Modeling the biomass allocation of tree resprout in a fire-prone savanna

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A B S T R A C T

Young savanna trees can quickly grow back from belowground storage structures after topkill. This capacity is a tolerance trait that confers persistence at the plant individual level, enabling them to survive diverse disturbance regimes.

We simulated the growth of a single resprouting stem (without and with fire) of a deciduous tree species that allocates its photo-assimilates during the vegetation season to reserves, belowground and aboveground parts (leaves and stem). As savannas grow under highly seasonal climates, the model considers that trees are leafless during the dry season and following growth is only possible thanks to reserves. Stem architecture constrains the leaf biomass to be proportional to stem length rather than biomass. We compared the success of different allocation strategies, with and without fire and according to the seasonality. To do so, the height of the resprouting stem after 50 yrs and the time to reach 2 m were modeled for three species of a humid savanna.

The viable and faster growth strategies are those for which allocation to belowground parts is <40%. There is very little sensitivity to allocation to reserves since successful growth is observed for allocation to reserves between 0.5% and 85% of photo-assimilates. In the literature and in our results, there is little impact of fire on the stem height or the time needed to escape the fire trap. Our model suggests that (1) allocation to leaves is determinant as leaves are the primary source of assimilates that can then be turned into fire-resistant structures (reserves and roots) and (2) fire only weakly slows down the plant growth compared to dry season..

1. Introduction

Savanna is a vegetation type characterized by the coexistence of grasses and trees (Higgins et al., 2000). In most savanna ecosystem, fire occurs frequently and strongly affects tree mortality and the recruitment of saplings into the larger size classes (Govender et al., 2006). Savanna tree species are adapted to fire: after a top kill – the loss of all or part of their aboveground biomass – they are able to quickly grow back from belowground storage structures such as lignotubers (Lehmann et al., 2014). Topkill is mainly due to fire (Archibald and Bond, 2003; Bellingham and Sparrow, 2000; Wigley et al., 2009), and herbivores (Sankaran et al., 2005). The ability to grow back (resprouting) is a tolerance trait that confers persistence to the plant individuals, enabling them to survive diverse disturbance regimes (Clarke et al., 2013). At the community level, this gives rise to an ecosystem that is resilient to severe disturbance such as very frequent fires. The resprouting ability is determined by the development and protection of a viable bud bank (Blarer and Doebeli, 1996; Charles-Dominique et al., 2015) and the

storage of carbon reserves that are replenished between fires (Hoffmann et al., 2000). It also depends on plant anatomy or architecture (Verdaguer and Ojeda, 2002), plant size before disturbance (Canadell and López-Soria, 1998; Pate et al., 1990), disturbance intensity (Kambo and Mapauret, 2006; Vesk and Westoby, 2004), disturbance frequency (Morrison and Renwick, 2000), nutrients and water availability (Cruz et al., 2003). Resprouting ability is thought to increase with stem size (Moreno and Oechel, 1993), but in some tree species, decreases in the largest size classes (Trollope, 1974). The survival of a young tree and its recruitment into the reproductive adult stage depend on its ability to escape the 'fire trap' (Bond and Keeley, 2005), i.e. the flame zone (usually from 0 to 3 m high; (Menaut and César, 1979; N'Dri et al., 2014)) where young tree resprouts can survive but are prevented from producing a perennial stem by repeated top-kill for many consecutive years. Establishing such a perennial stem requires accumulating enough photo-assimilates to develop, between two fires events, a stem that is tall enough for its terminal bud to be above the flame zone. Allocation of carbon in all compartments (leaves, stems, roots, reserves) of the

resprout is also constrained by its architecture (leaf to stem ratio, dependent on stem height, stem diameter, internode length, number of leaves per node…).

Thornley (1972) argues that for plant growth (without disturbances), two processes are important: the first is the utilization of substrate for growth and how this utilization depends upon substrate concentration, the second concerns the transport of substrate between different plant parts (roots, shoots and leaves) and how this depends upon the substrate concentrations in the plant parts. For this model, the growth pattern of a plant depends upon the mechanisms by which substrate is transported around the plant, and the way in which substrate is utilized for growth of the plant parts. For Lacointe (2000) carbon assimilates flow during plant growth from "source" areas such as leaves to "sink" areas where they are taken up and used. The assimilate fluxes from sources to sinks are mainly dependent on the source-sink distances and on the respective abilities of the different sinks to take up and use the assimilates that are available to them. Both models use quite complex representations of allocation. Müller et al. (2000) compare two different conceptions of carbon allocation in plants, the *ratio* and *allometric* views. In the ratio view, a plant has a certain biomass at any point in time and allocates it proportionally to different structures. In the allometric view, allometry is seen as the quantitative translation of growth into allocation. Plants evolve allometric patterns in response to numerous selection pressures and constraints such as fire. Also, models of tree growth and assimilate movement have been developed to study resprouting in savanna and have been used to compare the consequences of contrasted tree strategies (Bond and Midgley, 2001; Clarke et al., 2013; Bond and Midgley, 2003), such as seeding (investment into the next generation) or resprouting (investment into the current generation) (Bellingham and Sparrow, 2000). These models suggested that the success of these allocation strategies depends on ecosystem productivity, disturbance regime and competition for resources (nutrients and light). However, they did not consider the allocation of carbon reserve contained in belowground parts and stems, though these reserves may play an important role to escape the fire trap. Reserves of carbon in belowground parts and stems are vitally needed to resume growth at the beginning of the rainy season after a top kill or a drought event. Previous reviews (Bellingham and Sparrow, 2000; Bond and Midgley, 2001,2003) of resprouting ecology were based on models of how trees escape fire effects, concentrating on the role of fire frequency and severity and their interaction with basal sprouting and other types of resprouting (Clarke et al., 2013).

Here, we propose a new model simulating the allocation of carbon reserve between belowground and aboveground parts, to determine the range of allocation strategies allowing a resprout to grow and escape the fire trap in fire prone savannas. The model is based on field observations from Schutz et al., 2009 where the carbon allocation and biomass partitioning patterns have been measured and studied. It simulates the growth of a single resprouting stem that allocates its photo-assimilates during the vegetation season between reserves, belowground parts, and aboveground parts, and compares the success of different allocation strategies with or without fire, seasonality and according to plant architecture characteristics. We considered as successful strategies those allowing a resprout to escape the fire trap (assuming an average flame height of 2 m) after some time and as unsuccessful all the other. We aim at answering the following questions: (1) which biomass allocation strategies allow escaping the fire trap in fire-prone savannas? (2) Are the best allocation strategies the same with and without fire? and seasonality? (3) Does resprout architecture influence the success of allocation strategies? (4) What is the effect of the photosynthesis and translocation rates on the allocation strategy success?

2. Materials and methods

The model consists of a system of differential equations and aims at simulating the allocation of biomass between reserves, belowground parts (roots), aboveground parts (leaves and stem) of an individual tree

with a single resprout stem and the consequences of this biomass allocation strategies for its growth and survival against fire.

The main assumption of our model (Fig. 1) is that plant reserves allow regrowth after a loss of leaves either due to the dry season in the case of deciduous species or to the removal of all aboveground parts by fire. The individual tree (called 'resprout' hereafter) is described by the biomass of leaves B_l, stems B_s, belowground parts B_r and reserves B_p with a minimal architecture description (Table 1). Reserves are located in the belowground parts and the stem. Seasonality is modelled by considering that active growth only occurs during the wet season (9 months each year) and that plants are in a dormant state (leafless) during the dry season (3 months each year). During the wet season, belowground parts, leaves and stem are present, and leaves can fix carbon. During the dry season, the resprout loses its leaves (we assume a deciduous species) and no photosynthesis occurs. At the beginning of the dry season, only belowground parts and stem remain. When fire occurs during the dry season, the stem burns and only belowground biomass persist. In the next parts, we will note D^+F^+ to describe simulations with seasonality (wet and dry season) and a yearly fire, D^+F^- for simulations with seasonality (wet and dry season) but no fire and D^-F^- for simulations with only wet season and no fire.

