeppigiana (Walpers) O.F. Cook (Leguminosae: Phaseoleae)) subjected to periodic prunings. At the present stage, the model does not simulate partitioning of assimilated carbon into different biomass compartments. We used the model to estimate the amount of carbon available for tree growth following a complete pruning.

Simulation model

Algorithm

The general algorithm of the CANEX model is presented in

![Figure 1. Simplified flow chart of the CANEX simulation model. Abbreviations: $a_0$ = assimilation rate, $r_n$ = night respiration rate, $A_d$ = diurnal assimilation of a phytoelement, $R_n$ = diurnal night respiration of a phytoelement.]

Canopy development

Canopy development is simulated on the basis of measured time series of canopy dimensions and whole-canopy leaf area plus field data on phytoelement expansion rate and life span. The phytoelement considered is a foliole of the trifoliolate leaf of E. poeppigiana. The folioles are large (1.9--2.7 dm$^2$) and the petioles are long (up to 15 cm). Thus, folioles are considered as independent phytoelements in the description of the canopy structure. The daily development of canopy dimensions is computed by linear interpolation from the measured time series of canopy height and diameter after pruning. The canopy envelope area and volume are computed assuming that the canopy is a semi-ellipsoid, with the origin at the center of the canopy base.

The distribution of phytoelements within the canopy is computationally described by placing a three-dimensional grid within the canopy envelope. Each node of the grid represents a point where a phytoelement may be situated. The early development of the canopy is presented by means of a grid with a 6.5 $\times$ 6.5 cm spacing, and later the phytoelements are placed on a grid with a 13 $\times$ 13 cm spacing.

Based on the observed phytoelement emergence pattern (Rebottaro 1992), the new phytoelements are placed in the grid nodes located within the canopy volume formed during the day of emergence. If there are more emerging phytoelements than free grid nodes, the number of excess phytoelements is recorded and their emergence is “allowed” once there are enough free grid nodes. This procedure is used to describe canopy development immediately after pruning. If there are more free grid nodes than emerging phytoelements, which is the case in the later phases of canopy development, new phytoelements
are allocated randomly to free nodes. This produces a semi-random spatial distribution of the foliage that differs in different runs of CANCEX with the same input tree data.

We assume that (i) the phytoelement emergence rate between two leaf area measuring dates is constant, although it may vary from one measuring interval to another, and (ii) leaf shedding is caused by the aging of leaves only. The observed whole-canopy leaf area at the end of interval $j$ between two measurements of canopy leaf area, $L_{A_{obs}}(j)$, is formed by the phytoelements that have emerged during the previous intervals and are retained during interval $j$, and phytoelements emerged during interval $j$. Let $N_a(h)$ denote the number of phytoelements of leaf age $a$ at moment $h$ (in days) from the beginning of interval $j$, $h$, the end of interval $j$ (in days) and $a_m$ the leaf shedding age. If $a \leq a_m$ and $h \leq a$, the number of phytoelements retained at moment $h$ is:

$$N_a(h) = N_{a-a_m}(0),$$

and the phytoelement emergence rate (phytoelements per day) during interval $j$, $k_d(j)$, can be solved from:

$$L_{A_{obs}}(j) = \sum_{a-a_m}^{a} N_{a-a_m}(0) S_a + k_d(j) \sum_{i=0}^{\min(a+h)} S_i,$$

where $S_a$ is the area of a phytoelement formed before interval $j$ at age (in days) $a$, $S_i$ is the area of a phytoelement formed on $i^{th}$ day of interval $j$. Average leaf shedding age varies between 73 and 87 days (Nygren 1995a). Foliole area of *E. poeppigiana* is described as a function of leaf age:

$$S_a = \frac{S_m}{1 + \exp(\gamma_t - k_d a)},$$

where $S_m$ is the area of the mature foliole, $k_t$ is the initial foliole expansion rate and $\gamma_t$ is a parameter. Equation 3 is parameterized so that $S_a$ approaches the $S_m$ value (1.93–2.72 dm$^2$, depending on tree source) in about 2 weeks (Nygren 1995b).

*Incident radiation*

Model input weather data include measured global short-wave radiation and global photosynthetic photon flux density; the direct and diffuse components of photon flux are estimated separately according to Weiss and Norman (1985).

In the absence of clouds, direct beam radiation, $r_d$, is estimated as (derived from Gates 1980, Ross 1981, Forseth and Norman 1993):

$$r_d = r_0(\bar{d}/d)^2 \sin(\phi)\tan(p_{0.5} s^{-1} \phi),$$

where $r_0$ is the average value of the solar constant, $\bar{d}$ is the yearly average of the distance between the Earth and the Sun, $d$ is the actual distance between the Earth and the Sun calculated according to McCullough and Porter (1971), $\phi$ is the solar elevation angle relative to the horizon (the apparent solar position in the sky was calculated as described by Ross (1981)), $\tau$ is atmospheric transmittance, $p_a$ is atmospheric pressure at the study site and $p_0$ is the atmospheric pressure at sea level. The $r_0$ value used to estimate total solar short-wave radiation (SWR; 280–3000 nm) was 1380 W m$^{-2}$ (Ross 1981), and the value used to estimate photosynthetically active radiation (PAR; 400–700 nm) was 600 W m$^{-2}$ (Weiss and Norman 1985).

