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Mummy, why do you keep on growing?

Impacts of environmental variability on optimal growth and reproduction allocation strategies of annual plants

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Abstract. In their 1990 paper *Optimal reproductive efforts and the timing of reproduction of annual plants in randomly varying environments*, Amir and Cohen considered stochastic environments consisting of i.i.d. sequences in an optimal allocation discrete-time model. We suppose here that the sequence of environmental factors is more generally described by a Markov chain. Moreover, we discuss the connection between the time interval of the discrete-time dynamic model and the ability of the plant to rebuild completely its vegetative body (from reserves). We formulate a stochastic optimization problem covering the so-called linear and logarithmic fitness (corresponding to variation within and between years), which yields optimal strategies. For "linear maximizers", we analyse how optimal strategies depend upon the environmental variability type: constant, random stationary, random i.i.d., random monotonous. We provide general patterns in terms of targets and thresholds. We also provide a partial result on the comparison between '"linear maximizers" and "log maximizers". Numerical simulations are provided, allowing to give a hint at the effect of different mathematical assumptions.

Contents

1. Introduction

The theoretical body on evolution of energy allocation between growth and reproduction is substantial in the ecological and biological litterature, with recurrent themes and questions. One of them is the *determinate growth* life-history pattern: mammals and many other organisms stop growth when they become mature and start to reproduce. But other animals and plants, such as fishes, snakes, clams, etc. experience *indeterminate growth*: their life-history shows mixed growth and reproduction. The role of the environment in allocation strategies and the question of phenotypic plasticity, that allows individuals to adapt their phenotype to their actual environment, are also largely debated [HM99].

Concerning plant growth, different papers identify optimal strategies as those which maximize a certain measure of fitness. In [Pug87], optimal strategies of perennial plants in a deterministic environment are those which maximize the Malthusian population rate of increase. Optimal strategies of plants in stochastic environments are studied in [AC90, IK97, Iwa00]. In stochastic environments, two different measures of fitness are available for annual plants. When variability is between individuals within the year, optimal plants are "linear fitness maximizers"; when variability is between years for the same individual, optimal plants are "log fitness maximizers". Although maximizing the expected value of the logarithm of the annual reproductive

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yield seems more appropriate in stochastic environments, it is unfortunately a mathematical challenge compared to maximizing the expected value. Amir and Cohen attacked this problem in [AC90] in the case of i.i.d. stochastic environmental factor sequences. We try and extend their work for general stochastic sequences, with the goal of studying the impacts of environmental variability on optimal strategies. Doing this, we shall contest some of their assertions as to stationarity of optimal strategies.

In section 2, we present the basic model by Amir and Cohen in [AC90], together with its extension to general Markovian environments. We discuss the biological content of the time unit (time interval of the discrete-time dynamic model), in connection to the ability of the plant to rebuild completely its vegetative body (from reserves). We also try to justify the two different measures of fitness presented hereabove. Optimal strategies are defined as those maximizing fitness: we cover both linear and logarithmic fitnesses under a common mathematical treatment. In section 3, we study how optimal strategies for "linear maximizers" depend upon environmental variability. We show that they are characterized by means of what we call *targets* and *thresholds*. This allows us to study the influence of different types of environmental variability: constant, random stationary, random i.i.d., random monotonous. A rich variety of patterns emerges from the property that targets and thresholds are generally functions of time and of the environmental factor. In section 5, we provide a partial result on the comparison between "linear maximizers" and "log maximizers". We do not insist on such a comparison which is a difficult task in all generality (some elements of discussion may be found in [AC90]). In the conclusion 6, we sum up our main results, discuss the limitations of our assumptions, and provide some numerical simulations to illustrate different options. The Appendix collects all proofs.

2. A discrete-time model of annual plant growth in general stochastic environments

We present here an extension of the basic model of [AC90] to the case where the sequence of environment factors in the year is not necessarily i.i.d.