Different constraints are considered to account for plant architecture: (1) the size of belowground parts and stem limits the size of the reserve compartment; (2) the sum of the allocation coefficients (Table 1) is equal to 1 due to mass conservation; (3) the stem biomass limits leaf biomass as leaves are carried by the stem.

The next part presents how reserve biomass are created, lost, and allocated to resprout compartments.

2.1. Production of new biomass (G)

New biomass that is allocated during each time step results from the net photosynthesis aB_l and use of reserves bB_P, where a is the rate of photosynthesis (gg^{-1}month^{-1}) and b is the translocation rate between 0.1 and 0.9 (gg^{-1}month^{-1}) (Table 1). We assume that the resprout cannot transfer all reserve without loss so the maximum translocation is 90% of reserve and the minimum we can interpret is 10%.

When leaves are absent, growth is only possible by the translocation of reserves to aboveground parts. Afterwards, the growing leaves start to produce photosynthates that are allocated to the different compartments (belowground and aboveground parts).

2.2. Respiration costs

Stem and belowground parts have a maintenance cost proportional to their biomass (rate q) whatever the season. The respiration cost in the dry season represents 1/10 of respiration in the wet season (to take
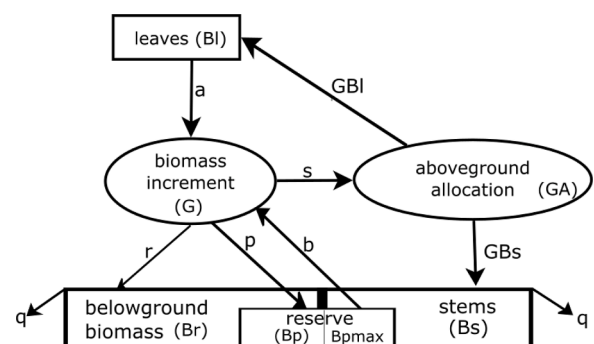

Fig. 1. Conceptual model of resprout biomass allocation where s, r, p, q, GB_l, GB_s, a, b and *Bpmax* are respectively the allocation rates to aboveground parts, to belowground parts, to reserves, the rate of biomass lost due to respiration, allocation to leaves, allocation to stem, photosynthesis rate, translocation rate and the maximum reserve that resprout can contains (see text).

Table 1
Parameters of model.

Definition	parameter	Units	values		
Photosynthesis rate	a	g g^{-1}month^{-1}	2* and 3*		
Translocation rate	b	g g^{-1}month^{-1}	0.1 and 0.9		
Maintenance cost	q	g g^{-1}month^{-1}	15%*		
Belowground parts allocation rate	r	g g^{-1}	From 0 to 1		
Stem and leaves allocation rate	s	g g^{-1}	From 1-r to 1		
Reserves allocation rate	p	g g^{-1}	1-r-s		
Maximal reserves	$pmax$	g g^{-1}	65%*		
Species specific parameters			*Piliostigma thonningii*	*Crossopterix febrifuga*	*Bidelia ferruginea:*
Ratio h/d	f	-	39.73	82.5	93.23
Mean inter-node length	e	cm	3.73	3.3	3.35
Number of leaves per node	n	-	1	2	1
Mean stem density**	m	gcm^{-3}	0.65 ±0	0.8 ± 0	0.59 ± 0.08
Mean leaf biomass	ml	g	3.98±2.12	5±4.6	5.25 ± 6.8

* Values were adjusted to produce realistic resprout growth, because data was not available for savanna species.
** Online database of tree functional and ecological attributes (Tree functional attributes and ecological database, 2020).

active growth in account).

2.3. Allocation to reserves

Reserves consist in starch or other photo-assimilates, stored in stem and roots. This imposes a limit on the pool of reserves, which must be kept lower than a maximal proportion of these compartments. This leads to the following equation:

$$B_{Plim} = 1 - \frac{B_P}{B_{Pmax}}(B_r + B_s)$$

where B_{Plim} represents the decrease in the transfer to reserves and B_{Pmax} the maximum proportion of reserves within plant organs (Fig. 1). The allocation to reserves B_P is therefore:

$$pB_{Plim}(aB_l + bB_P)$$

and the dynamic of reserves biomass is:

$$\frac{dB_P}{dt} = pB_{Plim}(aB_l + bB_P) - bB_P \quad (1)$$

2.4. Allocation to belowground parts

The imposition of constraints on the size of the reserve pool ensure that the allocation coefficients sum to 1. To satisfy this, we pose the correction term α :

$pB_{Plim} + \alpha(r+s) = 1$, so $pB_{plim} + \alpha(1-p) = 1$ and finally $\alpha = 1 - p\frac{B_{Plim}}{1-p}$. With the maintenance cost, the roots biomass dynamic is:

$$\frac{dB_r}{dt} = r\left(1 - p\frac{B_{Plim}}{1-p}\right)(aB_l + bB_P) - qB_r \quad (2)$$

Note that $\frac{dB_r}{dt}$ can be negative if the respiration (qB_r) exceeds the biomass allocation to belowground parts. This matches the common observation that plants can lose parts to adjust their growth to their carbon budget.

2.5. Allocation to aboveground parts

First, the part of G allocated to aboveground parts (GA), is computed from the allocation coefficients and the corrective term α as:

$$GA = s\alpha G = s\left[1 - p\frac{B_{Plim}}{1-p}\right][aB_l + bB_P]$$

Where s represents the allocation coefficient to aboveground parts (Fig. 1). Then, this biomass is distributed between leaves and stem, according to architecture constraints. Here, we assume that all aboveground growth after fire is allocated to a single stem and that there are

strong architectural relations between leaf biomass and stem biomass. h (cm) represents the height of the stem and d (cm) its basal diameter. The stem has a constant volumetric mass m characteristic of the species (g cm^{-3}) relating its biomass to its volume: $Bs = mv$, where v is the stem volume. The height/diameter ratio ($f = h/d$) is constant and species-specific. The stem has a paraboloid profile relating the volume to the stem diameter and height $v = \pi d^2\frac{h}{8}$. This profile is a frequently used, simple but realistic representation of the stem taper (Gignoux et al., 2016). The number of leaves per stem length is characterized by two parameters: e the average internode length and n the number of leaves per node. We therefore assume that (1) if the stem is less than one year old then the leaves were formed at the same time as the stem, (2) if the stem is older and has lost its leaves, these leaves are replaced by short axes having a negligible stem biomass and bearing a foliar surface and biomass equivalent to that formerly set during the previous growing season. Leaves have a constant average biomass m_l (g). From these constraints, we calculate:

- The stem height h from stem biomass: $v = \pi d^2\frac{h}{8}$ so $h = \left(8f^2\frac{B_s}{\pi m}\right)^{\frac{1}{3}}$
- The leaf biomass B_l carried by a stem of height h: $B_l = nm_l\frac{h}{e}$
- Finally, the leaf biomass from the stem biomass: $B_l = \frac{nm_l}{e}\left(8f^2\frac{B_s}{\pi m}\right)^{\frac{1}{3}}$

We pose:

$$\beta = \frac{nm_l}{e}\left(\frac{8f^2}{\pi m}\right)^{\frac{1}{3}}, \text{ Thus:}$$

$$B_l = \beta B_s^{\frac{1}{3}}.$$

For the new growth to take place in accordance with this relation, the respective growth rates of B_l and B_s (hence their derivatives) must verify:
$\beta^3\frac{dB_s}{dt} = 3B_l^2\frac{dB_l}{dt}$. Since,

$$GA = GB_l + GB_s,$$

where GB_l and GB_s are respectively the leaves and stem growth, we solve the system to find:

$$GB_l = \left(\frac{\beta^3}{\beta^3 + 3B_l^2}\right)GA$$

and

$$GB_s = \left(\frac{3B_l^2}{\beta^3 + 3B_l^2}\right)GA.$$

Equations for the dynamics of leaf biomass B_l and stem biomass B_s then follow:

$$\frac{dB_l}{dt} = s\left[\frac{\beta^3}{\beta^3 + 3B_l^2}\right]\left[1 - p\frac{BPlim}{1-p}\right][aB_l + bB_p] \quad (3)$$

$$\frac{dB_s}{dt} = s\left[\frac{3B_l^2}{\beta^3 + 3B_l^2}\right]\left[1 - p\frac{BPlim}{1-p}\right][aB_l + bB_p] - qB_s \quad (4)$$