Diffuse sky radiation, $r_g$, under clear skies is estimated by (cf. Forseth and Norman 1993):

$$r_g = 0.5 r_0(\bar{d}/d)^2 \sin(\phi)\tan(1 - \frac{\tau}{\tan(p_{0.5} \sin^{-1} \phi)}),$$

Combining Equations 4 and 5 yields an estimate of potential global radiation under clear skies,

$$r_g = 0.5 r_0(\bar{d}/d)^2 \sin(\phi)\tan(1 + \frac{\tau}{\tan(p_{0.5} \sin^{-1} \phi)}).$$

The direct fraction of photosynthetically active radiation, $\Phi_b$, is estimated (Weiss and Norman 1985):

$$\Phi_b = \frac{r_d(PAR)}{r_g(PAR)} \left[1 - \left(\frac{0.9 - r_{obs}/r_g(SWR)}{0.7}\right)^{\frac{2}{5}}\right],$$

where $r_d(PAR)$ and $r_g(PAR)$ are potential direct and global radiation of the photosynthetically active wave band, respectively, computed from Equations 4 and 6 using $r_0 = 600$ W m$^{-2}$, $r_{obs}$ is measured global short-wave radiation and $r_g(SWR)$ is potential global short-wave radiation, computed from Equation 6 using $r_0 = 1380$ W m$^{-2}$. To avoid negative beam fraction values, the ratio of $r_{obs}$ to $r_g(SWR)$ is not allowed to exceed 0.9 (Weiss and Norman 1985).

Measured photosynthetic photon flux density, $q$, is divided into the direct and diffuse components, $q_d$ and $q_g$ respectively:

$$\begin{cases} q_b = \Phi_b q \\ q_d = (1 - \Phi_b) q \end{cases}$$

*Penetration of photon flux into the canopy*

If we assume that (i) the phytoelements are opaque horizontal plane objects, (ii) the phytoelements have a uniform azimuthal distribution, (iii) the penumbra is negligible because of the size of the phytoelements, and (iv) the distribution of diffuse sky radiation is uniform, then the photon flux density on a phytoelement inside the canopy is only formed by the direct and diffuse photon fluxes that penetrate the canopy. Diffuse photon flux density incident on phytoelement $p$ inside the canopy, $q_d(p)$, can be estimated by considering the average gap frequency of the canopy over the phytoelement, $\bar{F}_d(p)$, as the proportion of the above-canopy diffuse photon flux density that penetrates to $p$ (Nilson 1992):

$$q_d(p) = \bar{F}_d(p) q_d.$$  

Penetration of direct photon flux to phytoelement $p$ (existence of sunflecks) is a binary random phenomenon that depends on
the existence of a gap between the phytoelement and the sun (Nilsen 1992). Global photon flux density incident on phytoelement \( p \), \( q_d(p) \), thus depends on the existence of a sunfleck:

\[
\begin{align*}
q_d(p) &= q_0 + \bar{F}_d(p)q_\alpha, & \text{if } p \text{ is in a sunfleck} \\
q_d(p) &= \bar{F}_d(p)q_\alpha, & \text{if } p \text{ is not in a sunfleck} ,
\end{align*}
\]

where \( q_0 \) and \( q_\alpha \) are computed according to Equation 8.

The probability of a canopy gap occurring between the sun and phytoelement \( p \), \( P_g(p,p,\Theta) \), is estimated as a function of the path length (m) between the canopy envelope and phytoelement toward the sun (direction of direct photon flux), \( s(p,\phi,\Theta) \), and the extinction coefficient, \( k_\phi \) (dimension m\(^{-1}\)), which integrates the effects of foliage density and distribution on gap probability (cf. Nygren et al. 1993a):

\[
P_g(p,p,\Theta) = \exp[-k_\phi s(p,p,\Theta)].
\]

The average gap frequency over the phytoelement \( p \) is estimated by integrating the directional gap probabilities, computed in directions \( (\phi',\Theta') \) according to Equation 11, over the hemisphere above \( p \) (Nilsen 1992):

\[
\bar{P}_d(p) = \int_0^{\pi/2} \int_0^{\pi/2} P_g(p,\phi',\Theta') \cos \phi' \sin \phi' d\phi' d\Theta'.
\]

Equation 12 is estimated as the average of gap probabilities in 24 directions.

Shoot growth of \( E. poeppigiana \) follows a periodic pattern; periods of abundant leaf flush alternate with cycles of slow growth (Borchert 1980). Under humid tropical conditions, the periodicity of shoot growth may be observed even at pruning intervals of 5–6 months (Rebottaro 1992, Nygren et al. 1993a). The periodicity of leaf flush and shoot growth also affects the optical properties of the canopy. Nygren et al. (1993a) observed that, within the canopy of \( E. poeppigiana \), the value of the extinction coefficient followed a cyclic pattern during a pruning interval. Using the age of the canopy as an indicator of canopy development, the value of the extinction coefficient can be estimated by applying an empirical function (Nygren et al. 1993a):

\[
k_\phi = \alpha_\phi + 0.57 \sin(0.24 t_w),
\]

where \( t_w \) is the time from pruning in weeks and \( \alpha_\phi \) is a parameter that effectively describes the average optical density of the foliage. The amplitude (0.57) and longitude (0.24) of Equation 13 were reproduced when the equation was adjusted to another field data set (Rebottaro 1992); however, the value of \( \alpha_\phi \) is variable; e.g., Nygren et al. (1993a) reported a value of 2.25, whereas adjustment to the data of Rebottaro (1992) gave 3.32.