2.1. A dynamic and stochastic growth model

The model is a discrete time one with time variable $t \in \{0, \ldots, \tau\}$. A time unit may typically be either a day ($t \in \{0, \ldots, 364\}$), a month ($t \in \{0, \ldots, 11\}$), or a season ($t \in \{0, 1, 2, 3\}$), where, in the whole paper, season is to be understood in the usual sense of winter, spring, summer, autumn.

We choose a discrete time model for different reasons. First, the original model of [AC90] is in discrete time (where, surprisingly, the time unit is not formally defined[1]). Second, when the effect of the environment may be summed up in a global factor over, for instance, a month (mean temperature, enlightment, etc.), a monthly discrete time unit is appropriate. Third, when time unit is the day, a continuous time model might be an alternative; however, our position is that the introduction of an adapted mathematical apparatus of continuous time stochastic processes and stochastic control would introduce technicalities that one may avoid with discrete time stochastic control. Here is the model.

1. At the beginning of each time interval $[t, t+1[$,
   (a) the plant is characterized by its vegetative biomass $k_t \in [0, +\infty[$ and by the cumulated reproductive biomass $S_t \in [0, +\infty[$;
   (b) an environmental factor $w_t \in \mathbb{W}$ affects the total biomass $f(k_t, w_t)$ which will be allocated between vegetative and reproductive biomass during $[t, t+1[$ (depends on roots, leaves, environmental factors, etc.); for instance, when time unit is a day, w may be the mean temperature, humidity, enlightment, etc. belonging to $\mathbb{W} = \mathbb{R}^n$; when time unit is a season, w may take discrete values corresponding to a global characterization of the season (for instance, $\mathbb{W} = \{\text{winter, spring, summer, autumn}\}$); the same holds for a month; in all generality, $\mathbb{W}$ is a Borel space, equipped with σ-algebra $\mathcal{W}$.
2. At the end of each time interval $[t, t+1[$,
   (a) the plant allocates biomass u_t − bounded above by $f(k_t, w_t)$ and below by a fraction α ($0 \leq \alpha \leq 1$) of its vegetative biomass − as vegetative biomass and $f(k_t, w_t) - u_t$ as reproductive biomass in the interval $[t, t+1[$; the constraint $\alpha k_t \leq u_t \leq f(k_t, w_t)$ will be commented in the following subsection;
   (b) the cumulated reproductive biomass is $S_{t+1} = S_0 + \sum_{s=0}^{t}[f(k_s, w_s) - u_s] = S_t + [f(k_t, w_t) - u_t]$;

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[1] Some references to "daily state of the environment" suggest that the time unit might be the day.

(c) the plant biomass is
  - either $k_{t+1} = u_t$ with probability β_t (survival), where β_t is a deterministic number in $[0,1]$;
  - or $k_{t+1} = 0$ with probability $1 - \beta_t$ (death);
(d) the environment is characterized by w_{t+1} randomly drawn according to law $\pi_t(dw_{t+1} \mid w_t)$; π_t is a stochastic kernel on $\mathbb{W}$, that is for all $w \in \mathbb{W}$, $\pi_t(dw' \mid w)$ is a probability on $(\mathbb{W}, \mathcal{W})$; for instance, when time unit is a day, the daily environmental factor w_{t+1} is statistically related to w_t; when time unit is a season, (w_0, w_1, w_2, w_3) is the deterministic sequence (winter, spring, summer, autumn), which may be generated from a degenerate stochastic kernel on $\mathbb{W} = \{\text{winter, spring, summer, autumn}\}$; when time unit is a month, $(w_0, \ldots, w_{11})$ may follow a deterministic sequence (sinusoidal) with random perturbations.

This goes on till the last time interval $[\tau, \tau + 1[$ where the plant ultimately dies: $k_{\tau+1} = 0$ with probability 1 (that is $\beta_\tau = 0$). Thus, $\tau + 1$ is the *maximal life span*: when time unit is a day, $\tau = 365$ is the number of days in one year; when time unit is a month, $\tau = 12$, and when time unit is a season, $\tau = 4$. The cumulated reproductive biomass at terminal time $\tau + 1$ is $S_{\tau+1}$, released in the form of independent offspring.