Simulation experiment

The allocation parameters (r, s and p; Table 1) are unknown and we aim at determining the successful allocation strategies. Thus, we explored all possible combinations of the values of these allocation rates between 0 and 1 with a step of $5\,10^{-3}$. The others parameters (number of leaves per node (n), stem height (h) in cm, the diameter (d) of the trunk

in cm for 3 species (*Bridelia ferruginea, Crossopteryx febrifuga* and *Piliostigma thonningii*) were obtained from Gignoux et al., 2016 and had been collected at the Lamto ecological station in Ivory Coast (Menaut and César, 1979), which data we use as a baseline study case. The three species we have used are dominant species commonly found in all the Guinean savanna zone in Africa ("Guinean forest-savanna mosaic" WWF ecoregion). More specifically, in the Lamto savanna , more than 90% of the woody layer is composed of four species (Menaut and César 1979): *Bridelia ferruginea* Benth. (Phyllanthaceae), *Crossopteryx febrifuga* (Afzel. ex G. Don) Benth. (Rubiaceae), *Cussonia arborea* Hochst. ex A.Rich. (Araliaceae), and *Piliostigma thonningii* (Schum.) Milne-Redhead (Caesalpiniaceae). We chose three of these species to parameterize our model
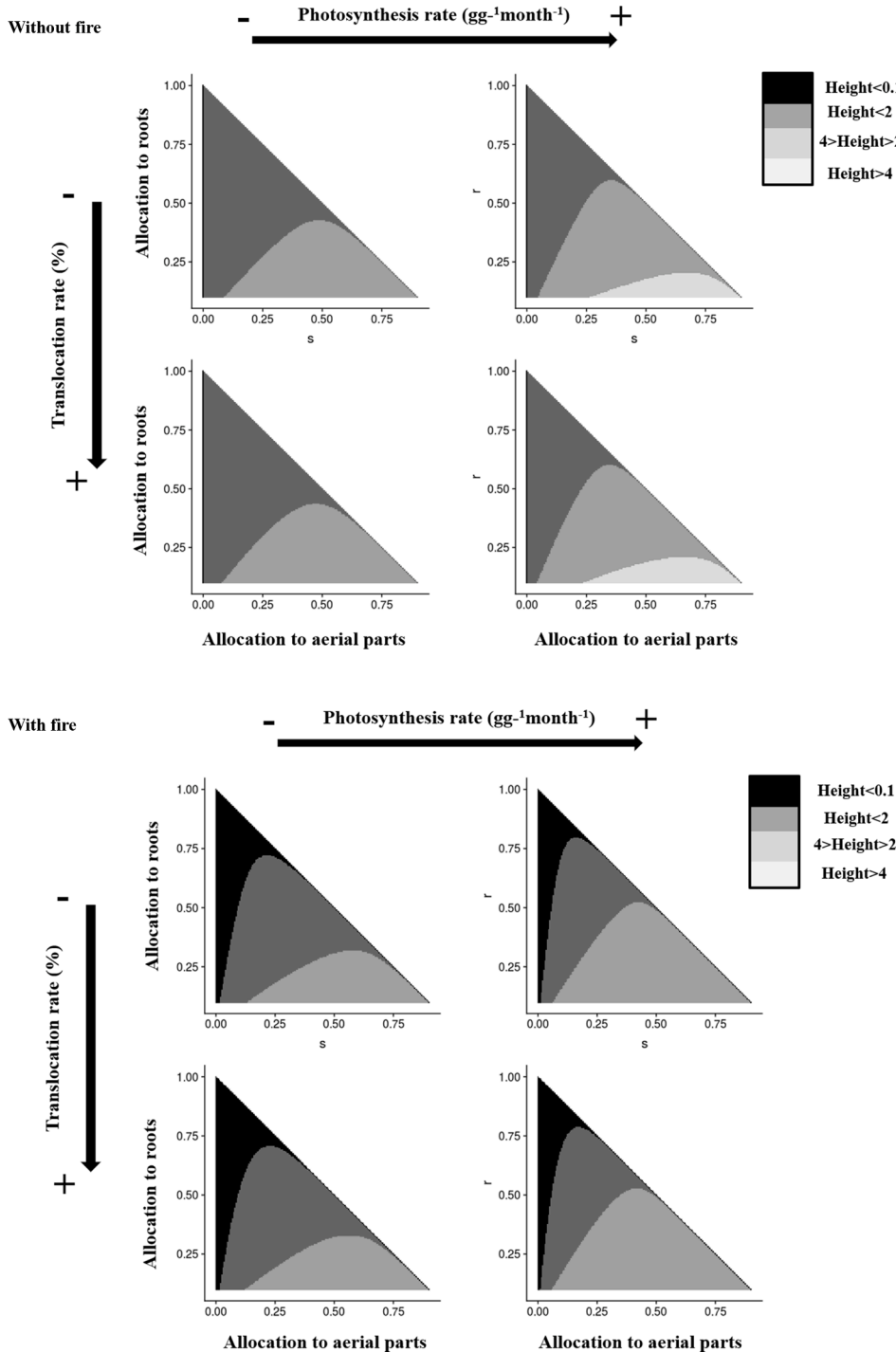

Fig. 2. Effect of allocation strategies on the height (m) of 50 yr old *Piliostigma thonningii* resprout, for 4 combinations of photosynthesis rate (a) and translocation rate of reserves (b), without and with fire. x axis: the allocation rates to aerial parts (leaves and stem), y axis: the allocation rates to roots. The first row represents simulation when $b = 0.1$ and the second when $b = 0.9$. The first column represents simulation when $a = 2$ g g^{-1}month^{-1} and the second when $a = 3$ g g^{-1}month^{-1}. Because the sum of the three allocation rates is always 1, all strategies lie within the bottom left triangle. Shade levels indicate the height of the resprouting stem after 50 years, from 0 to more than 4 m.

as they are representative of this ecosystem and their characteristics, such as photosynthetic and growth rates, are known (Gignoux et al., 2016). They also all display very strong resprouting abilities and have extensive belowground storage systems.

Stem wood densities (m in g cm^{-3}) were collected in an online database (Tree functional attributes and ecological database, 2020). The average constant biomass of well-developed leaves (m_l in g), and the mean inter-node length (e in cm) were calculated from data on single stem individuals (Gignoux et al., 2016). Then, we explored photosynthesis rate a (from 2 to 3 g g^{-1}month^{-1}) and translocation rate b (from 0 to 90% of reserve biomass), and we assumed that the maximum proportion of reserve $Bpmax$ represents 65% of reserve compartment $Bs + Br$ and the resprout maintenance rate (q) for the stem is 15% of the living parts of the plant.

Simulations were run for 50 years using a monthly time step. Differential equations were numerically integrated using the R package deSolve (Soetaert et al., 2010) under R 4.0 (R Core Team, 2020). We initially put r, s and p at zero; the initial belowground biomass at 10 g and reserve biomass at 6.5 g. Output variables were the height of resprout at the end of the 50th rainy season and the time to reach 2 m in height. Model was parameterized for the three tree species and three environmental conditions D^+F^+, D^-F^- and D^+F^- (Table 1). Results for D^+F^+, D^-F^- are given in the main text and those for D^+F^- are given in appendix.