Leaf CO\(_2\) exchange

A leaf CO\(_2\) exchange model developed for \( E. poeppigiana \) (Nygren 1995a) was used to estimate instantaneous assimilation rate. The model assumes that a phytoelement is uniformly irradiated and that there is no water deficit restricting leaf CO\(_2\) exchange. The environmental variables of the model are photon flux density incident on phytoelement \( p \), \( q_d(p) \), computed according to Equation 10, ambient CO\(_2\) concentration, \( c_a \), and leaf temperature, which is replaced by air temperature, \( T_a \), in CANEX. The assimilation rate of phytoelement \( p \), \( a(p) \), is computed as the difference between photosynthesis and daytime respiration (Nygren 1995a):

\[
a(p) = \pi_p \frac{k_\phi q_d(p) \kappa c_a}{k_\phi q_d(p) + \kappa c_a} - \left[r_m(20) \exp[k_r(T_a - 20)] + \alpha_r/c_a \right],
\]

where \( \pi_p \) is the relative photosynthetic capacity, \( k_\phi \) is the quantum yield for incident photon flux, \( \kappa \) is the product of total conductance of the CO\(_2\) pathway from the outside air to the chloroplast and carboxylation efficiency, \( r_m(20) \) is metabolic (dark) respiration rate at 20 °C, \( k_r \) is the rate of change of the metabolic respiration rate, and \( \alpha_r \) is the photosynthesis parameter. Leaf age, \( a \), is used to describe the effect of physiological leaf development on relative photosynthetic capacity (Nygren 1995a):

\[
\pi_p = \frac{\alpha_\pi - \beta_\pi a}{1 + \exp(\gamma_\pi - k_\pi a)} \text{ if } a \leq a_m - 6 \text{above } \pi_p = \alpha_\pi' - \beta_\pi' a, \text{ if } a >> -a \text{sub roman m}^\text{n}\wedge\text{6}.
\]

where \( k_\pi \) is the initial rate of change in relative photosynthetic capacity and \( \alpha_\pi, \beta_\pi, \gamma_\pi, \alpha_\pi', \beta_\pi' \) are parameters of the relative photosynthetic capacity function.

Field data

Study site

Field measurements were made at the experimental farm of the Centro Agronómico Tropical de Investigación y Enseñanza (CATIE), in Turrialba, Costa Rica (9°53’ N, 83°39’ W, 600 m a.s.l., humid tropical climate). The experiment consisted of two plots. One plot was composed of 30 trees, the root systems of which were separated by a plastic barrier down to a depth of 1 m and the ground was kept clear by manual weeding to facilitate root and nodule sampling. Another group of 30 trees was grown without root enclosures and weeding, but the herbaceous ground-cover was cut every two months. Hereafter, the plots will be referred to as the clear and ground-cover plots, respectively.

The experiment was established in March 1991 at a planting density of 4 × 4 m. Tree material consisted of four clones selected by the Nitrogen Fixing Tree Project of CATIE (Sources 2660, 2662, 2687 and 2693), planted as 1.5 m-tall, rooted cuttings, and a half-sib family (Source 2431 of the Latin American Forest Seed Bank, CATIE), planted as greenhouse-grown, 4-month-old seedlings. There were six trees of each source in each plot planted in a completely randomized design.

On December 12, 1991, trees was pruned completely and
pollarded to 1.5 m, except for Sources 2431 and 2687 in the ground-cover plot. A second and third pruning were carried out on all trees on June 12, 1992 and November 18, 1992, respectively, in accordance with the normal management practice for _E. poeppigiana_ on Costa Rican coffee farms and CATIE’s alley cropping experiments.

An automatic weather station (Delta-T Devices, Cambridge, U.K.) at the site recorded global short-wave radiation and photosynthetic photon flux density every 10 s, and the 10-min mean was stored in a data logger. Instantaneous air temperature was recorded every 10 min. The average atmospheric pressure in Turrialba is 94.2 ± 0.6 kPa throughout the year (Francisco Jiménez, CATIE, personal comm.), and the average atmospheric transmittance under clear skies is 0.610 from March to May and 0.674 during the rest of the year (P. Nygren, unpublished observations). The value for March, April and May is lower than for other months because of smoke from the burning of sugar cane fields in the Turrialba valley. Other climatic data have been described by Nygren (1995a).

**Input data for simulations**

The first leaves emerged 2–3 weeks after pruning. Whole-canopy leaf area and biomass were determined at 7 weeks after pruning and every 4 weeks thereafter by measuring the diameters of all branches and applying the equations presented by Nygren et al. (1993b) for the relationship between branch cross-sectional area and leaf biomass and area supported by it. Because the relationship is different for young unbifurcated branches than for fully lignified, bifurcated main branches, the relationship for young branches was used for the first measurements after each pruning (January 30 and July 29, 1992), and the relationship for bifurcated main branches was used for the other measurements. Canopy height and diameter were measured on the same occasions.

Average values for the development of canopy dimensions and leaf area between the first and second pruning, and between the second and third pruning, were used to estimate canopy CO$_2$ exchange. Hereafter, the intervals between prunings will be called the second and third interval, respectively. Simulations were carried out separately for each _E. poeppigiana_ source and both pruning intervals, and during the third interval for both plots. No simulations were performed with the tree data for the ground-cover plot during the second interval because of poor growth of the trees. The weather data sets measured during each interval were used in the simulations.

To test the assumption that phytoelements are horizontal plane objects, leaf inclination angle with respect to horizon was measured at 0800, 1200 and 1430 h solar time under clear skies on three occasions during the second interval (8, 13 and 17 weeks after pruning) in 30 randomly selected leaves.

