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A minimal model for forest fire regimes

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Summary

We show in this paper how the characteristics of fire recurrency in forests can be theoretically derived from simple informations concerning forest morphology. The task is accomplished by means of a minimal model encapsulating a few assumptions on the interactions between overstorey and understorey species and on the mechanisms of fire development and transmission. The main difference with other models for fire prediction and simulation is that, here, fire is an endogenous variable with purely deterministic dynamics. Nevertheless, the analysis shows that fire recurrency can be chaotic for parameter values corresponding to mediterranean forests. By contrast, the model shows that boreal forests and savannas must experience periodic fires. These general results are in agreement with the studies carried out on many different forests in this century.

Non technical summary

Extensive research on forest fires has shown that fires are only accidental in rain forests, while they are recurrent in other forests. But fire regimes of boreal forests, savannas and mediterranean forests are remarkably different. Indeed, the fire return time is typically 50-200 years in boreal forests, 1-2 years in moist savannas and 5-10 years in arid savannas, and 10-100 years in mediterranean forests. Moreover, the variability of the return time at a given site is not very pronounced in boreal forests and savannas while it is in mediterranean forests. By oversimplifying a bit the overall picture, one could say that fires are: absent in rain forests; periodic at low frequency in boreal forests; periodic at high frequency in savannas; chaotic in mediterranean forests.

We show in this paper how these characteristics can be derived from a simple but general model based only on a few classical assumptions on the interactions between overstorey and understorey species and on the mechanisms of fire development and transmission. The model is purely deterministic and should not be confused or compared with numerous stochastic models for fire prediction. In the model the forest is idealized as two homogenous interacting layers. Each layer is composed of two compartments, the green and the red biomass, the second one identifying the burning biomass. The dynamic behavior of the model is studied through bifurcation analysis and the result is surprisingly neat. It shows that depending upon the value of some strategic parameters the forest can behave in four possible ways corresponding, indeed, to the four distinct fire regimes outlined above. The conclusion is that the assumptions we have incapsulated in our simple model have the power of explaining the fire regimes of rain forests, boreal forests, savannas, and mediterranean forests.

The theory presented in this paper is based on very rough assumptions. For this reason it cannot explain a number of interesting characteristics of forest fires, like those related with diffusion and spatial heterogeneity. In order to deal with these problems one should use a much more complex model which however would make the analysis very heavy if not impossible. By contrast, a remedy for some weaknesses of the present study could be found by slightly modifying the assumptions. For example, post-fire successions or particular surface fires not explained by the present model should become explainable by enlarging the minimal model.

Introduction

Forests can be classified in different ways depending upon the characteristics one likes to focus on. Four important groups are present in many, if not all, classifications (Spurr 1964, Walter 1985, Archibold 1995): 1. rain forests; 2. boreal forests; 3. savannas; 4. mediterranean forests. The definition of each class is usually based on forest morphology. Rain forests are dense and humid and stratification is not marked (Longman and Jeník 1974, Richards 1996). Boreal forests are characterized by high density of large conifers and scarcity of bush (Viereck *et al.* 1983), the prevalent understorey species being bryophytes and lichens (Johnson 1981). By contrast, trees are quite rare while herbs are very dense in savannas (Menaut and Cesar 1979, Huntley and Walker 1982). Finally, in mediterranean forests, both understorey and overstorey species are important and quite interacting (di Castri and Money 1973). The same classification is sometimes based on different arguments, like the characteristics of fire regimes. Indeed, fires are only accidental in rain forests (Sanford *et al.*, 1985, Saldarriaga and West 1986), while they are recurrent in other forests. But fire regimes of boreal forests, savannas and mediterranean forests are remarkably different. Indeed, the fire return time is typically 50-200 years in boreal forests (Rowe and Scotter 1973, Zackrisson 1977, Engelmark 1984, Payette 1989), 1-2 years in moist savannas (Scott 1971, Goldammer 1990) and 5-10 years in arid savannas (Tyson and Dyer 1975, Rutherford 1981), and 10-100 years in mediterranean forests (Kruger 1983, Davis and Burrows 1994). Moreover, the variability of the return time at a given site is not very pronounced in boreal forests (see Bonan 1989 and references therein) and savannas (see Goldammer 1983 and references therein) while it is in mediterranean forests (Kruger 1983). By oversimplifying a bit the overall picture, one could say that fires are: absent in rain forests; periodic at low frequency in boreal forests; periodic at high frequency in savannas; chaotic in mediterranean forests.

In conclusion, the same classification can be obtained in two different ways, namely by looking at forest morphology or at fire regimes. Thus, while it is true that savannas are "...tropical formations where the grass stratum is continuous and important but occasionally interrupted by trees and shrubs; the stratum is burnt from time to time..." (Bourlière and Hadley 1970), it is also true that such a definition contains some redundancy. In fact, the morphology of a given forest uniquely identifies its fire regime. Although this is *a priori* more than conceivable, we are not aware of any formal theoretical derivation of such a property. For this reason, we show in this paper how this property can be derived from a simple but general model based only on a few classical assumptions on the interactions between overstorey and understorey species and on the mechanisms of fire development and transmission. The model is purely deterministic and should not be confused or compared with numerous stochastic models for fire prediction (see, for instance, Van Wagner 1978, Johnson and Wan Wagner 1985, Davis and Burrows 1994, Chao *et al.* 1997). In the model the forest is idealized as two homogenous interacting layers, called upper (*u*) and lower (*l*) layers. Each layer is composed of two compartments, the green (*G*) and the red (*R*) biomass, the second one identifying the burning biomass. The dynamic behavior of the model is studied through bifurcation analysis and the result is surprisingly neat. It shows that depending upon the value of some strategic parameters the forest can behave in four possible ways corresponding, indeed, to the four distinct fire regimes outlined above. The conclusion is that the assumptions we have encapsulated in our simple model have the power of explaining the fire regimes of rain forests, boreal forests, savannas, and mediterranean forests.

A minimal model

We now describe the model on which our analysis is based. It is such a crude simplification of reality that the word model is almost inappropriate. Indeed, models which neglect many of the mechanisms that are known to operate in the field, are sometimes called “minimal” in order to distinguish them from detailed simulation models. Minimal models are based only on a few basic facts which are related with the property one likes to discuss. Thus, a minimal model for forest exploitation (Clark, 1976) will be different from a minimal model for pest outbreak prediction (Ludwig, 1978), or from a minimal model describing the impact of acidic deposition (Gatto and Rinaldi, 1989). In general, simulation models are tuned on a specific forest, while minimal models are used to characterize and classify the behaviors (for example the fire regimes) of large classes of forests.

The identification and the classification of all modes of behavior of a model requires a paramount effort if the model is complex, i.e., if it has more than a few variables and parameters. Spatial heterogeneity is systematically ruled out in minimal models, because it would require to work with partial differential equations or with a great number of ordinary differential equations, thus making the problem untractable. For the same reason, species diversity, seasonalities, age structure and plant physiology are also not considered, unless they are strategically important. Thus, in our minimal model we look only at total biomass (see, for example, Chapter 6 in Shugart 1984) but in order to distinguish crown fires from surface fires, we consider an upper vegetational layer, in general composed of trees of various species, and a lower vegetational layer which, depending upon the forest, is composed of bryophytes, herbs, shrubs, or any mix of these plants.