3. Results

3.1. Effect of the allocation strategies on resprout height

Here, we analyze the effect of allocation strategies on resprout height after 50 years depending on fire presence. The successful allocation strategies are those with a high investment to the aboveground parts where (Fig. 2) $s>r$ and the maximum allocation to belowground part in these cases is generally less than 40%.

Fire mostly reduces the height of resprouts after 50 years, without changing qualitatively the distribution of successful allocation strategies. In D^+F^- (Fig. 2), only strategies for which $s = 0$ do not allow resprouts to grow and reach more than 0.1 m (minimum height we consider in our model), i.e. are unviable.

In the D^+F^+ model, no strategy allowed resprouts to reach more than 4 m (Fig. 2). There are more unviable strategies that do not allow respouts to reach 0.1 m. In D^+F^-, the maximum heights are respectively 8.7 m and 11.88 m, for $a = 2$ month^{-1} and $a = 3$ month^{-1}; and 6.53 m and 8.36 m (for the same a value) for D^+F^+. Overall, the parameter space of successful strategies (Fig. 2) is larger in D^+F^- than D^+F^+ for all combination of translocation rate b and photosynthesis rate a.

The parameter space of successful strategies does not change with the translocation rate (Fig. 2, vertical comparison) in D^+F^- and D^+F^+, whereas the photosynthesis rate increases the parameter space of successful strategies (Fig. 2, horizontal comparison).

3.2. Effect of the allocation strategies on the time to reach 2 m

Overall, the number of years necessary to reach 2 m as a function of the allocation rates follows the same pattern as the height reached by resprouts after 50 years. In D^+F^+ and D^+F^-, the more the resprouts allocate biomass to their aboveground parts, the faster they reach 2 m (Fig. 3). The increase in the photosynthesis rate has a positive impact on the parameter space of successful strategies, compared to the translocation rate (Fig. 3). The minimum time for successful strategies to reach 2 m is similar for *Piliostigma thonningii* and *Bridelia ferruginea* with and without fire and is about 0.5 year (6 months) when $a = 3$ gg^{-1}month^{-1} and $b = 0.9$ gg^{-1}month^{-1} for, and 0.42 years (5 months) for *Crossopteryx febrifuga* for the same values. We did distinguish between resprouts which reached 2 m before 2 years and those after 2

years to take in account field observation of plant growth (Fig. 3). Fire increases the time to reach 2 m and reduces the parameter space domain in which reaching 2 m is possible.

3.3. Effect of plant architecture on allocation strategies

Overall, the allocation strategies and their interactions with fire and the photosynthesis rate have a similar impact on the growth of the three species present (Fig. 4).

There are however some differences between species. In D^+F^+, the parameter space of successful strategies allowing a resprout to reach more than 4 m tends to decrease for *Crossopteryx febrifuga* and *Bridelia ferruginea* (Fig. 4). The parameter space of successful strategies is larger for *Crossopteryx febrifuga* than *Bridelia ferruginea* (Fig. 4), which is itself larger than *Piliostigma thonningii*. Unviable strategies that do not allow to reach 0.1 m remain the same for all species. Finally, *Piliostigma thonningii*, whatever its allocation strategy, never reaches 4 m.

4. Discussion

### 4.1. Which biomass allocations strategies allow resprout escaping the fire trap in fire-prone savannas?

In all simulations, successful strategies allowing to reach more than 2 m are those where $s>r$. The maximum allocation to belowground parts in these cases is when $r<50\%$. Allocation to belowground parts or reserves can be as low as 0.5% of reserves and still allows to reach 2 m. We think that this is likely because a higher allocation to aboveground parts in the growing season assures the production of foliar surface at the beginning of the rainy season. Schutz et al. (2009) measured the allocation to aboveground biomass in Acacia karoo after fire and found that leaves accounted for more than 75% of the total aboveground biomass.

In D^+F^+, the parameter space of allocation strategies that never allow resprouts to reach 0.1 m increases considerably (black regions of Figs. 2 and 4) and corresponds to resprouts allocating between 60 and 90% of their biomass to belowground parts. Thus, allocating biomass to aboveground parts in ecosystems with an annual fire does seem to be a favorable survival strategy. Indeed, large reserves are not necessary in this model as photosynthesis, quickly after the beginning of the rainy season, ensures the production of biomass. This result is unexpected, because the commonly accepted view is that plants need to build up large reserves to resume their growth as quickly as possible at the beginning of the vegetation season in fire prone savannas.

However Schutz et al. (2009); Gignoux et al. (2016) noted that resprouts of savanna tree species first invested in leaf biomass, with leaves accounting for up to 75% of the total aboveground biomass to ensure a faster growth in the beginning of growth season when reserve in belowground part decreases considerably. These experimental measurements support our model results suggesting that allocating most resources to aerial parts at the beginning of the growth season can be an efficient strategy. We observe the same trend for the time to reach 2 m as for the height after 50 years: successful strategies are those with an allocation to aboveground parts higher than 12.5%. Such strategies allow a quick regrowth, which leads both to a short time to reach 2 m and a tall stem after 50 yrs. On the other hand, it would be logical that later in the season, there would be a greater allocation to the reserve than to aboveground parts. One limitation of our model is thus the use of fixed allocation rates and using variable allocation rates with time might extend the range of allocation values for successful strategies. However, using variable allocation rates increases the complexity of the model and was beyond the scope of this work.