**Estimation of whole-tree carbon balance**

The complete carbon balance of _E. poeppigiana_ was analyzed over the whole pruning interval. Total assimilation and foliage respiration at night were estimated by CANCEx. The production (i.e., sum of biomass increment and turnover) of foliage, branches (divided into unliignified green twigs and woody branches), nodules and fine roots and increment of stem wood and transport roots was determined. Because no loss of branches was observed during a pruning interval, branch biomass at pruning was used as the estimate of branch production. Assimilated CO$_2$ was converted to dry matter equivalents by multiplying by 28.5 g mol$^{-1}$ (Landsberg 1986), which assumes a dry matter C content of 42% (Grace et al. 1987).

Foliage and branch biomass at pruning, and litterfall and stem increments during a pruning interval were determined as described by Nygren (1995a). Nodules were analyzed for three periods to study the development of the carbon assimilatory system following pruning.

**Simulation procedure**

Because the output of CANCEx depends on two probabilistic phenomena—the spatial distribution of the foliage and the occurrence of sunflecks—sample runs are made to obtain a reliable average of whole-canopy assimilation. The number of sample runs required for each day of the simulation period was estimated from a presample of 10 runs by (Roberts et al. 1993):

$$n = \left(\frac{10}{\sigma^2} \right) \frac{1}{L},$$  

(16)

The ratio of fine root production to total foliage production, which was 0.12 in both Sources 2431 and 2687, was used to estimate fine root production in the other sources, as well as in all sources during the third interval.

To estimate transport root (diameter > 2 mm) increment, we computed the average ratio of root to stem biomass from data compiled by Cannell (1982). Root biomass was one fourth of stem biomass, so we estimated the transport root increment from the stem increment by multiplying it by 0.25. To estimate the amount of carbon used in nodule respiration, we calculated the ratio of C lost in nodule respiration to C used in nodule production from the data presented by Hoo et al. (1990). The amount of carbon used in fine root respiration was estimated from the ratio of C lost in fine root respiration to C used in fine root production in the same data set. The ratios were 2.51 and 1.48 for nodules and fine roots, respectively.

Carbon assimilation and foliage night respiration were computed for each 4-week-period between the determinations of canopy leaf area and biomass. These data were compared with the measured canopy foliage biomass and litter fall during the respective periods to study the development of the carbon balance of the assimilatory system following pruning.
where \( n \) is the number of sample runs needed, \( t \) is the Student’s \( t \)-value for 9 degrees of freedom in the two-tailed test at 5%, \( \sigma \) is the standard deviation of diurnal assimilation in the trial runs, \( t \) is the required length of the confidence interval of the mean as a proportion of the mean, and \( \bar{A}_d \) is the mean of diurnal assimilation in the trial runs. The number of simulations to be run for each tree and weather data combination was determined such that the length of the confidence interval was less or equal to 10% of the diurnal mean assimilation on a minimum of 95% of the days included in a pruning interval.

The number of runs needed to fulfill our criteria varied from 30 to 50 for the third interval and from 40 to 70 for the sunnier second interval. The variation in diurnal assimilation was higher on sunny days (Figure 2). However, the total assimilation over longer periods appeared to be conservative; the coefficient of variation of total assimilation over a 5- to 6-month period was less than 5%. We present and analyze the assimilation results were within one standard deviation of the measured mean, except for Source 2660 during the second interval (Figure 3) coincided with a severe defoliation of young leaves caused by an attack of adult June beetles (Phyllophaga menetriesi, Coleoptera: Scarabaeidae) at the beginning of May 1992 (21 weeks after pruning).

To compare measured leaf litter mass with simulated values (which are true model generated values), the measured leaf litter mass was converted to leaf litter area by dividing by the leaf mass to area ratio of senescent leaves, which varies from 58.9 (2687) to 70.3 \( \text{g m}^{-2} \) (2431) (Nygren 1995a). The simulation results were within one standard deviation of the measured mean, except for Source 2660 during the second interval (Figure 4). The proportion of explained variance was only 0.28, but no systematic bias was observed.

The assumption of phytoelements as horizontal plane objects is supported by the finding that 55% of the leaves were horizontal, or diverged from it by less than 10°, and 80% diverged from it by less than 30° (Figure 5). No solar tracking was observed. In the morning, there were fewer completely horizontal leaves, but the total number of horizontal leaves and leaves inclined 5° from the horizontal was the same at noon and during the afternoon (Figure 5).

For all sources, simulated leaf area density (LAD = canopy leaf area/canopy volume) and the value of \( \alpha_L \) observed in the clear plot. The values of parameter \( \alpha_L \) used in the simulations are presented in Table 1.

Because of the importance of parameter \( \alpha_L \) for whole-canopy assimilation and carbon balance, we studied the sensitivity of total assimilation to changes in \( \alpha_L \) during the third interval in Sources 2431 (highest value of \( \alpha_L \)) and 2660 (lowest value of \( \alpha_L \), excluding Source 2662). The value of \( \alpha_L \) changed by ±10, 20 and 40% from the value that complied with the carbon balance.

### Results

#### Canopy development

There were significant differences between sources in tree dimensions and leaf areas at the time of the prunings and the trees growing in the ground-cover plot were smaller than those growing in the clear plot (Table 2). Typical simulated canopy leaf area development patterns are presented in Figure 3. Equation 2 provided a satisfactory description of the canopy leaf area during different phases of canopy development. The cessation in simulated leaf area development during the second interval (Figure 3) coincided with a severe defoliation of young leaves caused by an attack of adult June beetles (Phyllophaga menetriesi, Coleoptera: Scarabaeidae) at the beginning of May 1992 (21 weeks after pruning).