At time t a tree (or a part of it) is either burning or not burning, so that the biomass of the upper layer can be subdivided into green component, indicated by $G_u(t)$, and red component indicated by $R_u(t)$. Similarly, the biomass of the lower layer is subdivided into green biomass $G_l(t)$ and red $R_l(t)$. Obviously, $R_u(t)$ and $R_l(t)$ are indicators of fire intensity in the two layers at time t . The instantaneous rate of variation of each biomass can be specified through a simple mass balance equation. In particular, the rate of variation of the green biomass of each layer $\dot{G} = dG / dt$ is the difference between a growth rate g (taking into account productivity, natural mortality and competition) and the rate f at which green biomass is attacked by fire. Since fire transforms green biomass into red biomass, the rate of variation $\dot{R} = dR / dt$ of the red biomass of each layer is the difference between f and the rate e at which such a biomass goes extinct. Thus, the minimal model is a fourth order continuous-time model of the form:

$$\dot{G}_u = g_u - f_u \quad (1)$$

$$\dot{R}_u = f_u - e_u \quad (2)$$

$$\dot{G}_l = g_l - f_l \quad (3)$$

$$\dot{R}_l = f_l - e_l \quad (4)$$

where the first two equations describe the upper layer and the last two the lower layer.

In order to specify the model, we must first define the arguments of the functions e , f and g . Of course, this must be done by trading-off between two conflicting objectives: the realism of the model and its simplicity. Our choice is that the combustion processes of a burning plant are practically uninfluenced by the surrounding biomasses, i.e.,

$$e_u = e_u(R_u)$$

$$e_l = e_l(R_l)$$

As for the fire attack rates, we assume

$$f_u = f_u(G_u, R_u, R_l) \qquad f_l = f_l(G_l, R_u, R_l)$$

because the burning biomass of each layer attacks the green biomasses of both layers. Finally, shadowing and competition for nutrients among plants of different layers imply that both growth rates g_u and g_l depend, in principle, upon green biomasses of both layers. Nevertheless, in the following, we consider the asymmetric case

$$g_u = g_u(G_u) \qquad g_l = g_l(G_u, G_l) \qquad \frac{g_l}{G_u} < 0$$

corresponding to forests in which interlayer competition for nutrients is negligible and understorey species are negatively influenced by shadowing.

Figure 1: Influence graph of the minimal model (a) and Vandermeer's model (b). Both models can be interpreted as two coupled oscillators: in case (a) each layer can be an oscillator, while in case (b) each prey--predator pair can be an oscillator.

The structure of the model is described by the influence graph of Fig.1a, which shows that each layer can be interpreted as a prey-predator assembly, where the prey is the green biomass and the predator the red one. As is well known (May 1976) such an assembly can be a biological oscillator, i.e., for suitable functions e, f, g , each single layer can experience periodic fires. Thus, the model is composed of two coupled oscillators. The literature on this topic is very rich (see Strogatz 1994a). It is rooted in a study of Huygens who in the 17th century discovered that two asynchronous clocks could lock their frequencies when they were hanging on the same wall. But frequency locking is only one of the many complex and intriguing behaviors (including deterministic chaos) that can occur when coupling nonlinear oscillators (Strogatz 1994b). In the ecological context, coupled oscillators have been used by Vandermeer (1993) to explain the complex dynamics of communities composed of two populations preyed upon by two predator populations. But the influence graph of Vandermeer's model, see Fig. 1b, is radically different from that of our model. In fact fire transmission between layers corresponds to a beneficial influence between predators, a fact usually not present in other ecosystems where different predators do not interact or interact negatively through interference. In conclusion, even if our model is composed of two prey-predator submodels, the coupling is not standard and the results obtained by Vandermeer cannot be used to predict the fire regimes. In other words, our minimal model is a new model and must be studied *per se*.

The analysis will not be carried out in general, but for a significant class of the functions e, f and g giving rise to the following model:

$$\dot{G}_u = r_u G_u \left(1 - \frac{G_u}{k_u}\right) - \alpha_u \frac{G_u}{G_u + h_{uu}} R_u - \alpha_{ul} \frac{G_u}{G_u + h_{ul}} R_l \quad (5)$$

$$\dot{R}_u = \alpha_u \frac{G_u}{G_u + h_{uu}} R_u + \alpha_{ul} \frac{G_u}{G_u + h_{ul}} R_l - \mu_u R_u \quad (6)$$

$$\dot{G}_l = r_l G_l \left(1 - \frac{G_l}{k_l}\right) - \alpha_{lu} \frac{G_l}{G_l + h_{lu}} R_l - \alpha_{ll} \frac{G_l}{G_l + h_{ll}} R_u \quad (7)$$

$$\dot{R}_l = \alpha_{lu} \frac{G_l}{G_l + h_{lu}} R_l + \alpha_{ll} \frac{G_l}{G_l + h_{ll}} R_u - \mu_l R_l \quad (8)$$

All parameters are indicated by lower case letters and are constant in time, while the four state variables are indicated by capital letters. In the absence of fire ($R_u=R_l=0$), trees grow logistically toward the carrying capacity k_u (see eq. (5)). By contrast, plants of the lower layer do not tend toward their carrying capacity k_l because tree canopy reduces light availability. This has been taken into account by introducing a mortality rate proportional to G_u into eq. (6). Thus, if there is no fire and trees tend toward their carrying capacity, the green biomass of the lower layer tends toward $(1 - k_u/r_l)k_l$.

The fire attack rate f_u and f_l appearing in eqs.(1)-(4) are the sum of two components representing the fire attacks due to the burning biomasses of the two layers. Each component is the product of a burning biomass and a Monod function of green biomass. This means that the amount of green biomass to which the fire is transmitted by each unit of burning biomass increases with the amount of green biomass. In particular, it vanishes when there is no green biomass and tends toward a plateau when green biomass becomes abundant. The half saturation constant h appearing in the Monod function is the density of green biomass at which the fire transmission rate of the burning biomass is half maximum. The maximum fire attack rates within the same layer are denoted by α_u , while the interlayer fire attack rates are denoted by α_{ul} . Finally, as for the functions e , the parameters

in eqs. (5) and (8) represent the rate at which burning trees and burning plants of the lower layer become extinct. In the extinction phase of a severe fire, when G_u is negligible, eq. (6) becomes $\dot{R}_u = -\mu_u R_u$ so that $R_u = R_u(0)\exp(-\mu_u t)$. In other words, crown fires decay exponentially with a time constant $1/\mu_u$. Similarly, surface fires decay exponentially with a time constant $1/\mu_l$. Model (5-8) has fifteen parameters. Five of them ($r_u, k_u, r_l, k_l, \alpha_{ul}$) specify vegetation growth in the two layers, while the others are related to fire characteristics. In order to adapt the model to different classes of forests, the parameters must be assigned properly. The lowest and the highest values of the parameters often refer to savannas and boreal forests, respectively, because in these forests the upper and the lower layer morphologies are somehow extreme.

Table 1 reports the net primary productivity ranges, the biomass ranges and the parameter values we have used in our analysis. Minimum and maximum values of growth rates r and carrying capacities k have been derived from various sources. The range of α_{ul} has been fixed in such a way that the green biomass of the lower layer at equilibrium $(1 - k_u/r_l)k_l$ is between 40% and 90% of its carrying capacity k_l . This reduction is in agreement with studies on savannas and mediterranean forests (Grunow *et al.* 1980, Specht *et al.* 1983). Notice that α_{ul} is minimum in boreal forests, where the plants of the lower layer are shade tolerant, and maximum in savannas.