However, our model does not take in account the functional role of belowground parts, they are not only reserve storage organs, but they also absorb water or mineral nutrients. This implies that water and mineral nutrients are not limiting, which is unlikely. Considering the limitation by water and mineral nutrients would necessarily give more
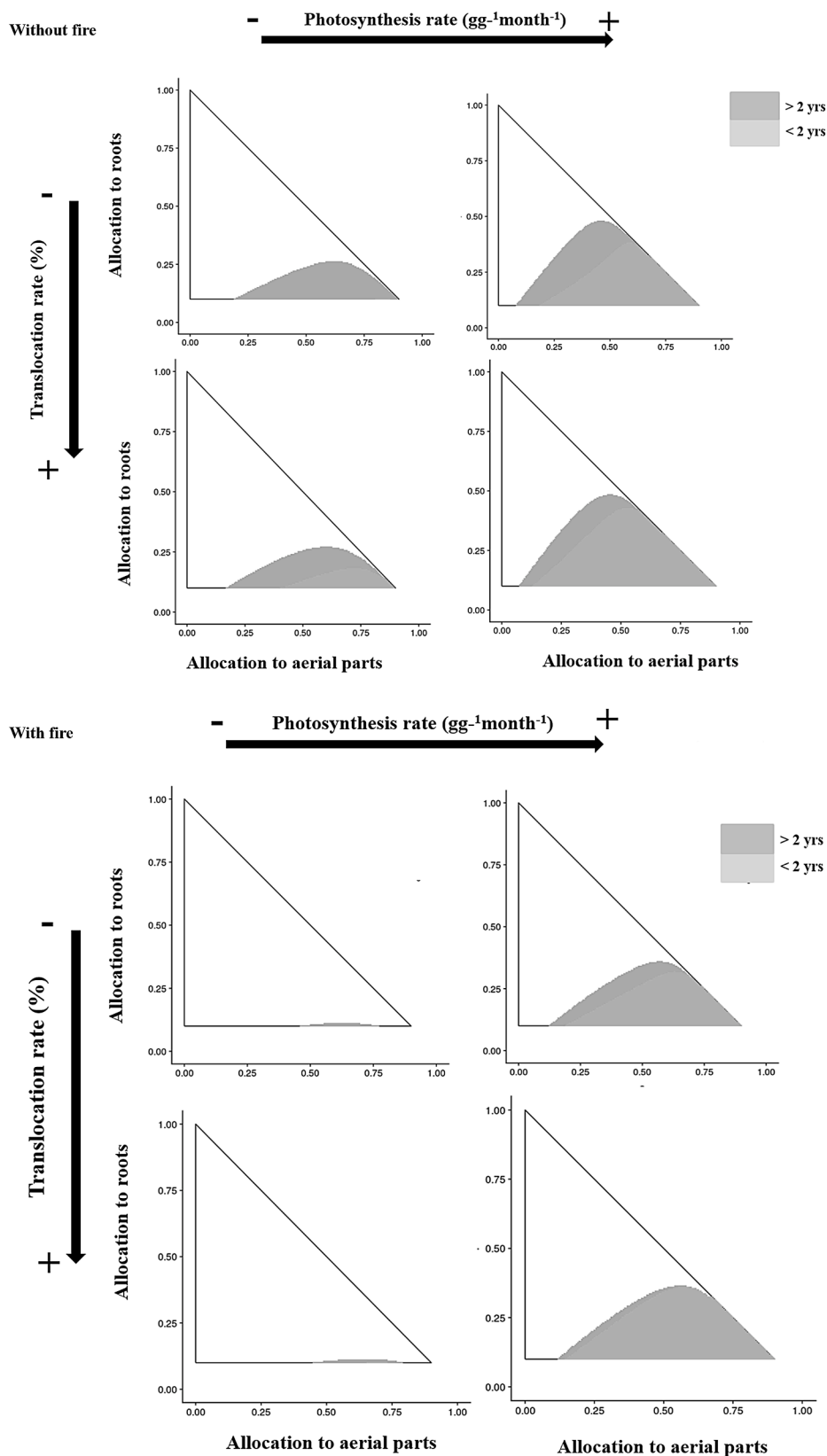
Fig. 3. Comparison of the time to reach 2 m for *Piliostigma thonningii* resprout. Panel and axis description as in Fig. 2. In this figure, when light gray becomes dark, the time to reach 2 m becomes bigger and bigger (from 6 month to 20 years).
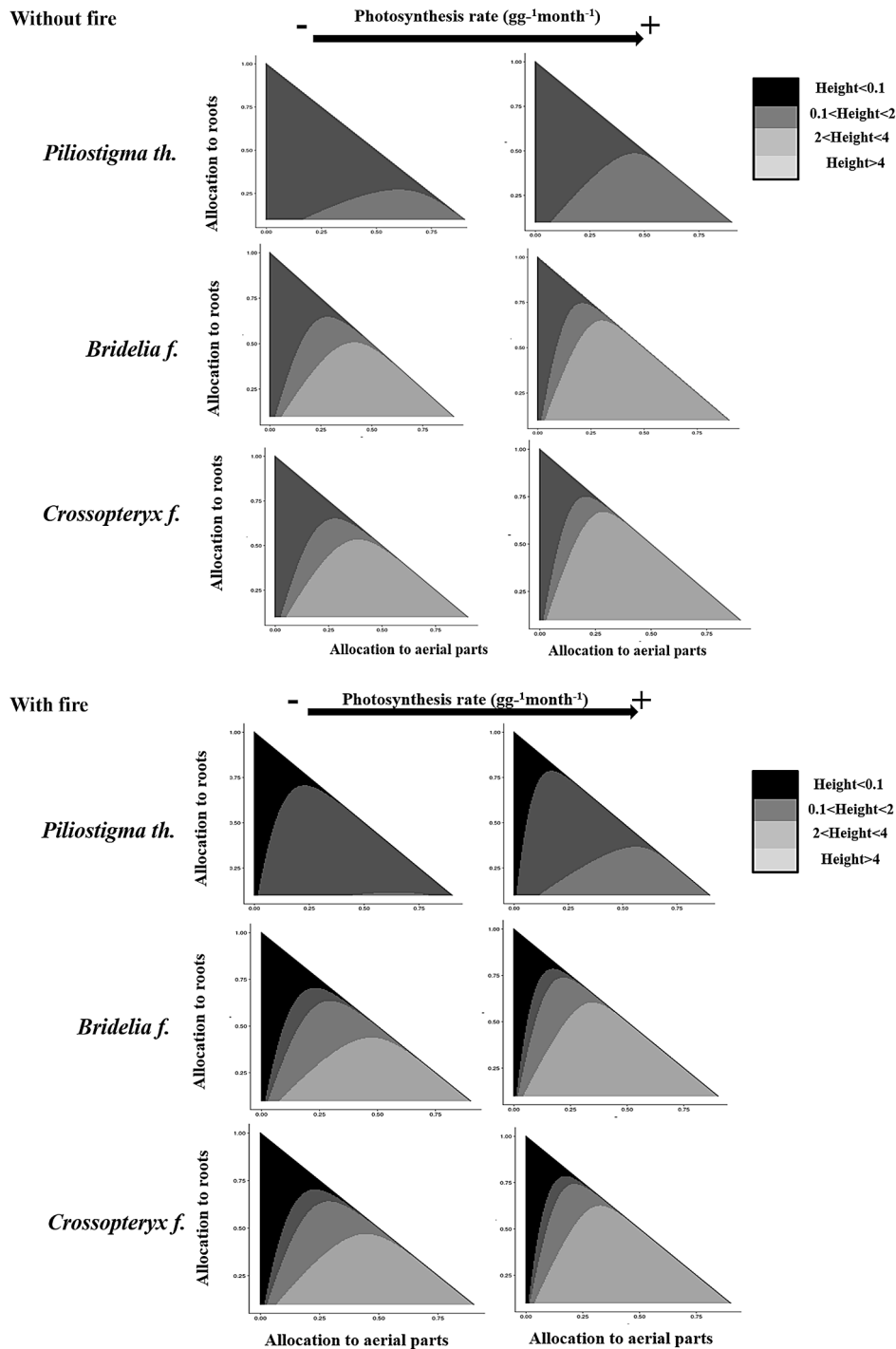
Fig. 4. Comparison of *Piliostigma thonningii, Bridelia ferruginea* and *Crossopteryx febrifuga,* according to effect of the allocation strategies on the height (m) of 50 yr old resprout for 4 combinations of photosynthesis rate (a) and translocation rate of reserves (b) for b = 0.9 g g^{-1}mont^{-1}. Panel and axis description as in Fig. 2.

importance to allocation to belowground parts and this consideration could alter our results on the successful strategies of allocation of biomass by increasing available biomass each time and its translocation in all parts of the resprout.

4.2. Are the best allocation strategies the same with and without fire, and seasonality?

In D^+F^- and D^-F^-, resprouts grow with less disturbance than in $D+F+$ and almost any set of allocation parameter leads to successful strategies, in contrast to D^+F^+ (Appendix 3). The height of resprouts

after 50 yrs in the D^+F^+ regime is lower than in D^+F^-; and the parameter space leading to successful strategies is also smaller. This difference may be due to the reserves accumulated in belowground parts during the first year before fire. Thus, resprouts begin the growth season in the second year with more reserve in belowground parts than in first year (appendix 4). The effects of fire on savanna plants have been studied by several authors (Gignoux et al., 1997) that have shown that fire slows the growth of resprouts by topkill. In our model, fire reduces resprout biomass and the parameter space of successful strategies. These results are consistent.