<table>
<thead>
<tr>
<th>Tree source</th>
<th>Second interval</th>
<th>Third interval</th>
</tr>
</thead>
<tbody>
<tr>
<td>Clear</td>
<td>Ground-cover</td>
<td></td>
</tr>
<tr>
<td>2431</td>
<td>2.11</td>
<td>1.75</td>
</tr>
<tr>
<td>2660</td>
<td>1.80</td>
<td>1.34</td>
</tr>
<tr>
<td>2662</td>
<td>1.32</td>
<td>1.10</td>
</tr>
<tr>
<td>2687</td>
<td>2.17</td>
<td>1.44</td>
</tr>
<tr>
<td>2693</td>
<td>2.05</td>
<td>1.53</td>
</tr>
</tbody>
</table>

Table 1. Values of \( \alpha_L \) (in Equation 13), used in the simulations for the four clones and a half-sib family (2431) of Erythrina poeppigiana.
second interval, there was a steady decline in LAD in Sources 2660 and 2662, whereas a minimum LAD was observed at 17 weeks after pruning in Sources 2431 (Figure 6), 2687 and 2693, which coincided with a heavy litterfall. Shedding of old leaves (> 87 days in Source 2431; Figure 6) formed an empty volume inside the canopy that was subtracted from the total volume in the computation of LAD. During the third interval there was a steady decline in LAD in all sources.

Extinction coefficient
The extinction coefficient, $k_g$, was higher during the second interval (Figure 6), indicating a smaller canopy gap frequency according to Equations 11 and 12. The extinction coefficient generally followed LAD development, except at the end of both intervals, when the extinction coefficient increased and LAD declined.

The value of parameter $\alpha_g$ in Equation 13, which determines the average value of the extinction coefficient, was closely correlated with average LAD (computed from 7 weeks after pruning onward) during a pruning interval (Figure 7). When the outlying data for Source 2662 were excluded, the value of $\alpha_g$ could be estimated from the average leaf area density, $\bar{D}_l$, by linear regression ($R^2 = 0.93$):

$$
\alpha_g = 0.50 + 0.38\bar{D}_l.
$$

Table 2. Average tree dimensions ± standard deviation measured at the second and third prunings in the clear plot and at the third pruning in the ground-cover plot. Means followed by the same letter within a date and item do not differ significantly (Duncan’s multiple range test at 5%).

<table>
<thead>
<tr>
<th>Tree source</th>
<th>Total height (m)</th>
<th>Canopy height (m)</th>
<th>Canopy diameter (m)</th>
<th>Leaf area ($m^2$)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Clear plot on June 12, 1992 (second pruning)</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2431</td>
<td>3.3 ± 0.59 abc</td>
<td>2.8 ± 0.56 b</td>
<td>3.0 ± 0.88 b</td>
<td>26.3 ± 9.25 bc</td>
</tr>
<tr>
<td>2660</td>
<td>3.7 ± 0.27 a</td>
<td>3.6 ± 0.28 a</td>
<td>4.2 ± 0.36 a</td>
<td>43.9 ± 4.45 a</td>
</tr>
<tr>
<td>2662</td>
<td>3.4 ± 0.61 ab</td>
<td>2.9 ± 0.59 b</td>
<td>4.0 ± 0.79 a</td>
<td>32.5 ± 9.41 bc</td>
</tr>
<tr>
<td>2687</td>
<td>2.9 ± 0.55 bc</td>
<td>2.8 ± 0.58 b</td>
<td>3.6 ± 0.51 ab</td>
<td>33.9 ± 8.43 b</td>
</tr>
<tr>
<td>2693</td>
<td>2.6 ± 0.67 c</td>
<td>2.4 ± 0.62 b</td>
<td>3.3 ± 0.43 b</td>
<td>22.8 ± 6.51 c</td>
</tr>
<tr>
<td><strong>Clear plot on November 18, 1992 (third pruning)</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2431</td>
<td>3.7 ± 0.36 b</td>
<td>3.2 ± 0.26 bc</td>
<td>3.3 ± 0.79 c</td>
<td>27.6 ± 11.04 c</td>
</tr>
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<td>4.4 ± 0.30 a</td>
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<td>48.2 ± 6.20 a</td>
</tr>
<tr>
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<td>4.3 ± 0.59 ab</td>
<td>38.0 ± 9.95 b</td>
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<tr>
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<td>3.7 ± 0.59 b</td>
<td>4.4 ± 0.61 ab</td>
<td>36.4 ± 7.08 bc</td>
</tr>
<tr>
<td>2693</td>
<td>3.4 ± 0.50 b</td>
<td>3.3 ± 0.51 bc</td>
<td>3.9 ± 0.46 b</td>
<td>27.4 ± 4.87 c</td>
</tr>
<tr>
<td><strong>Ground-cover plot on November 18, 1992 (third pruning)</strong></td>
<td></td>
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<td></td>
<td></td>
</tr>
<tr>
<td>2431</td>
<td>2.4 ± 0.54 ab</td>
<td>1.4 ± 0.33 b</td>
<td>1.9 ± 0.43 b</td>
<td>7.4 ± 3.42 b</td>
</tr>
<tr>
<td>2660</td>
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<td>3.1 ± 0.49 a</td>
<td>21.2 ± 3.36 a</td>
</tr>
<tr>
<td>2662</td>
<td>2.8 ± 0.63 a</td>
<td>2.0 ± 0.93 b</td>
<td>3.1 ± 0.92 a</td>
<td>19.3 ± 11.97 a</td>
</tr>
<tr>
<td>2687</td>
<td>2.5 ± 0.57 ab</td>
<td>2.2 ± 0.48 ab</td>
<td>2.6 ± 0.81 ab</td>
<td>13.6 ± 5.82 ab</td>
</tr>
<tr>
<td>2693</td>
<td>1.9 ± 0.71 b</td>
<td>1.7 ± 0.61 b</td>
<td>2.3 ± 0.63 ab</td>
<td>8.3 ± 5.22 b</td>
</tr>
</tbody>
</table>