2.2. Biological comments

In the above model, the environmental factor w_t is realized and known at the beginning of the time interval $[t, t + 1[$. By "known", we simply mean that the decision at the end of the time interval $[t, t + 1[$ may depend upon w_t, just as it may depend upon the vegetative biomass k_t. This does not mean that the plant has a clairvoyance ability, but simply that allocation between vegetative and reproductive biomass is made at the end of the time interval, depending on observed environmental conditions.

As to the constraint $\alpha k_t \leq u_t \leq f(k_t, w_t)$, where $0 \leq \alpha \leq 1$, we shall discuss three cases.

$\alpha = 0$. The constraint $0 \leq u_t$ captures the assumption that the plant can rebuild completely its vegetative body (from reserves) during every time interval. Such a hypothesis requires a large time interval, as for a month or for a three-months season but not for one day. Let us insist upon the fact that
  - $u_t = 0$ is a possible decision, meaning that the plant can "decide" to die, transforming all vegetative biomass into reproductive one;
  - $u_t \leq k_t$ is a possible decision, meaning that the plant can reduce its present size.
$\alpha = 1$. The constraint $k_t \leq u_t$ is adapted to organisms which cannot, for structural reasons, reduce their body in a short time interval. In that case $F(k, w) = f(k, w) - k$ is nonnegative[2] and represents biomass produced in the time interval $[t, t + 1[$.
$0 < \alpha < 1$. This accounts for an intermediate situation, where the plant body decrease is possible but limited to a fraction of its body.

To end up, notice that the plant biomass is driven by the stochastic environmental factor $w_t \in \mathbb{W}$, through the control $u_t \in [\alpha k_t, f(k_t, w_t)]$, while the environmental factor w_t is affected neither by k_t, nor by S_t. Hence, an important implicit assumption is the absence of density-dependence effects.

2.3. Mathematical assumptions

Random environments Environmental randomness has two independent sources in the above model.

One is a sequence of independent Bernoulli random variables taking value 0 for death and 1 for survival: $d_0, \ldots, d_\tau$ are independent and such that $\mathbb{P}(d_t = 1) = \beta_t = 1 - \mathbb{P}(d_t = 0)$[3]. Such a sequence is characterized by (deterministic) parameters $\beta_0 \in [0, 1], \ldots, \beta_{\tau-1} \in [0, 1]$, $\beta_\tau = 0$.

The second source of randomness is a sequence of environmental factors $w_0, \ldots, w_\tau$, taking values in a Borel space $\mathbb{W}$ with σ-algebra $\mathcal{W}$, which affect the growth function $f(k, w)$. The family of stochastic kernels $(\pi_t)_{t=0,\ldots,\tau-1}$ on the Borel space $\mathbb{W}$, together with an inital law for w_0, generate a Markov chain $(w_t)_{t=0,\ldots,\tau}$

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[2] If, for some w_t, $F(k_t, w_t) < 0$, the constraint $k_t \leq u_t \leq f(k_t, w_t)$ cannot be satisfied, some additional assumptions must be made, as to decide that the organism must die. We shall make an *ad hoc* assumption to avoid such a situation.

[3] An equivalent formulation, as in [AC90], requires a random integer T having values in $\{0, 1, \ldots, \tau\}$ corresponding to death date. The link between both approaches is given by the formula $\mathbb{P}(T = t \mid T \geq t) = 1 - \beta_t = \mathbb{P}(d_t = 1)$.

of environmental factors. For technical reasons, we assume that the kernels satisfy the Feller property: for all continuous function $V : \mathbb{R}_+ \times \mathbb{W} \to \mathbb{R}$, the function $(k, w) \hookrightarrow \int V(k, w')\pi_t(dw' \mid w)$ takes finite values and is continuous.