Despite differences, the D^+F^- has substantially the same effects as

the D^+F^+ on successful allocation strategies. In D^+F^- and D^+F^+, the successful strategies always correspond to a large investment in aerial parts (>12.5%, appendix 3). The similarity of D^+F^- and D^+F^+ effects on successful allocation strategies can be explained by the fact that the plant is dormant during the dry season (but stem is still there) and fire

occurs only in the dry season and destroys the stem, so that there is no new biomass production and biomass allocation in both cases, and during a part of the year production is lost and rebuild the year after. Fire effects seem to reinforce the dry season effect, i.e. they do not change the pattern of responses, but increase their intensity.
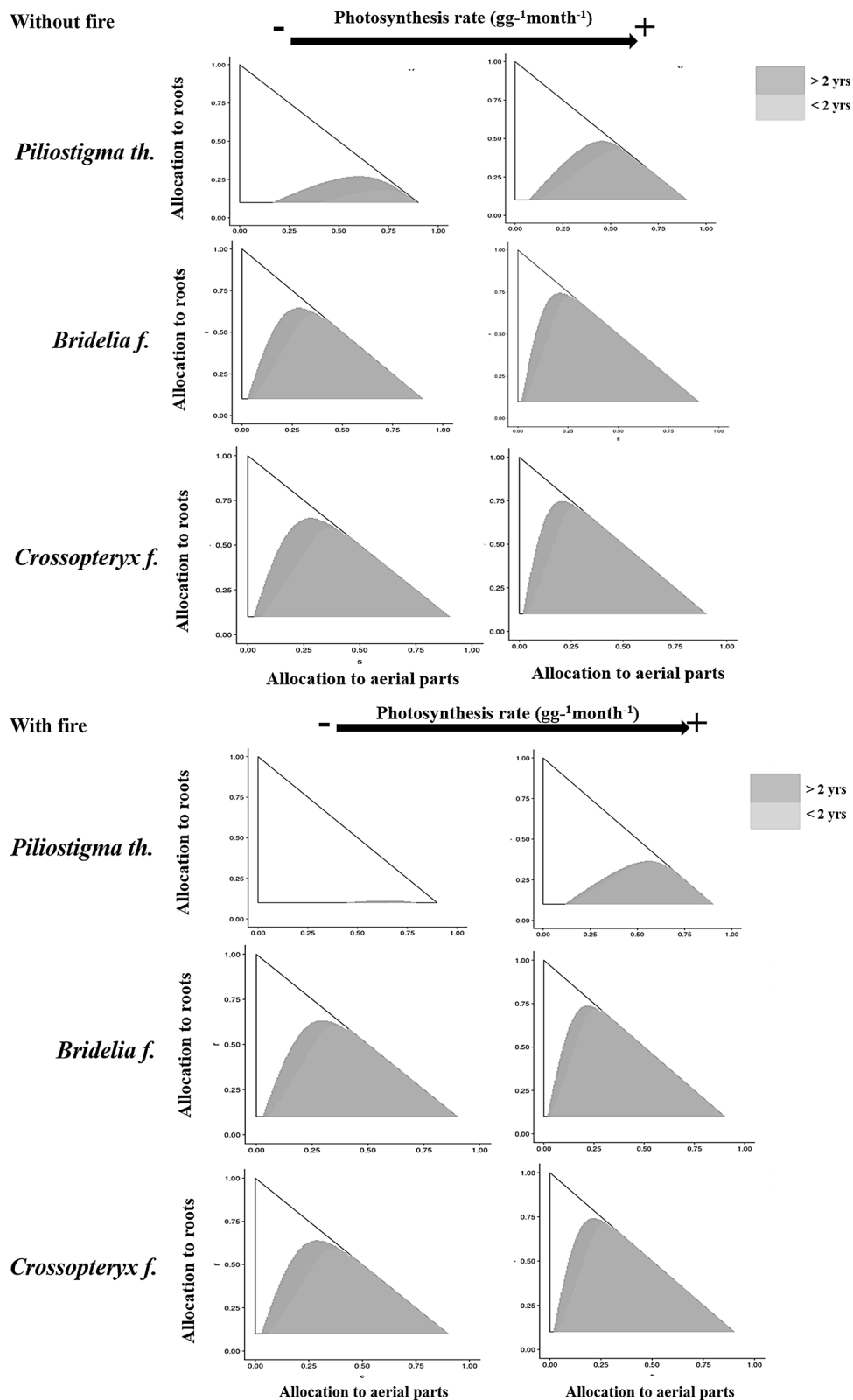

Fig. 5. Comparison of the time to reach 2 m for *Piliostigma thonningii, Bridelia ferruginea* and *Crossopteryx febrifuga* according to the rate of allocation to belowground parts (y axis) and the rate of allocation to aboveground parts (x axis) for b = 0.9 g g^{-1}mont^{-1}. Panel and axis description as in Fig. 2.

By contrast, in the D^-F^- model, resprouts have successful allocation strategies even when they allocate between 60 and 90% of their biomass to belowground parts and the parameter space of successful strategies is much larger than in the other cases (appendix 3). This may be due to the fact that, in the wet season, the plants grow normally without major disturbances, hence without biomass losses to fire or dry season.

In summary the biomass allocation strategies allowing resprouts to escape the fire trap are those with more than 12.5% allocation to aboveground parts (stem and leaves) and there are more successful allocation strategies without fire than with fire. Also, D^+F^- and D^+F^+ are similar in their impact on resprouts success allocation strategy, and we offer that D^+F^+ (model with dry season and fire) are like drought (like in D^+F^-) when we compare both with wet season model (appendix 3).

4.3. Does resprout architecture influence the success of allocation strategies?

The parameter space leading to successful strategies is larger for *Crossopteryx febrifuga* than for the other two species (Figs. 4 and 5) in all simulations (D^+F^+, D^+F^-, and D^-F^-). This suggests that *C febrifuga* has better allocation strategies than *Piliostigma thonningii* and *Bridelia ferruginea* in fire prone ecosystems (as savannas). In the model, the only differences between these species are their architecture. This implies that plant architecture could significantly influence the success of their biomass allocation strategies and plant growth (Kaggwa-Asiimwe et al., 2013). In our model, *C. febrifuga* and the two other species mainly differ by the number of leaves per node (*C. febrifuga* has 2 while others have only 1) and the internode length (Table 1). Indeed, *C. febrifuga* has the smallest internode length (3.33 cm) and *P. thonningii* (3.75 cm) the 14% biggest (Table 1). If we assume the same internode length and individual leaf surface for all species, the species with 2 leaves per node will carry twice more leaf surface for the same stem length than a species with 1 leaf per node. This is certainly an advantage when putting up leaves quickly at a low cost in stem biomass is important.

However, we did not take into account the impact of the architecture on the survival of the stem, while indeed plant architecture can significantly affect light distribution and penetration in the crop canopy, and thus change plant growth, biomass partitioning, boll distribution, and yield potential (Kaggwa-Asiimwe et al., 2013). Furthermore, we used the same respiration cost for aboveground and belowground parts, because of lack of information about plant belowground parts respiration cost in savanna species. This consideration could have influenced biomass loss or gain by respiration. In fact, respiration cost can differ between stem and roots according to plant species and environmental condition (Anekonda et al., 1994; Hansen et al., 1994). In summary, the success of allocation strategies depends on the tree architecture and especially the parameters which decrease stem biomass necessary for the establishment of a given quantity of leaves such as the internode length and the numbers of leaves per node. The cubic relation between stem and leaf biomass, which constrains the quantity of leaves available to grow, emphasize the role of plant architecture on plant growth.

4.4. What is the effect of the photosynthesis and translocation rates on the allocation strategies success?

High photosynthesis rate increases the parameter space allowing for successful strategies (either in terms of height after 50 yrs, or the time needed to reach 2 m). This is due to the increase in biomass that is permitted when photosynthesis increases but this does not change the

general pattern of successful strategies. However, because of the lack of information concerning savanna tree photosynthesis rate, the value for this parameter might not be correct. In Figs. 3 and 5, we have thus distinguished resprouts that reach 2 m within 2 years from those that reach 2 m after two years. The second case seems more realistic (field observation where plant cannot reach to meters before 2 years), and the first may be due to our estimation.

Nevertheless, this result helps us to analyze how photosynthesis rate alters plant allocation strategies to escape fire trap. In the D^+F^+ model, resprouts grow more quickly than in the D^+F^- model at the beginning of the growing season. This may be due to the architecture constraints we implemented for stem and leaves production (see appendix 4 in which we compared of the growth rate of the resprout with and without fire). Schutz et al. (2009) compared photosynthetic rates of individual plants of *Acacia karroo* without and with fire and found that growth of plants in burnt area was significantly greater than that of plants in unburnt areas. Our result is supported by this study considering only resprouts growth in burnt and unburnt area.