Figure 3. Simulated (lines) leaf area development of Source 2660 of *Erythrina poeppigiana* and leaf areas measured in the field experiment (points) during the second and third intervals in the clear plot and during the third interval in the ground-cover plot.

Figure 4. Litterfall from four clones and a half-sib family (2431) of *Erythrina poeppigiana*, simulated by CANCEX (columns) and measured average ± standard deviation (circles with error bars), during the second and third pruning intervals in the clear plot.
Combining Equations 13 and 17 gives a new expression for the extinction coefficient:

$$k_g = 0.38\overline{D_l} + 0.50 + 0.57\sin(0.24t_w).$$  

(18)

Defining the periodic factor of Equation 18 as:

$$\mu = 0.50 + 0.57\sin(0.24t_w).$$  

(19)

we can combine Equations 11 and 18 to get a new expression for the computation of gap probability:

$$P_g(p,\phi,\Theta) = \exp\left[-(0.38\overline{D_l} + \mu)s(p,\phi,\Theta)\right].$$  

(20)

These formulations are similar to the theoretical model presented by Nilson (1992) for computing canopy gap frequency in an isolated plant. Thus, the gap frequency over a point at depth $s$ in the canopy depends on the average LAD, the mean projection of the unit foliage area onto a plane perpendicular to the direct photon flux, 0.38 in Equation 20, and the path length from the point to the canopy envelope. The parameter $\mu$ is a correction factor describing the effect of canopy development on LAD and foliage distribution. This interpretation of $\mu$ is consistent with the simulated development of an $E. poeppigiana$ canopy, as well as with field observations (Rebottaro 1992). The value of $\mu$ is highest at the beginning of a pruning interval when the canopy is small and dense, and it decreases, reaching a minimum at 20 weeks after pruning (cf. Figure 6) when all the denser foliage is shed and the canopy is non-homogeneous. Theoretically, the gap frequency is lower in homogeneous canopies than in non-homogeneous canopies (Nilson 1971).

**Carbon dioxide assimilation and carbon balance**

Simulated daily assimilation was a function of canopy leaf area and daily photon flux (Figure 8). Canopy leaf area determined the general trend during a pruning interval, whereas daily photon flux caused considerable variation between days with roughly the same canopy leaf area. Cumulative assimilation increased linearly as a function of intercepted photon flux in all sources (Figure 9). The molar ratio of total assimilation to intercepted photon flux varied from 1.26 to 1.69%, except in Source 2662 where it was 1.03–1.12% (Table 3). The overall ratios in Table 3 were the same as the slopes of the lines in Figure 9. The intercepts were small (−4.22 to 2.27) although statistically significant. Potential photon exposure was computed by integrating the product of the canopy leaf area and daily photon flux over the whole simulation period. The ratio of intercepted photon flux to potential photon exposure was higher in Source 2662 than in the other sources (39.9–52.1 versus 27–35%) (Table 4).

Carbon balance estimates for trees growing in the clear plot during the second and third intervals are presented in Table 3. Simulated whole-canopy CO$_2$ assimilation varied from 3.37 kg of C (281 mol) in Source 2693 to 6.83 kg (569 mol) in Source 2660 during the second interval and the corresponding values during the third interval were 3.89 kg (324 mol) to 7.22 kg (602...
mol. Although the second interval was 3 weeks longer than the third interval, the total assimilation was lower during the second interval. This may have been partly caused by a beetle attack at the beginning of May 1992. The coefficient of variation of the biomass components of the carbon balance, determined from field data, was typically 20–35%. It was highest in Source 2431, at 59 and 43% during the second and third intervals, respectively. In Source 2660, which showed least within-source variation, the respective coefficients of variation for the second and third intervals were 10 and 15%, respectively.

About 16–24% of assimilate was lost from the foliage as night respiration. The proportion of harvestable biomass (leaves, green twigs and woody branches at pruning) was highest (45% during both intervals) in Source 2662, and varied from 32 to 41% in other sources. Allocation to below-ground biomass was highest (10% during both intervals) in Source 2431. The proportional differences in carbon allocation between sources was small, and the between-source productivity differences in harvestable biomass seemed to be more affected by differences in total assimilation.

At the beginning of both intervals, a high proportion of carbon was allocated to the production and maintenance of the assimilatory system (Figure 10). At 7 weeks after pruning, carbon allocation to the assimilatory system was higher or only slightly less than the cumulative assimilation in all sources (average 110 and 100% during the second and third intervals, respectively), indicating the important role of reserve carbohydrates for growth. In the fast-growing Sources 2660 and 2662, allocation to the assimilatory system slightly exceeded the cumulative assimilation even at 11 weeks after pruning, whereas a positive balance was observed in the other sources. At 19 weeks after pruning, proportional allocation to the assimilatory system was 50–65% in all sources, and varied between 45 and 57% (Sources 2660 and 2693, respectively) at the end of both pruning intervals.