In what follows, a general *random environment* is a sequence $(\beta_t, \pi_t)_{t=0,\dots,\tau-1}$ of deterministic numbers in $[0, 1]$ and of stochastic kernels as above[4]. By general random environment, we also mean the stochastic process $(d_t, w_t)_{t=0,\dots,\tau}$.

We shall particularly be concerned with *random stationary environments*. This is a special case where all β_t are equal to a fixed $\beta \in [0, 1]$ (except $\beta_\tau = 0$) and all π_t are equal to a fixed π. The Markov chain $(w_t)_{t=0,\dots,\tau}$ of environmental factors is then stationary.

Gross growth function Concerning the *(gross) growth function* $f : \mathbb{R}_+ \times \mathbb{W} \to \mathbb{R}$, we make the following assumptions:

- f is continuous;
- for all $w \in \mathbb{W}$, $f(0, w) = 0$ and $f(k, w) > 0$ for $k > 0$;
- for all $w \in \mathbb{W}$, $k \in \mathbb{R}_+ \hookrightarrow f(k, w)$ is increasing (and we denote by $k \in \mathbb{R}_+ \hookrightarrow f^{-1}(k, w)$ its inverse[5]);
- for all $w \in \mathbb{W}$, $k \in \mathbb{R}_+ \hookrightarrow f(k, w)$ is strictly concave.

All these assumptions are classical in an economic framework where the trade-off is, for instance, between consumption and investment [BM72].

For simplicity reasons (see footnote 2), we add the following assumption:

- for all $w \in \mathbb{W}$, $f(k, w) \geq \alpha k$ for $k \geq 0$; when $\alpha = 0$, this assumption is a consequence of our second assumption hereabove; when $\alpha > 0$, this is an *ad hoc* assumption to avoid problems with empty constraints sets.

As an illustration, the growth function

$$f(k, w) = wk^\gamma \quad \text{with} \quad w \in \mathbb{R}_+, \quad k \in \mathbb{R}_+, \quad 0 < \gamma < 1 \tag{1}$$

satisfies the above assumptions for $\alpha = 0$. For $0 < \alpha \leq 1$, one would rather take $f(k, w) = k + wk^\gamma$.

2.4. Two measures of fitness

We try here to make explicit the assumptions leading to two different measures of fitness (see [Coh66, LC69, Cas01]). By a strategy, we mean here a Markovian strategy, that is a feedback $u_t = \varphi(t, k_t, S_t, w_t)$ depending both upon the time interval and upon the state at this date (vegetative biomass, cumulated offspring, environment).

Variability between individuals within year We consider N annual plants following the same strategy in one year. Each plant i is submitted to death occurences $(d_t^i)_{t=0,\dots,\tau}$ and environmental factors $(w_t^i)_{t=0,\dots,\tau}$. We assume that the sequence $(d_t^1, w_t^1)_{t=0,\dots,\tau}, \dots, (d_t^N, w_t^N)_{t=0,\dots,\tau}$ is i.i.d. Thus, plants only differ by the realizations of the environment. The total annual reproductive yield by the N plants is $S_{\tau+1}^1 + \dots + S_{\tau+1}^N$. If we assume that N is large, then $S_{\tau+1}^1 + \dots + S_{\tau+1}^N \approx N\mathbb{E}(S_{\tau+1})$, by the law of large numbers.

This is why $\mathbb{E}(S_{\tau+1})$, expected value of the annual reproductive yield, is the appropriate measure of fitness when variability is between individuals within the same year and the populations are sufficiently large.

Variability between years for the same individual Here, we follow a single plant from year to year during N years (and not N plants during one year).

At the beginning at year 1, the plant has vegetative biomass k_0; at the end, it yields $S_{\tau+1}^1$ offspring, depending on death occurences $(d_t^1)_{t=0,\dots,\tau}$ and environmental factors $(w_t^1)_{t=0,\dots,\tau}$ (recall that index t measures time intervals within a year). We write $S_{\tau+1}^1 = \Phi((d_t^1, w_t^1)_{t=0,\dots,\tau})$.