VEGETATIONAL DATA				
FOREST TYPE	NPP [Kg m ⁻² y ⁻¹]		BIOMASS [Kg m ⁻²]	
	<i>min</i>	<i>max</i>	<i>min</i>	<i>max</i>
Rain	1	3.5	6	80
Boreal	0.4	2	6	40
Savanna	0.2	2	0.2	15
Mediterranean	0.5	1.5	0.7	26

VEGETATIONAL PARAMETERS					
<i>Parameter</i>		<i>min</i>		<i>max</i>	
r_u	[y ⁻¹]	0.05	(<i>b</i>)	1	(<i>s</i>)
r_l	[y ⁻¹]	0.1	(<i>b</i>)	4	(<i>s</i>)
k_u	[10 Kg m ⁻²]	0.15	(<i>s</i>)	3	(<i>b</i>)
k_l	[10 Kg m ⁻²]	0.05	(<i>b</i>)	3	(<i>r</i>)
	[0.1 m ² (Kg y) ⁻¹]	0.003	(<i>b</i>)	16	(<i>s</i>)
FIRE PARAMETERS					
<i>Parameter</i>		<i>min</i>		<i>max</i>	
u	[y ⁻¹]	18	(<i>b</i>)	50	(<i>s</i>)
l	[y ⁻¹]	20	(<i>b</i>)	90	(<i>s</i>)
u	[y ⁻¹]	15	(<i>b</i>)	60	(<i>s</i>)
l	[y ⁻¹]	25	(<i>b</i>)	75	(<i>s</i>)
u	[y ⁻¹]	0.01	(<i>b</i>)	5	(<i>r</i>)
l	[y ⁻¹]	0.01	(<i>b</i>)	5	(<i>r</i>)
h_{uu}	[10 Kg m ⁻²]	0.0015	(<i>s</i>)	0.15	(<i>b</i>)
h_{ul}	[10 Kg m ⁻²]	0.0015	(<i>s</i>)	0.15	(<i>b</i>)
h_{ll}	[10 Kg m ⁻²]	0.0005	(<i>b</i>)	0.15	(<i>r</i>)
h_{lu}	[10 Kg m ⁻²]	0.0005	(<i>b</i>)	0.15	(<i>r</i>)

Table 1: Vegetational data (minimum (*min*) and maximum (*max*) values of net primary productivity (NPP) and biomass) and ranges of vegetational and fire parameters used in the model. Data for rain forests, boreal forests and savannas, are derived from Whittaker and Woodwell (1971) and Whittaker and Likens (1975), while those for mediterranean forests are taken from Lieth (1975), De Bano and Conrad (1978), Hoffmann and Kummerow (1980), Malanson and Trabaud (1987). The type of forest (*r* = rain, *b* = boreal, *s* = savanna) corresponding to extreme parameter values is indicated in parenthesis.

The identification of realistic ranges for the fire parameters is not an easy task because available data are scarce. Let us start from the parameters u and l and recall that their inverses are fire extinction times (see eq. (6) with $G_u=0$ and eq. (8) with $G_l=0$). Thus, the figures reported in Table 1 simply say that extinction of herb fires in savannas is of the order of one week, while extinction of conifer fires in boreal forests can take more than three weeks (see, for example, the data of the Chinchaga River fire of 1950, reported by Johnson 1992). The same figures indicate that the time of fire extinction $1/u$ is higher, in each given forest, in the upper layer and increases from savannas to mediterranean forests and from mediterranean forests to boreal forests, as one should indeed expect by considering the different morphologies of these forests.

In order to estimate β_u and β_l , one should use data on the rate at which fire develops among crowns and among bryophytes, herbs and shrubs at different latitudes. Since good data of such sort are not available, we have followed a simple reasoning based on two facts. First, notice that when the upper layer is at its carrying capacity ($G_u = k_u$) and there is no fire in the lower layer ($R_l = 0$) the rate of variation of the upper layer red biomass (see eq. (6)) is given by

$$\dot{R}_u = \beta_u \frac{k_u}{k_u + h_{uu}} - \beta_u R_u$$

Thus fire cannot develop in the upper layer of a forest if

$$\beta_u \frac{k_u}{k_u + h_{uu}} - \beta_u < 0$$

Since we will assume that $h_{uu} \ll k_u$, this condition is equivalent to

$$\beta_u < \beta_u$$

Similarly, fire cannot develop within the lower layer if $\beta_l < \beta_l$. In the following we will refer to the reverse inequalities $\beta_u > \beta_u$ as conditions for fire development in a single layer. On the other hand, the morphology of the various forests obviously implies that fire development in the upper layer (when the lower layer is not burning) is possible only in boreal and mediterranean forests, while fire can develop in the lower layer (when the upper layer is not burning) only in savannas and mediterranean forests. From the above two facts one can infer that in the two dimensional parameter space (β_u / β_l) the four types of forests should be located as shown in Fig. 2.

Figure 2: Partition of the two dimensional parameter space (β_u / β_l) in four regions corresponding to rain forests, boreal forests, savannas and mediterranean forests. Fire cannot develop in a single layer if the corresponding value of β_u / β_l is greater than unity.

The fire parameters reported in Table 1 are in agreement with Fig. 2 and show that the highest rate of fire development ($\beta_u - \beta_l$) in a single layer is that of the lower layer in savannas.

The two parameters β_u and β_l are coupling parameters (in fact, if β_u were equal to zero, the upper layer would be fully independent of the lower layer). Interlayers fire transmission is rather small, since the inflammable parts of the two layers are often quite separated in space. For this reason, we have chosen $\beta_u \ll \beta_u$ and $\beta_l \ll \beta_l$.

Finally, the half saturation constants h_{uu} and h_{ll} have been fixed between 1% and 5% of the carrying capacity k_u , thus implying that crown fires develop at least at 90% of their maximum speeds (β_u and β_u) even in forests which are at 50% of their upper layer carrying capacity, since

$$\frac{k_u / 2}{k_u / 2 + 0.05 k_u} = 0.90$$

The same criterion has been used to fix the ratios of h_{ll} and h_{lu} to k_l . With this choice, the half saturation constants have practically no role during severe fires, but inhibit the occurrence of fires in immature forests.

Model behavior

In this section we show how model (5-8) behaves for four different parameter settings, corresponding to a typical rain forest, boreal forest, savanna and mediterranean forest, respectively.

Rain forests

In order to determine the parameter setting of a rain forest we first fix the values of r_u , r_l , k_u and k_l in such a way that the point $(r_u/r_l, k_u/k_l)$ falls in the region indicated by "rain forest" in Fig. 2. Since upper and lower layers can hardly be distinguished in rain forests, we have identified them in the model with the same parameter values $r_u = r_l = 23$ and $k_u = k_l = 30$. The other parameter values have been selected within the ranges indicated in Table 1, far from the extreme values which are typical of boreal forests and savannas. Simulations of model (5-8) show that the forest tends toward the same equilibrium independent of initial conditions. Fig. 3 reports the time patterns of green biomasses as predicted by the model starting from the following initial conditions

$$G_u(0) = G_l(0) = \frac{1}{2} k_u \quad R_u(0) = R_l(0) = \frac{1}{10} k_u$$

The patterns of red biomasses are not shown in the figure because they are smaller than 10^{-3} [Kg/m²] after a few weeks, while green biomasses tend toward a plateau. The time needed to reach the equilibrium is of the order of 70 years for both layers. Similar transients are obtained from different initial conditions, and the conclusion is that such a forest tends toward a steady state in which fire is absent. Assuming that this example is a good representative of all rain forests, we could conclude that the minimal model explains why fires can only be accidental (but not recurrent) in rain forests.