Equation 17 was used to compute $\alpha_g$ for the trees in the ground-cover plot during the third interval in all sources except Source 2662. The value of $\alpha_g$ for Source 2662 was computed by applying the ratio of $\alpha_g$ to average LAD in Source 2662 in the clear plot (0.37). Because not all biomass items were determined for the ground-cover plot, the ratio of harvestable biomass to total assimilation was computed, and compared to the respective ratio in the clear plot (Table 3). The proportion of harvestable biomass was 39% in Source 2662 compared to only 21–24% in the other sources, indicating higher allocation to the belowground biomass and consequently higher below-ground respiration in trees growing in the ground-cover plot. Foliar night respiration as a proportion of total assimilation varied from 14 to 18%, which was slightly less than in the clear plot.

Total assimilation was sensitive to $\alpha_g$ (Figure 11). A 10% change in the value of $\alpha_g$ caused about the same change in total assimilation. However with reductions of 20 to 40% in the value of $\alpha_g$, total assimilation increased in a much higher proportion. When the value of $\alpha_g$ was increased, total assimilation decreased in a slightly higher proportion. The effect of $\alpha_g$ on the intercepted photon flux followed the same pattern. Thus, the model is sensitive to the value of $\alpha_g$, or more generally, the value of the extinction coefficient.
Table 3. Carbon balance (g C tree\(^{-1}\)) of *Erythrina poeppigiana* trees growing in the clear plot during the second (December 12, 1991 to June 12, 1992) and third (June 12, 1992 to November 18, 1992) pruning intervals and in the ground cover plot during the third pruning interval (June 12, 1992 to November 18, 1992).

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Tree source</th>
<th>2431</th>
<th>2660</th>
<th>2662</th>
<th>2687</th>
<th>2693</th>
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<td></td>
<td></td>
<td></td>
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<td></td>
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<tr>
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<td>4835</td>
<td>3715</td>
<td>3368</td>
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<td>884</td>
<td>786</td>
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<td>160</td>
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<td>259</td>
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<td>198</td>
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<td>1.52%</td>
<td>1.03%</td>
<td>1.26%</td>
<td>1.46%</td>
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<td>884</td>
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<td>2487</td>
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<td>1.63%</td>
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<td>1.37%</td>
<td>1.59%</td>
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<td>1560</td>
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<tr>
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<td>590</td>
<td>364</td>
<td>341</td>
<td>289</td>
</tr>
<tr>
<td>Foliage at pruning(^2)</td>
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<td>495</td>
<td>634</td>
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<td>909</td>
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<td>519</td>
<td>325</td>
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<td>24%</td>
<td>39%</td>
<td>23%</td>
<td>21%</td>
</tr>
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<td>Reference proportion(^6)</td>
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<td>36%</td>
<td>45%</td>
<td>40%</td>
<td>35%</td>
</tr>
<tr>
<td>Assimilation/Intercepted PF(^5)</td>
<td></td>
<td>1.46%</td>
<td>1.69%</td>
<td>1.12%</td>
<td>1.40%</td>
<td>1.58%</td>
</tr>
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</table>

\(^1\) Simulated value.
\(^2\) Value determined indirectly from literature data.
\(^3\) Value from direct field measurements.
\(^4\) Value determined indirectly from field data.
\(^5\) PF = photon flux.
\(^6\) Harvestable biomass/assimilation in trees growing in the clear plot.
Discussion

Because no measurements of whole-canopy CO$_2$ exchange of *E. poeppigiana* exist, and we did not have the facilities to perform them, the validation of the presented model is based on partial validation of its submodels. We focus on the canopy development and radiation regime submodels, because the leaf CO$_2$ exchange model has been discussed in detail elsewhere (Nygren 1995a).

Equations 2 and 3 describing canopy leaf area development and foliole area growth fitted the field data well. The June beetle attack on the young leaves was severe enough to be observed in the time series of canopy leaf area development, and CANEX simulated the phase correctly by adjusting the phytoelement emergence rate to zero (cf. Figure 3). The most important insect pests observed in *Erythrina* spp. in Costa Rica all attack the young leaves (Hilje et al. 1993), and CANEX appears to simulate leaf area development satisfactorily despite the damage to young leaves. The omission of explicit insect damage from the model is thus not a severe restriction to its application. The leaf angle distribution appeared to be planophile, as assumed in the model development.

The simulated litterfall did not coincide with the field data as well as the simulated leaf area development. However, the litterfall measurements are subject to two uncertainties. First, the applied leaf mass/leaf area ratio does not necessarily apply to all leaf litter collected, because the leaves of *E. poeppigiana* start to decompose rapidly, and even weekly sampled litterfall may contain partially decomposed, lighter material. Second, the weevil *Chalcodermus dentipes* (Coleoptera: Curculionidae) lays eggs inside the young *Erythrina* shoots, resulting in the shedding of young leaves (Hilje et al. 1993), which are lighter than senescing leaves (Nygren 1995a). *Chalcodermus dentipes* was also observed at our study site. Thus, the correlation between the simulated and measured litterfall may be considered satisfactory, and the canopy development submodel as a whole seems to be reasonably accurate.