We assume that this offspring gives $n_1 = \lfloor \frac{S_{\tau+1}^1}{k_0} \rfloor$ plants ($\lfloor s \rfloor$ is the largest integer $\leq s$) of vegetative biomass k_0. Thus, all "sons" become new plants at the beginning of year 2, and the process starts with null

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[4] We do not insist on the initial law for w_0 which plays little role in the sequel.
[5] With the convention that $f^{-1}(+\infty, w) = +\infty$, for all $w \in \mathbb{W}$.

offspring. Since there are no density-dependence effects in our model, we have $S_{\tau+1}^2 = n_1 \times \Phi((d_t^2, w_t^2)_{t=0,\ldots,\tau})$, and thus $n_2 = \lfloor \frac{S_{\tau+1}^2}{k_0} \rfloor \approx n_1 \frac{\Phi((d_t^2, w_t^2)_{t=0,\ldots,\tau})}{k_0}$.

Pursuing this process, we see that the total reproductive yield at the end of year N is $n_1 \cdots n_N k_0 \approx \frac{\Phi((d_t^1, w_t^1)_{t=0,\ldots,\tau})}{k_0} \cdots \frac{\Phi((d_t^N, w_t^N)_{t=0,\ldots,\tau})}{k_0} k_0$. The *long-run annual yield of seeds* is $\lim_{N \to +\infty} [n_1 \cdots n_N k_0]^{1/N}$. If the sequence $(d_t^1, w_t^1)_{t=0,\ldots,\tau}, \ldots, (d_t^N, w_t^N)_{t=0,\ldots,\tau}$ is i.i.d., the *time-averaged growth rate* is then

$$\log([n_1 \cdots n_N k_0]^{1/N}) \approx \frac{1}{N}[\log \frac{\Phi((d_t^1, w_t^1)_{t=0,\ldots,\tau})}{k_0} + \cdots + \log \frac{\Phi((d_t^1, w_t^1)_{t=0,\ldots,\tau})}{k_0} + \log k_0]$$

$$\to_{N \to +\infty} \mathbb{E}(\log \frac{\Phi((d_t^1, w_t^1)_{t=0,\ldots,\tau})}{k_0}) = \mathbb{E}(\log \frac{S_{\tau+1}^1}{k_0}) \tag{2}$$

by the law of large numbers. This is why $\mathbb{E}(\log S_{\tau+1})$, expected value of the logarithm of the annual reproductive yield, is the appropriate measure of fitness when variability is between years.

Notice that the assumption that the sequence $(d_t^1, w_t^1)_{t=0,\ldots,\tau}, \ldots, (d_t^N, w_t^N)_{t=0,\ldots,\tau}$ is i.i.d. implies that for all t, $d_t^1, \ldots, d_t^N$ are i.i.d. This precludes dependence between years, such as would be the effect of global warming for instance.

2.5. Fitness maximization in a stochastic environment

We shall now formulate an optimization problem which covers both cases of fitness. Let $U : \text{Dom}(U) \to \mathbb{R}$ be a concave increasing function, which will be either $U(y) = y$ ($\text{Dom}(U) = [0, +\infty[$) or $U(y) = \log y$ ($\text{Dom}(U) =]0, +\infty[$). Maximizing linear or logarithmic fitness amounts to solving the optimization problem

$$\begin{cases} \sup \mathbb{E}\left(U(S_{\tau+1})\right) \\ (k_t, S_t, w_t) \quad \text{controlled Markov chain with transition defined above} \\ \quad \text{under constraint} \quad \alpha k_t \leq u_t \leq f(k_t, w_t). \end{cases} \tag{3}$$

Classically, stochastic dynamic programming ([Ber00]) gives optimal strategies which are feedback strategies: they depend both upon the time interval and upon the state at this date (vegetative biomass, cumulated offspring, environment), that is $u_t = \varphi(t, k_t, S_t, w_t)$. It is clear that optimal strategies are defined in terms of regions in the state space: at each date, there is one domain in which full allocation to growth is optimal ($u_t = f(k_t, w_t)$), and the complement domain where some reproduction occurs ($u_t < f(k_t, w_t)$). For "linear maximizers", these domains do not depend upon the cumulated offspring, as is shown in [AC90].