Figure 3: Transients of green biomasses as predicted by the minimal model for a rain forest after an accidental fire. Parameter values are $r_u = 0.15$, $r_l = 0.25$, $k_u = 2$, $k_l = 3$, $\alpha = 0.07$, $r_u = r_l = 23$, $k_u = k_l = 5$, $r_u = r_l = 30$, $h_{uu} = h_{ul} = h_{lu} = h_{ll} = 0.045$. The dot on the left border of the figure indicates initial conditions (see text).

Boreal forests

In agreement with Fig.2, one example of boreal forest has been obtained by letting $r_u = 18$, $r_l = 20$, $k_u = 16.5$, $k_l = 21$ so that $r_u/r_l < 1$ and $k_u/k_l > 1$, while the remaining parameters have been fixed in accordance with Table 1. Simulations of model (5-8) show that the forest tends toward the same cyclical behavior independent of the initial conditions. Fig.4, which is in agreement with many data and studies on boreal forests at high latitudes, shows the cyclical patterns of the green biomasses of the upper and lower layer (parameter values are reported in the caption). The patterns of the red biomasses identifying the fires are not shown because, at the scale of the figure, they correspond to impulses with a return time of about 100 years, (the so called "fire frequency", Yarie 1981). Actually, in the simulations the red biomass remains very low (i.e., of the order of 10^{-20} - 10^{-3} [Kg/m²]) during most of the cycle and then jumps to very high values for a few months, during which the green biomass of the lower layer is reduced only by 50% (as indicated in Kasischke *et al.* 1995). After a fire, the green biomass of the lower layer increases for 20-30 yr (while conifers, which grow very slowly, are still almost absent) and then decreases and reaches the pre-fire level

within 60-100 yr, as theorized by Viereck (1983). Finally, when the upper layer green biomass reaches a threshold, a new devastating crown fire very quickly develops. In conclusion, the cycle is set up by the upper layer while the lower layer (which, as a single layer, would not experience recurrent fires because $u/l > 1$) is simply entrained in the fire cycle (Engelmark 1987).

It is worth noticing that some boreal forests experience recurrent surface fires due to litter accumulation on the ground (Kilgore and Taylor 1979). Obviously, such kind of fire cannot be explained by model (5-8), which does not account for litter. It is also important to remark that the fire regime predicted by the minimal model is rigorously periodic, while in reality the fire return time has some variability. An obvious remedy for this would be to add to eqs. (6) and (8) a suitable noise interpreting the randomness of environmental factors facilitating fire development. But this would be somehow against the spirit that supports minimal models, and would, indeed, hide the crude but clear message of our study: the fire return time of a boreal forest is constant and due to the endogenous mechanisms of growth and interactions among layers.

Figure 4: Cyclical patterns of green biomasses as predicted by the minimal model for a boreal forest. Parameter values are $r_u = 0.1$, $r_l = 0.3$, $k_u = 3$, $k_l = 0.1$, $\alpha_u = 0.045$, $\alpha_l = 18$, $\beta_u = 20$, $\beta_l = 0.1$, $\gamma_u = 0.02$, $\gamma_l = 16.5$, $\delta_u = 21$, $h_{uu} = h_{ul} = 0.045$, $h_{lu} = h_{ll} = 0.0015$

Savannas

The case of savannas is somehow dual to that of boreal forests, because the upper layer, cannot experience, as a single layer, recurrent fires, while the lower layer, mainly composed by herbs, can. The selected parameter values are $\alpha_u = 50$, $\alpha_l = 80$, $\beta_u = 53$, $\beta_l = 72$ so that $\alpha_u/\alpha_l > 1$ and $\beta_u/\beta_l < 1$ (see Fig. 2), while the remaining parameters are in agreement with Table 1. Fig. 5 shows the fire cycle which is, again, periodic, but at high frequency (fire return time of about 5 years as in Gill 1975, in Birk and Simpson 1980 and in Rutherford 1981). The cycle is set up by the lower layer and in fact the fire is a surface fire devastating the herbs (the loss in this layer is 90% of the pre-fire biomass), while tree biomass remains almost constant (the loss in this layer is less than 10%, as observed by Hopkins 1965).

Figure 5: Cyclical patterns of green biomasses as predicted by the minimal model for a savanna. Parameter values are $r_u = 0.8$, $r_l = 2.0$, $k_u = 0.5$, $k_l = 0.4$, $\alpha_u = 2$, $\alpha_l = 50$, $\beta_u = 80$, $\beta_l = 1$, $\gamma_u = 53$, $\gamma_l = 72$, $h_{uu} = h_{ul} = 0.0075$, $h_{lu} = h_{ll} = 0.006$.

Mediterranean forests

In accordance with Fig. 2 and following the classification of flammability given in Valette (1990), we have fixed the parameters α_u and α_l of mediterranean forests at $\alpha_u = \alpha_l = 25$, $\beta_u = \beta_l = 0.85$ $\gamma_u = 21.25$, while the other parameters have been fixed in agreement with the data reported by Trabaud *et al.* (1985) and Keeley (1986). Conditions $\alpha_u/\alpha_l < 1$ and $\beta_u/\beta_l < 1$ imply that fires can independently develop in both layers. In other words, in this forest the fire regime is really due to the interactions among two coupled oscillators, and strange attractors (i.e., chaotic regimes) can be expected (Strogatz 1994). Numerous simulations of the model have confirmed this guess and have shown that

the same strange attractor is reached no matter what the initial conditions of the forest are. Fig. 6 refers to this strange attractor by showing the patterns of the green biomasses in the two layers. Fires are recurrent but not periodic and the return time varies from 10 to 36 years, in good agreement with a number of studies (see, for instance, Hanes 1971, Le Houérou 1974, Keeley 1977, Schlesinger and Gill 1978, Horne 1981). Three types of fires can be identified:

1. surface fires (point 1 in Fig. 6) characterized by a very small reduction of tree biomass,
2. mixed fires (point 2 in Fig. 6) characterized by a more important, but not devastating, impact on tree biomass,
3. crown fires (point 3 in Fig. 6) characterized by a severe depletion of tree biomass.

Figure 6: Chaotic behavior of a mediterranean forest: the fire return time varies randomly, as well as the peaks of green biomasses. Parameter values are $r_u = 0.25$, $r_l = 1.5$, $k_u = k_l = 1$, $\alpha = 0.5$, $\beta_u = \beta_l = 25$, $\gamma_u = \gamma_l = 0.1$, $\delta_u = \delta_l = 21.25$, $h_{uu} = h_{ul} = h_{lu} = h_{ll} = 0.015$

After a fire, the shrub biomass first increases, but then decreases when tree canopy intercepts light, in agreement with Schlesinger and Gill (1980) and Trabaud (1994). This can be put into better evidence by a post-fire recovery diagram obtained by plotting $G_l(t)$ versus $G_u(t)$ in the period between two successive fires. This is done in Fig. 7a using the data from year 95 to year 120 of Fig. 6 and in Fig. 7b for an Australian forest (see Specht and Morgan 1981).

(a)

(b)

Figure 7: Two post-fire recovery diagrams: (a) is obtained from the minimal model, by plotting the data of Fig. 6 (years 95-120); (b) is taken from Specht and Morgan (1981) and refers to an Australian forest.