The applied leaf CO$_2$ exchange model explains the photosynthetic capacity as a function of leaf age (Nygren 1995a), and, when combined with the canopy development model, takes into account the stratification of photosynthetic characteristics within the canopy. A more sophisticated stratification

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**Table 4.** Photon flux intercepted (simulated value) as a proportion of the total potential photon exposure to whole leaf area in four clones and a half-sib family (2431) of *Erythrina poeppigiana*.

<table>
<thead>
<tr>
<th>Tree source</th>
<th>Second interval</th>
<th>Third interval</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Clear</td>
<td>Ground-cover</td>
</tr>
<tr>
<td>2431</td>
<td>28.3%</td>
<td>27.8%</td>
</tr>
<tr>
<td>2660</td>
<td>26.1%</td>
<td>28.8%</td>
</tr>
<tr>
<td>2662</td>
<td>39.9%</td>
<td>44.6%</td>
</tr>
<tr>
<td>2687</td>
<td>27.0%</td>
<td>31.5%</td>
</tr>
<tr>
<td>2693</td>
<td>29.4%</td>
<td>31.1%</td>
</tr>
</tbody>
</table>
model, based on changes in leaf nitrogen concentration within the canopy, has recently been presented by Wu (1993).

We combined a realistic canopy development pattern with an idealized radiation regime submodel. Although the canopy development model would allow the application of more sophisticated models for the penetration of photon flux into the canopy, including the procedural approach presented by Myneni and Impens (1985a), the idealized model provided a good empirical fit to measured data of the photon flux density profiles in the canopy (Rebottaro 1992, Nygren et al. 1993a).

The extinction coefficient integrated the effects of LAD, leaf angle and clumping of the foliage on the penetration of photon flux into the canopy (Nygren et al. 1993a). The importance of these effects was studied by deriving Equation 20 from Equations 11 and 13 on the basis of the simulation results. Equation 20 is in accordance with theoretical considerations about the effect of canopy structure on gap frequency (cf. Nilson 1971, 1992). The ratio of intercepted photon flux to the potential photon exposure was of about the same order as the values that can be calculated from the data presented by Green (1993) for an isolated walnut tree.

The extinction coefficient integrated the effects of LAD, leaf angle and clumping of the foliage on the penetration of photon flux into the canopy (Nygren et al. 1993a). The importance of these effects was studied by deriving Equation 20 from Equations 11 and 13 on the basis of the simulation results. Equation 20 is in accordance with theoretical considerations about the effect of canopy structure on gap frequency (cf. Nilson 1971, 1992). The ratio of intercepted photon flux to the potential photon exposure was of about the same order as the values that can be calculated from the data presented by Green (1993) for an isolated walnut tree.

The sources with a low LAD, and consequently high gap frequency, had higher total assimilation during a pruning interval. Sensitivity analysis indicated a strong dependence of total assimilation on the extinction coefficient, as measured by value of the parameter $\alpha_g$. Although the relationship between LAD and gap frequency appeared to be approximately the same within four of the sources included in this study, Source 2662 was an outlier. The ratio of intercepted photon flux to potential photon exposure was highest in Source 2662 (Table 4), but the quantum yield of Source 2662 was lower than that of the other sources (Nygren 1995a). Low quantum yield decreased the assimilation rate in the low-light conditions of the inner canopy, and this was reflected in the ratio of total assimilation to intercepted photon flux (Figure 9 and Table 3).

The higher carbon allocation to the below-ground parts of trees in the ground-cover plot may have been caused by root competition with grasses. Lower allocation to the assimilatory system resulted in lower total assimilation during the pruning interval (Table 3). The degree to which competition affected total assimilation was surprising because production of tree biomass in alley cropping experiments (Kass et al. 1989) is about the same as in the clear plot without competition in our experiment. We assume that alley crop management (e.g., weeding and pest control) favors tree growth to an extent that negates the effect of crop competition.

The change in carbon allocation to the assimilatory system during a pruning interval has important implications for the management of agroforestry trees. *Erythrina poeppigiana* is apparently dependent on reserve carbohydrates until 11 weeks after pruning, and allocation to the assimilatory system remains high at 15 weeks after pruning. From 19 weeks after pruning onward, the proportion of carbon allocated to foliage is more stable, though a slight decrease was observed toward the end of the pruning intervals. These results are in accordance with the conclusion of Russo and Budowski (1986) that the proportion of leaves in the aboveground biomass (harvested biomass + litterfall) of *E. poeppigiana* is highest at a pruning interval of four months, but the total amount of leaves produced increased slightly with increasing length of the pruning interval. The same pattern has been observed in other woody legumes (Duguma et al. 1988, Catchpoole and Blair 1990).

If *E. poeppigiana* is cultivated to produce forage, then a pruning interval of four months might be considered optimum: the harvest would contain a high proportion of leaves, and almost no leaves would be lost through litterfall. However, it is uncertain whether the reserve carbohydrate pool could fully recover with such a high pruning frequency because of the high carbon allocation to growth and maintenance of foliage until 19 weeks after pruning. Although no reduction in biomass production of *E. poeppigiana* pruned every four months has been observed in short-term studies (Russo and Budowski 1986, Borel and Benavides 1993), long-term data are lacking. In green manure systems, e.g., shade trees with perennial crops (Beer 1988) or alley cropping (Kass et al. 1989), *E. poeppigiana* is pruned twice a year. In these systems, litterfall is not a loss of material as in forage production, but it may be an important factor in the nutrient cycling of the system (Beer 1988).

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