Menaut and César 1979 measured that after burning, root biomass decreased because of transfers (translocation) of reserves from belowground parts to the growing shoots. In our results, the increase of translocation rate facilitates the increase of the size of the parameters space that leads to successful strategies. Thus, the higher this rate, the larger the amount of biomass available for resprout growth, at least at the beginning of the rainy season. Increasing the translocation rate has thus the same effect as increasing the photosynthesis rate. In summary, the increase of both the rate of photosynthesis and the translocation rates has a positive effect on resprout growth and increases the parameter space leading to successful strategies.

5. Conclusion

Our model allows for the study of how allocation strategies of resprouts affect stem growth in a fire- prone savanna considering some architecture and seasonality. This model be a general simple model of tree resprouting that can be easily adapted to other situations such as arid savannas or forests by incorporating new mechanisms (plant resistance, fire frequency, roots which absorb soil carbon…). We conclude that (1) allocation to leaves is determinant as leaves are the primary source of assimilates that can then be turned into fire-resistant structures (reserves and belowground parts) and (2) fire only weakly slows down the plant growth compared to the dry season. These results allowed us better interpret field observations about savanna trees resprouting concerning allocation strategy. Finally, our model suggests that fire act in a similar way as a severe dry season on tree resprouting when we compare both with wet season.

### Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.
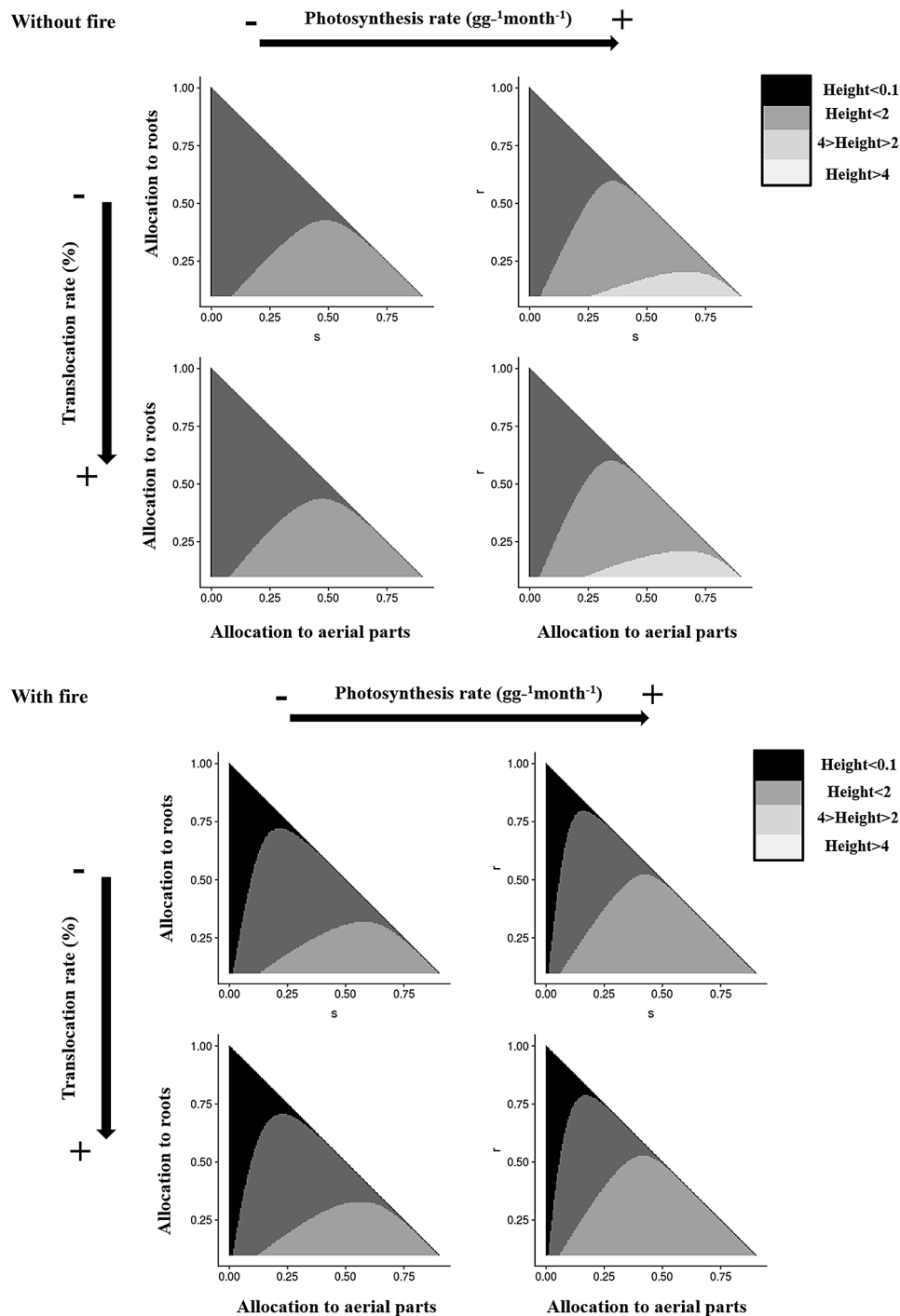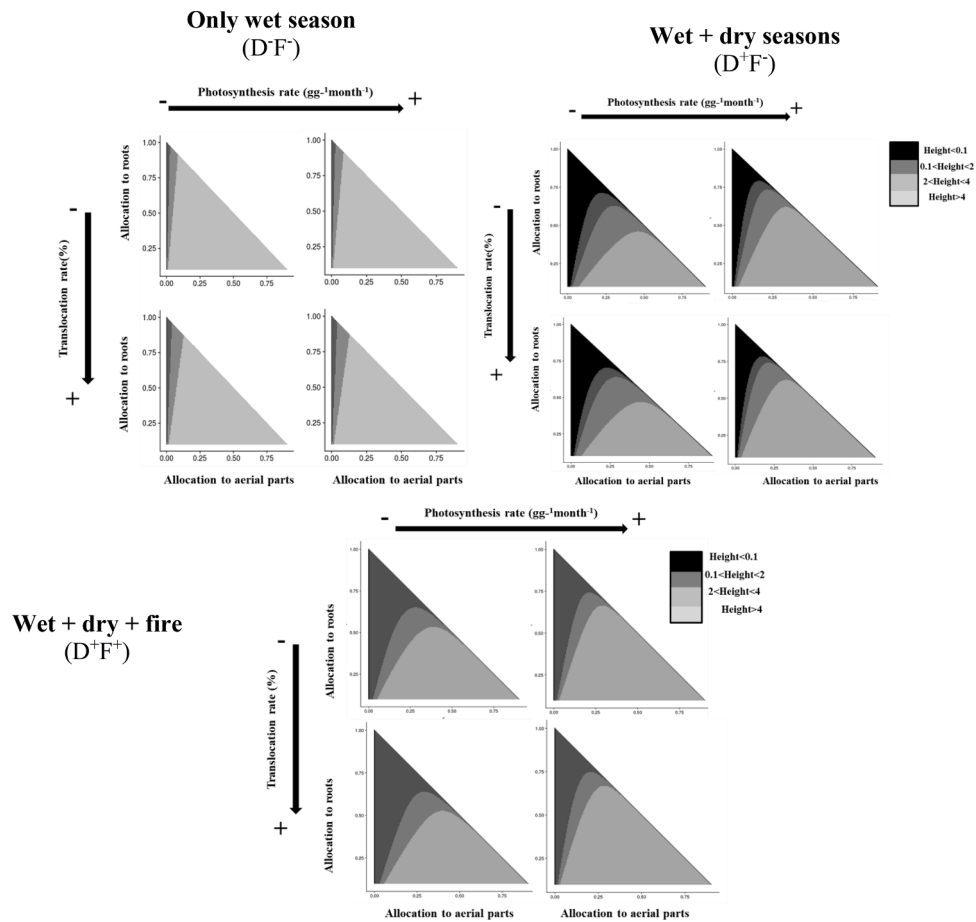
Appendix