Robustness of the results

We have shown in the previous section that the fire regime of a forest is a consequence of its morphology. But the result has been obtained by analyzing only one particular case for each type of forest, and needs, therefore, to be further validated. In other words, we must verify the robustness of our findings. The proper tool for this is bifurcation analysis (Strogatz 1994), a technique used to identify and classify all possible modes of behavior (the so-called attractors) of a given dynamical system in specified parameter ranges.

Since model (5-8) has four differential equations, its attractors (as well as its saddles and repels) can be equilibria and limit cycles, as in second order systems, but also strange attractors (as we have seen in the previous section). Each parameter setting corresponds to one model of our family (5-8) and therefore to one specific set of attractors, saddles and repellers. If one parameter is slightly perturbed, by continuity the position and the form of the attractors, saddles and repellers in state space will vary smoothly (e.g., a cycle might become slightly bigger and faster) but all trajectories will remain topologically the same (e.g., an attracting cycle will remain an attracting cycle). Only at some particular points in parameter space the above continuity argument will fail.

At these points, called bifurcations points, small variations of the parameters entail significant changes in model behavior. For example, an equilibrium can be stable (i.e., attract all nearby trajectories) for a given parameter setting, but lose its stability if one parameter is varied even of an infinitesimal amount. If this is the case, for the new parameter value the state of the system will not tend toward the equilibrium, but toward another attractor. In two dimensional parameter spaces, bifurcations points identify the so-called bifurcation curves and these curves partition the parameter space into subregions. All the models corresponding to the same subregion have the same qualitative behavior because they have topologically equivalent trajectories. Thus, if we like to produce a complete catalogue of the modes of behavior of a system we must simply determine all its bifurcation curves. This can be done by using specialized software implementing continuation techniques to carry out the computations (Khibnik *et al.* 1993, Kuznetsov 1995). Once a bifurcation point in the parameter space is found, this software produces the entire bifurcation curve passing through that point.

Figure 8: Bifurcation diagram of model (5-8) in the two dimensional parameter space $(u/l, u/l)$ (see Fig. 2). The curves denoted by T , H and F are, respectively, transcritical, Hopf and flip bifurcation curves. Parameter values are: $r_u = 0.25$, $r_l = 1.5$, $k_u = k_l = 1$, $\alpha = 0.5$, $\beta_u = \beta_l = 0.1$, $h_{uu} = h_{ul} = h_{lu} = h_{ll} = 0.015$.

Without going into more details, we show the results of this analysis in Fig. 8, where the two parameters are the nondimensional parameters u/l and u/l used in Fig. 2 to classify forests. All other parameters are fixed at the values indicated in the caption of Fig. 8. The nature of each bifurcation curve is identified by one of the following symbols

T	Transcritical bifurcation
H	Hopf bifurcation
F	Flip bifurcation

All these bifurcations are local bifurcations characterized by some kind of degeneracy of the eigenvalues of a suitable Jacobian matrix, and are, therefore, evaluated with high precision. In the region above curve T , roughly corresponding to rain forests (see Fig. 2), the attractor is a trivial equilibrium of the kind $(G_u, 0, G_l, 0)$, so that the model suggests that fires are absent in rain forests (in reality, accidental fires are possible). In the region above curve H_1 , corresponding to boreal forests (see Fig. 2), the attractor is a low frequency limit cycle, so that the conclusion is that boreal fire regimes are periodic with high return times (in reality, we should expect recurrent fires with low variability of return times). In the region between curves H_2 and F_1 the attractor is a limit cycle with frequency increasing from left to right. Thus, in savannas (see Fig. 2) the fire regime is cyclic (in reality almost cyclic) with low return times. Curves F_1 and F_2 are the first two curves of an infinite sequence of flip bifurcation curves, known as Feigenbaum's cascade (Strogatz 1994). Approaching curve F_1 from the right, the attracting limit cycle gradually loses stability. When curve F_1 is crossed such a limit cycle has a particular period, say T_1 , and becomes unstable, but a new attracting limit cycle appears with a period equal to $2T_1$. Thus, a stable limit cycle of period T_1 is replaced by a new stable limit cycle of period $2T_1$. This is why flip bifurcations are also called period doubling bifurcations. A second period doubling occurs on the second bifurcation curve F_2 , and then a third, a

fourth, and so on, period doublings occur on an infinite sequence of flip bifurcation curves F_3, F_4, \dots . But these curves accumulate very quickly on a curve F , after which the attractor becomes a genuine strange attractor. Actually, the rate of convergence of curves F_i to F is so high that, in practice, F can be hardly distinguished from F_2 . Thus, in the region of Fig. 8 bounded by curve F_2 , corresponding to a subset of mediterranean forests (see Fig. 2), the fire regime is chaotic. In the gray region of Fig. 8 delimited by curves T, H_1 and H_2 , the attractor is a positive equilibrium (G_u, R_u, G_l, R_l) with R_u and R_l very small (of the order of $10^{-3} - 10^{-5}$ of k_u and k_l). Because of the nature of our minimal model, forests of this kind could be interpreted as forests in which very small fires can often occur but never develop. Notice, however, that forests of this kind should be quite rare since the gray region of Fig. 8 is rather narrow. Another interesting feature pointed out by Fig. 8 is that mediterranean forests can also have periodic fire regimes: this happens when one of the two layers is characterized by β close to 1, i.e., when it has no marked tendency to experience fires. This is in agreement with intuition, because under these circumstances one of the two layers (being the dominant oscillator) sets up the cycle, while the other layer is simply entrained (frequency locking).

Fig. 8 proves that the fire regimes of the four particular forests analyzed in the previous section were, indeed, the typical fire regimes of rain forests, boreal forests, savannas and mediterranean forests. Thus, in conclusion, it is true that morphology determines fire regimes.

Discussion

We have shown in this paper that the fire regimes of rain forests, boreal forests, savannas and mediterranean forests can be theoretically derived from their morphologies. We have accomplished this through simulation and bifurcation analysis of an idealized forest model composed of four variables: burning (red) and not burning (green) biomass of the lower and upper layers of the forest. The novelties of this model, with respect to other models (see, for instance, Van Wagner 1978, Johnson and Wan Wagner 1985, Davis and Burrows 1994, Chao *et al.* 1997), are two. Firstly, fire is an endogenous variable of the model which is almost zero for very long periods of time and then suddenly explodes when the mix of green biomasses (fuels) in the two layers becomes critical. Secondly, and perhaps more interesting, the model is purely deterministic but can behave chaotically, for parameter values corresponding to mediterranean forests. By contrast, the model predicts that boreal forests and savannas must experience periodic fires. Since in real forests randomly varying environmental factors and hazards can anticipate or delay the occurrence of a fire with respect to the time dictated by the maturity of the forest, the message emerging from this study is that one should, a priori, expect more regularity in the fire regimes of boreal forests and savannas than in those of mediterranean forests and this is, as already pointed out, in agreement with the studies carried out on many different forests in this century.

The theory presented in this paper is based on very rough assumptions. For this reason it cannot explain a number of interesting characteristics of forest fires, like those related with diffusion and spatial heterogeneity. In order to deal with these problems one should use a much more complex model which however would make the analysis very heavy if not impossible. By contrast, a remedy for some weaknesses of the present study could be found by slightly modifying the assumptions. For example, post-fire successions or particular surface fires not explained by the present model should become explainable by enlarging the minimal model.