Appendix 1: Comparison of *Bridelia ferruginea, Crossopteryx febrifuga* and *Piliostigma thonningii,* according to effect of the allocation strategies on the height (m) of 50 yrs old resprouts for 4 combinations of photosynthesis rate (a) and translocation rate of reserves (b) for b = 0.1 g g^{-1}mont^{-1}. Panel and axis description as in Fig. 2.
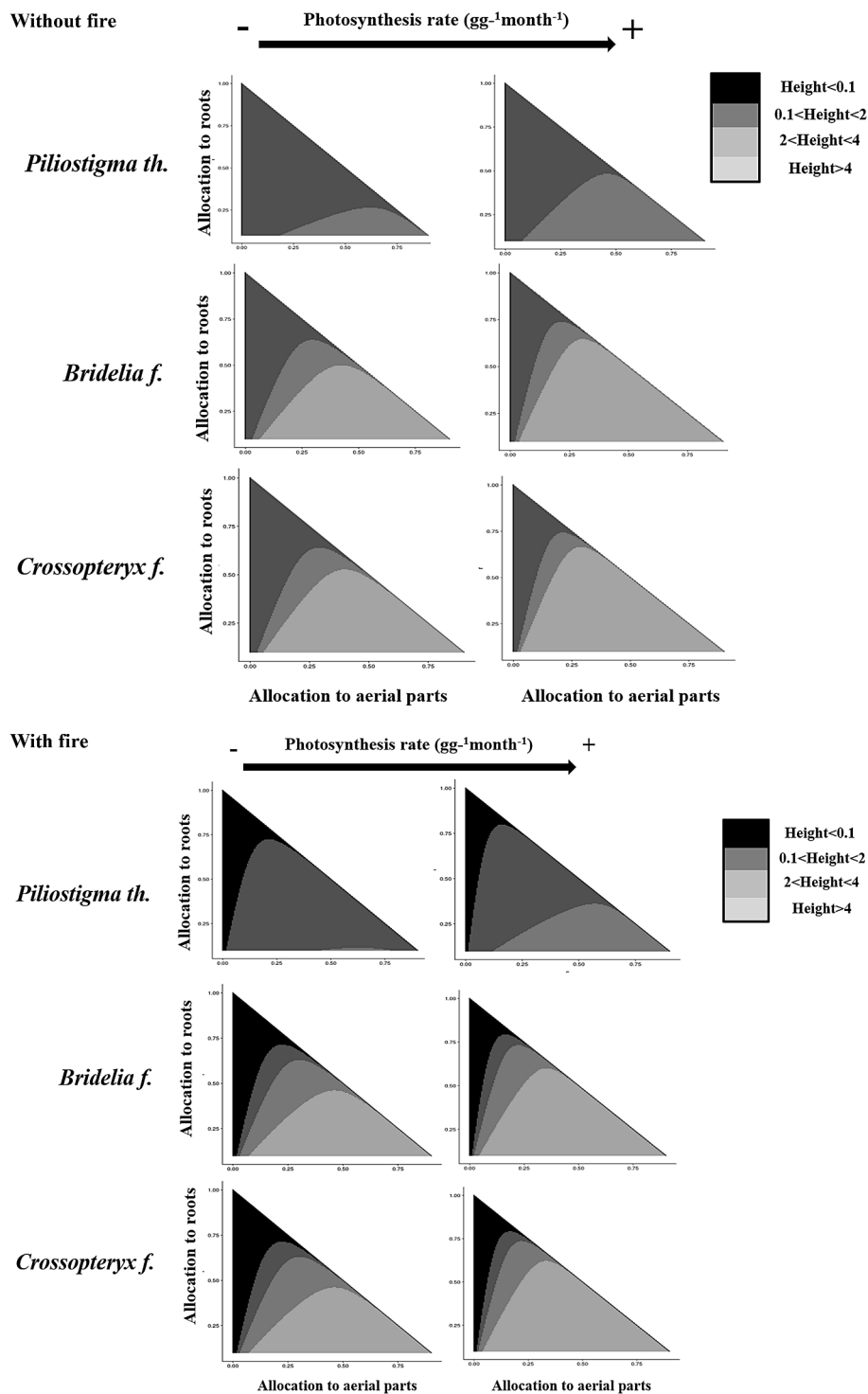
Appendix 2: Comparison of the time to reach 2 m for *Bidelia ferruginea, Crossopterix febrifuga* and *Piliostigma thonningii,* according to the rate of allocation to belowground parts (y axis) and the rate of allocation to aerial parts (x axis) for b = 0.1 g g^{-1}mont^{-1}. Panel and axis description as in Fig. 2.

Appendix 3: Comparison of allocation strategies between three simulations for *Crossopteryx febrifuga,* according to plant architecture after 50 yr old for 4 combinations of photosynthesis rate (a) and translocation rate of reserves (b). Panel and axis description as in Fig. 2.

Appendix 4: Comparison of resprout growth rate (by utilization of resprout height) of *Crossopteryx febrifuga* resprout height for 50 yr (600 month) with and without fire when $a = 3\,\mathrm{g\,g}^{-1}\mathrm{month}^{-1}$ and $b = 0.8$, allocation to belowground parts $r = 0.1$ and allocation to reserves $p = 0.69$ and allocation to aerial parts $s = 0.21$.
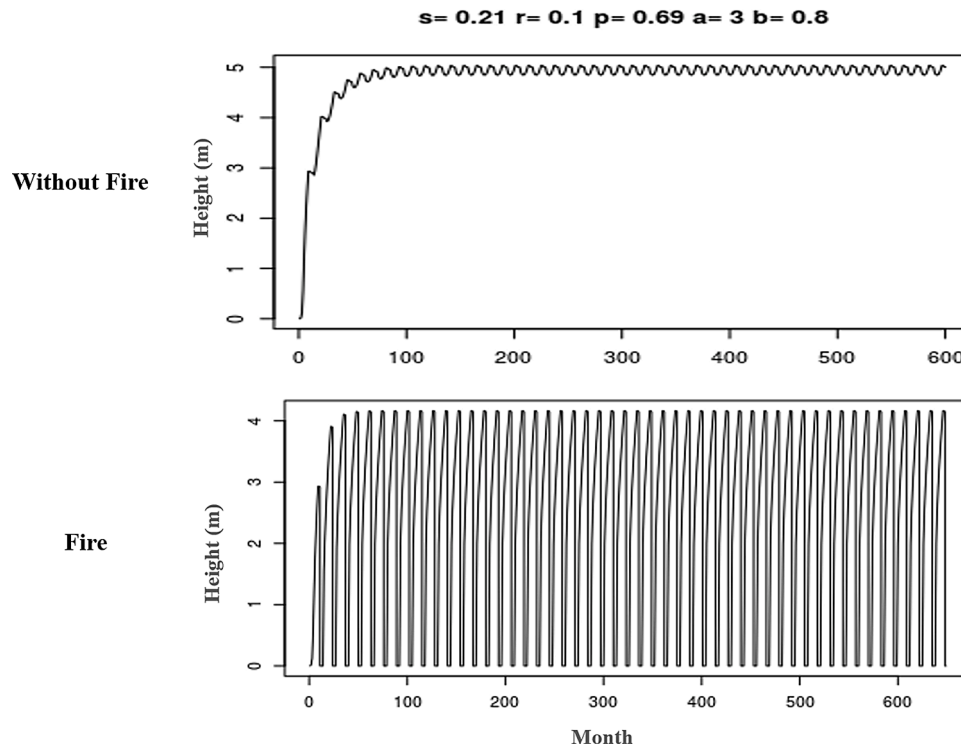
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