But even within the narrow context of the minimal model discussed in this paper, some work remains to be done. First of all, the minimal model could be used to determine, at least qualitatively, the most important impacts that different management policies have on fire frequencies and

intensities. Secondly, the model could perhaps be used to look at the problem of predictability of fires in mediterranean forests from a new perspective. In fact, notions like peak-to-peak dynamics (Schaffer and Kot 1985) could suggest ways for extracting from the minimal model more compact and operational models for fire prediction (see Rinaldi and Solidoro 1998 for a similar application concerning plankton blooms in eutrophic water bodies). Finally, for purely theoretical reasons, it would be interesting to compare the strange attractor we have discovered with strange attractors of other ecological models composed of coupled oscillators (Vandermeer 1993, Hastings *et al.* 1993).

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Literature Cited

- Archibold, O. W. 1995. Ecology of World Vegetation. Chapman and Hall, London.
- Birk, E. M., and Simpson, R. W. 1980. Steady state and the continuous input model of litter accumulation and decomposition in Australian eucalypt forests. *Ecology* 61:481-485.
- Bonan, G. B. 1989. Processes in boreal forest. Pages 9-12 *in* H. H. Shugart, R. Leemans, and G. B. Bonan, eds., *A Systems Analysis of the Global Boreal Forest*. Cambridge University Press, Cambridge.
- Bourlière, F., and Hadley, M. 1970. The ecology of tropical savannas. *Annual Review of Ecology and Systematics* 1:125-152.
- Chao, L., Ter-Mikaelian, M., and Perera, A. 1997. Temporal fire disturbance patterns on a forest landscape. *Ecological Modelling* 99:137-150.
- Clark, C. W. 1976. *Mathematical Bioeconomics: The Optimal Management of Renewable Resources*. John Wiley and Sons, New York.
- Davis, F. W., and Burrows, D. A. 1994. Spatial simulation of fire regime in mediterranean-climate landscapes. Pages 117-139 *in* *The Role of Fire in Mediterranean Type Ecosystems*. Springer Verlag, New York.
- De Bano, L. F., and Conrad, C. E. 1978. The effects of fire on nutrients in a chapparal ecosystem. *Ecology* 59:489-497.
- di Castri, F., and Mooney, H. A., eds. 1973. *Mediterranean Type Ecosystems: Origin and Structure*. Springer Verlag, Berlin.
- Engelmark, O. 1984. Forest fires in the Muddus National Park (Northen Sweden) during past 600 years. *Canadian Journal of Botany* 62:893-898.
- . 1987. Fire history correlations to forest type and topography in Northern Sweden. *Annales Botanici Fennici* 24:317-324.
- Gatto, M., and Rinaldi, S. 1989. Acidic deposition and catastrophes in forests: A tree nutrient model. *Coenoses* 89:81-90.
- Gill, A. M. 1975. Fire and the Australian flora: a review. *Australian Forestry* 38:1-25.
- Goldammer, J. G., ed. 1983. *Fire in Tropical Biota: Ecosystems Processes and Global Challenges*. Springer Verlag, Berlin. Figure 1.
- Grunow, J. O., Groeneveld, H. T., and Du Toit, S. H. 1980. Above-ground dry matter dynamics of the grass layer of a South African savanna. *Journal of Ecology* 68:877-889.
- Hanes, T. L. 1971. Succession after fire in the chapparal of Southern California. *Ecological Monographs* 41:27-52.

- Hastings, A., Hom, C. L., Ellner, S., Turchin, P., and Godfray, H. C. J. 1993. Chaos in ecology: Is Mother Nature a strange attractor? *Annual Review of Ecology and Systematics* 24:1-33.
- Hoffmann, A., and Kummerow, J. 1980. Root studies in the Chilean matorral. *Oecologia* 32:57-69.
- Hopkins, B. 1965. Observations on savanna burning in the Olokemeji forest reserve, Nigeria. *Journal of Applied Ecology* 2:367-381.
- Horne, I. P. 1981. The frequency of veld fires in the Groot Swartberg mountain catchment area, Cape Province. *South African Forestry Journal* 118:56-60.
- Huntley, B. J., and Walker, B. H. 1982. *Ecology of Tropical Savannas*. Springer Verlag, Berlin.
- Johnson, E. A. 1981. Vegetation organization and dynamics of lichen woodland communities in the Northwest Territories, Canada. *Ecology* 62:200-215.
- . 1992. *Fire and vegetation dynamics: studies from the North American boreal forest*. Cambridge University Press, New York.
- Johnson, E. A., and Van Wagner, C. E. 1985. The theory and use of two fire history models. *Canadian Journal of Forest Research* 15:214-219.
- Kasischke, E. S., Christensen, N. L., and Stocks, B. J. 1995. Fire, global warming, and the carbon balance of boreal forests. *Ecological Applications* 5:437-451.
- Keeley, J. E. 1977. Seed production, seed populations in soil and seedling production after fire for two generic pairs of sprouting and nonsprouting chaparral shrubs. *Ecology* 58:820-829.
- . 1986. Resilience of mediterranean shrub communities to fires. Pages 95-112 *in* Resilience in Mediterranean-Type Ecosystems. W. Junk Publishers.
- Khibnik, A. I., Kuznetsov, Y. A., Levitin, V. V., and Nikolaev, E. V. 1993. Continuation techniques and interactive software for bifurcation analysis of ODEs and iterated maps. *Physica D* 62:360-371.
- Kilgore, B. M., and Taylor, D. 1979. Fire history of a mixed conifer forest. *Ecology* 60:129-142.
- Kruger, F. J. 1983. Plant community diversity and dynamics in relation to fire. Pages 446-473 *in* F. J. Kruger, D. T. Mitchell, and J. U. Jarvis, eds., *Mediterranean-Type Ecosystems*. Springer Verlag, Berlin.
- Kuznetsov, Y. A. 1995. *Elements of Applied Bifurcation Theory*. Springer Verlag, New York.
- Le Houérou, . 1974. Fire and vegetation in the Mediterranean Basin. *Tall Timbers Fire Ecology Conference Proceedings* 13:237-277.
- Lieth, H. 1975. Primary production of the major vegetation units of the world. Page 207 *in* H. Lieth and R. H. Whittaker, eds., *Primary Productivity of the Biosphere*. Springer Verlag, New York. Table 10.2.
- Longman, K. A., and Jeník, J. 1974. *Tropical Forest and its Environment*. Longman, London.

- Ludwig, D., Jones, D. D., and Holling, C. S. 1978. Qualitative analysis of insect outbreak systems: the spruce budworm and forest. *Journal of Animal Ecology* 47:315-322.
- Malanson, G. P., and Trabaud, L. 1987. Ordination analysis of components of resilience of *Quercus coccifera* guarigue. *Ecology* 68:463-472.
- May, R. M. 1976. Models for two interacting populations. Pages 49-70 in R. M. May, ed., *Theoretical Ecology: Principles and Applications*. Blackwell Scientific Publications, Oxford.
- Menaut, J. C., and Cesar, J. 1979. Structure and primary productivity of Lamto savannas, Ivory Coast. *Ecology* 60:1197-1210.
- Payette, S. 1989. Fire as a controlling process in the North American boreal forest. Pages 145-169 in H. H. Shugart, R. Leemans, and G. B. Bonan, eds., *A Systems Analysis of the Global Boreal Forest*. Cambridge University Press, Cambridge.
- Richards, P. W. 1996. Stratification. Pages 26-48 in *The Tropical Rain Forest*. Cambridge University Press, Cambridge.
- Rinaldi, S., and Solidoro, C. 1998. Chaos and peak-to-peak dynamics in a plankton-fish model. *Theoretical Population Biology* 000-000.
- Rowe, J. S., and Scotter, G. W. 1973. Fire in the boreal forest. *Quaternary Research* 8:444-464.
- Rutherford, M. C. 1981. Survival, regeneration and leaf biomass changes in woody plants following spring burns in *Burkea africana* - *Ocoba pulchra* savanna. *Bothalia* 13:531-552.
- Saldarriaga, J. G., and West, D. C. 1986. Holocene fires in the northern Amazon Basin. *Quaternary Research* 26:358-366.
- Herrera]sanford85Sanford, R. L., Saldarriaga, J. G., Clark, K. E., Uhl, C., and Herrera, R. 1985. Amazon rain-forest fires. *Science* 227:53-55.
- Schaffer, W. M., and Kot, M. 1985. Nearly one dimensional dynamics in a simple epidemic. *Journal of Theoretical Biology* 112:403-427.
- Schlesinger, W. H., and Gill, D. S. 1978. Demographic studies of the chaparral shrubs, *Ceanothus Megacarpus*, in the Santa Ynez Mountains. *Ecology* 59:1256-1263.
- . 1980. Biomass, production, and changes in availability of light, water, and nutrients during the development of pure stands of the chaparral shrubs, *Ceanothus Megacarpus*, after fire. *Ecology* 61:781-789.
- Scott, J. D. 1971. Veld burning in Natal. *Proceedings of the Tall Timbers Fire Ecology Conference* 11:33-51.
- Shugart, H. H. 1984. *A Theory of Forest Dynamics*. Springer Verlag, New York.

Specht, R. L., and Morgan, D. G. 1981. The balance between the foliage projective covers of overstorey and understorey strata in Australian vegetation. *Australian Journal of Ecology* 6:193-202.

Sommerville]specht83Specht, R. L., Moll, E. J., Pressinger, F., and Sommerville, J. 1983. Moisture regime and nutrient control of seasonal growth in mediterranean ecosystems. Pages 120-132 in F. J. Kruger, D. T. Mitchell, and J. U. Jarvis, eds., *Mediterranean-Type Ecosystems*. Springer Verlag, Berlin.

Spurr, S. H. 1964. Forests of the World. Pages 306-320 in *Forest Ecology*, Chapter 18. Theronald Press Company, New York.

Strogatz, S. H. 1994a. Norbert wiener's brain waves. Pages 122-138 in S. A. Levin, ed., *Frontiers in Mathematical Biology*. Springer Verlag, Berlin.

———. 1994b. *Nonlinear Dynamics and Chaos with Applications to Physics, Biology, Chemistry and Engineering*. Addison-Wesley, Reading, Massachusetts.

Trabaud, L. 1994. Postfire Plant Community Dynamics in the Mediterranean Basin. Pages 1-15 in J. M. Moreno and W. C. Oechel, eds., *The Role of Fire in Mediterranean Type Ecosystems*. Springer Verlag, New York.

Trabaud, L., Michels, C., and Grosman, J. 1985. Recovery of burned *Pinus halepensis* Miller forests. Pine reconstitution after wildfire. *Forest Ecology and Management* 13:167-179.

Tyson, P. D., and Dyer, T. C. 1975. Mean annual fluctuations of precipitation in the summer rainfall regions of South Africa. *South African Geographic Journal* 57:2.

Valette, J. C. 1990. Inflammabilités des espèces forestières mediterranéennes. *Revue Forestière Francaise*. Numéro spécial (Espaces forestiers et incendies): 76-92.

Van Wagner, C. E. 1978. Age-class distribution and the forest fire cycle. *Canadian Journal of Forest Research* 8:220-227.

Vandermeer, J. 1993. Loose coupling of predator-prey cycles: entrainment, chaos, and intermittency in the classic MacArthur consumer-resource equations. *The American Naturalist* 141:687-716.

Viereck, L. A. 1983. The effects of fire in black spruce ecosystems of Alaska and northern Canada. Pages 201-220 in R. W. Wein and D. A. MacLean, eds., *The Role of Fire in Northern Circumpolar Ecosystems*. John Wiley and Sons, Chichester, England.

Viereck, L. A., Dyrness, C. T., Van Cleve, K., and Foote, M. J. 1983. Vegetation, soils and forest productivity in selected forest types in interior Alaska. *Canadian Journal of Forest Research* 13:703-720.

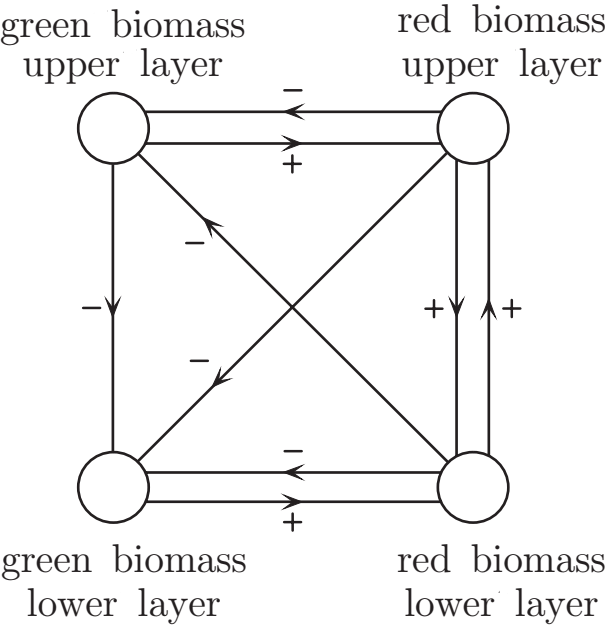
Walter, H. 1985. *Vegetation of the Earth and Ecological Systems of the Geo-Biosphere*. Springer Verlag, Berlin.

Whittaker, R. H., and Likens, G. E. 1975. The biosphere and man. Page 306 in H. Lieth and R. H. Whittaker, eds., *Primary Productivity of the Biosphere*. Springer Verlag, New York.

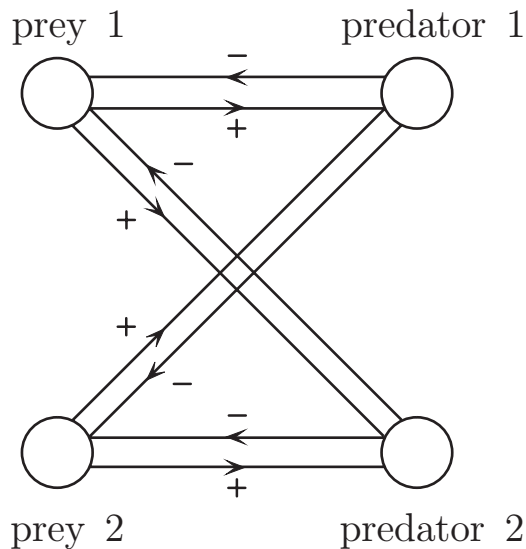
Whittaker, R. H., and Woodwell, G. M. 1971. Measurement of net primary production of forests. Page 167 *in* P. Duvigneaud, ed., Productivity of Forest Ecosystems. Unesco, Paris.

Yarie, J. 1981. Forest fire cycles and life tables: a case of study from interior Alaska. Canadian Journal of Forest Research 11:554-562.

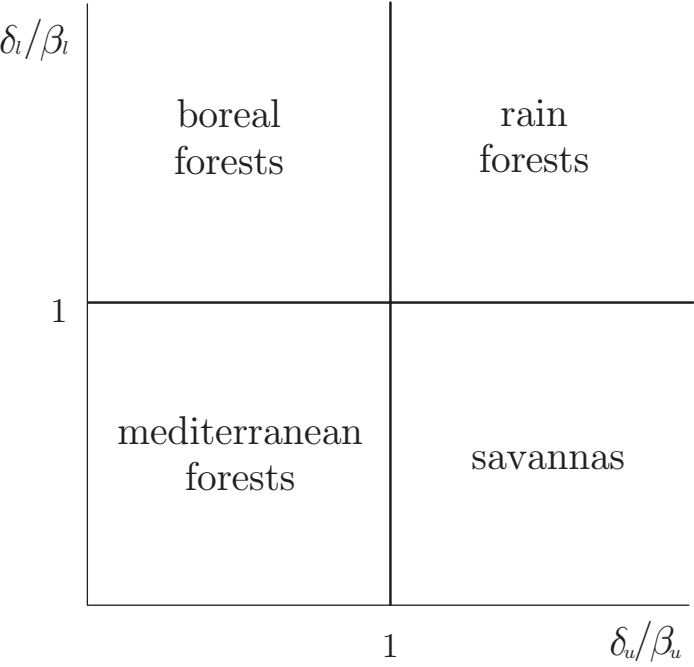
Zackrisson, O. 1977. Influence of forest fires on the North Swedish boreal forest. Oikos 29:22-32.



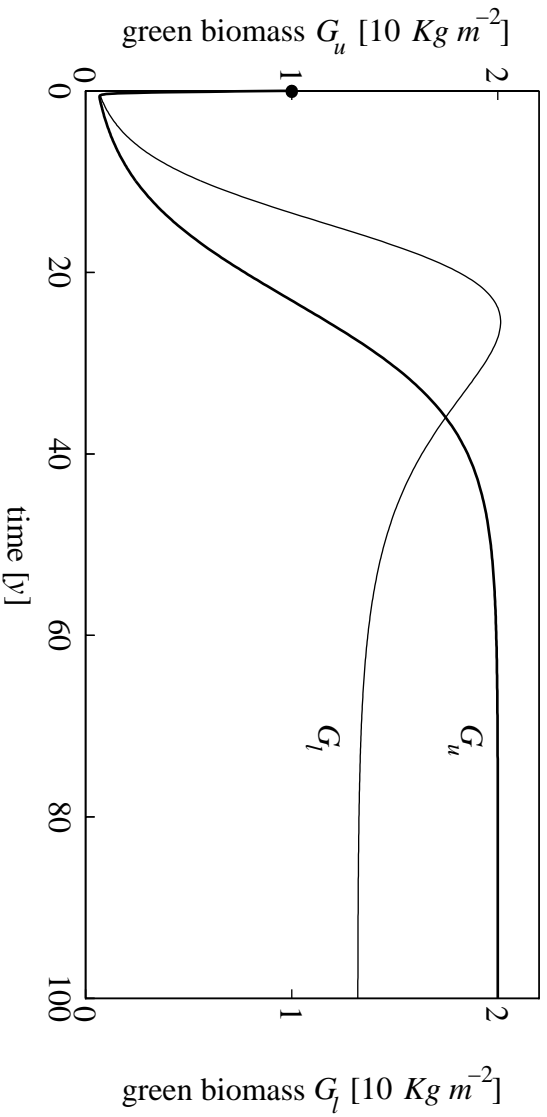
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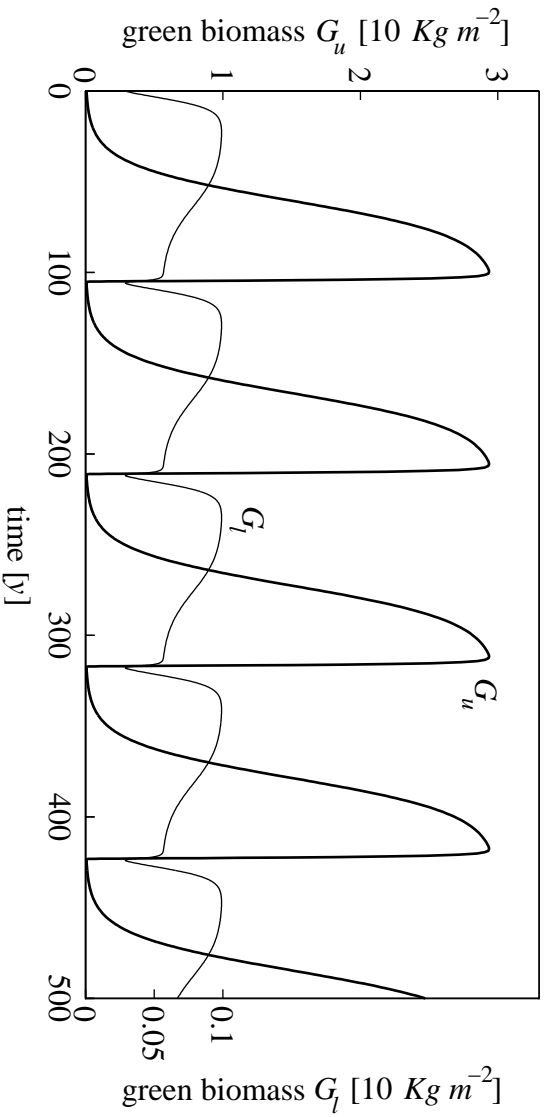
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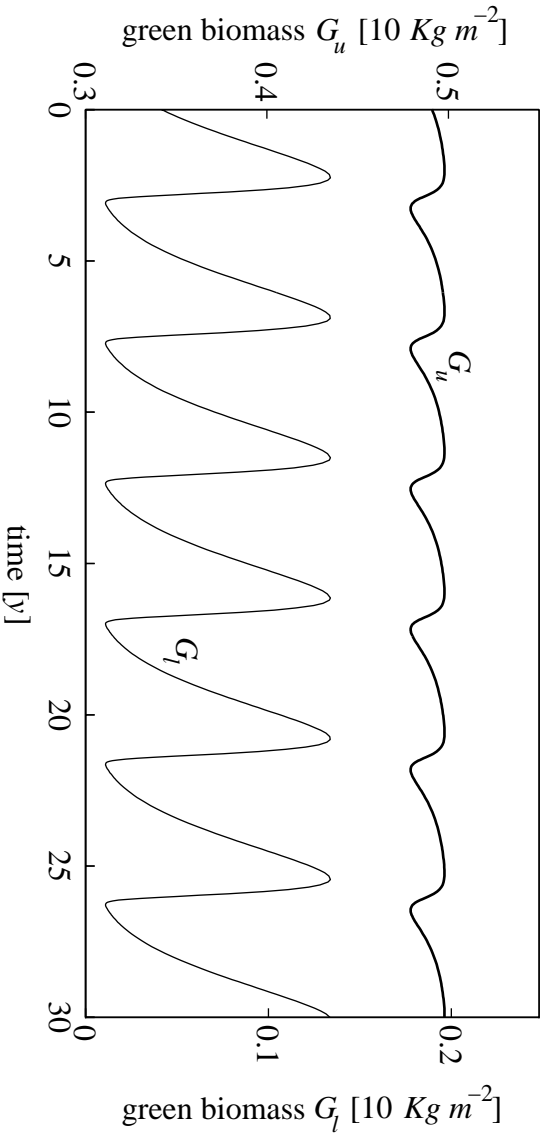
rain forest



boreal forest



Savanna



mediterranean forest