However, we depart from Amir and Cohen's mathematical characterizations of these domains. By a rigorous application of stochastic dynamic programming, we shall provide characterizations which lead us to question some of Amir and Cohen's assertions as to stationarity. Indeed, we shall show that, even for stationary environments, the domain in which full allocation to growth is optimal is generally different from time interval to time interval. This reflects the influence of the final horizon $\tau + 1$. However, we shall prove that there exist stationary strategies under specific assumptions.

The following Proposition describes the optimal strategy by means of three regions: one where the upper bound on u_t is binding, corresponding to full allocation to growth ($u_t = f(k_t, w_t)$); one where the lower bound on u_t is binding and where u_t sticks to αk_t due to impossibility of total rebuilding (this region is meaningless when $\alpha = 0$); one where none of these bounds is binding and where vegetative biomass reaches a target $\kappa_U^+(k_t, S_t, w_t, t)$, while remaining biomass is allocated to reproduction.

Proposition 1. *There exist mappings κ_U^+ and κ_U^- such that an optimal strategy for the stochastic optimization problem (3) is the following:*

$$\forall t = 0, \ldots, \tau - 1, \quad u^\sharp(k, S, w, t) = \begin{cases} f(k, w) & \text{if} \quad f(k, w) \leq \kappa_U^+(k, S, w, t) \\ \kappa_U^+(k, S, w, t) & \text{if} \quad \alpha k \leq \kappa_U^-(k, S, w, t) < f(k, w) \\ \alpha k & \text{if} \quad \alpha k \leq \kappa_U^+(k, S, w, t) \end{cases} \tag{4}$$

and $u^\sharp(k, S, w, \tau) = 0$.

Notice that $u^\sharp(k, S, w, \tau) = 0$ means that the plant ultimately dies to convert all its vegetative biomass into reproductive one. Indeed, the fitness is an increasing function of the cumulated offspring so that there is no gain in fitness by keeping vegetative biomass after the last time interval. Notice also that the full growth region $\{(k, S, w) \mid u^\sharp(k, w, t) = f(k, w)\} = \{(k, S, w) \mid f(k, w) \le \kappa_U^+(k, S, w, t)\}$ is generally nonstationary.

3. Impact of environmental variability on optimal strategies for "linear maximizers"

We take

$$U(y) = y, \quad \mathrm{Dom}(U) = [0, +\infty[\,. \tag{5}$$

This case is simpler to analyze than the "log maximizers" one ($U = \log$).

3.1. Optimal strategies for "linear maximizers" plants

In (stochastic) inventory control, (σ, Σ) policies are those for which there exists a stock threshold σ under which stocks have to be refilled up to the target Σ (see [Put94]). Here, optimal strategies are in the same vein but with moving thresholds and targets.

Proposition 2. *There exist mappings κ^+ and κ^- such that the optimal strategy for "linear maximizers" is the following:*

$$\forall k \in \mathbb{R}_+ \,, \, \forall w \in \mathbb{W}\,, \quad
\begin{cases}
\quad\quad\quad u^\sharp(k, w, \tau) = 0 \\[2mm]
\forall t = 0, \ldots, \tau - 1\,, \quad u^\sharp(k, w, t) =
\begin{cases}
f(k, w) & if \quad k \le \kappa^-(w, t) \\[2mm]
\kappa^+(w, t) & if \quad k > \kappa^-(w, t) \ \ and \ \ \alpha k \le \kappa^+(w, t) \\[2mm]
\alpha k & if \quad \alpha k > \kappa^+(w, t)\,.
\end{cases}
\end{cases} \tag{6}$$

The target $\kappa^+(w, t)$ *and the* threshold $\kappa^-(w, t)$ *are related by the following relationship*

$$\forall t = 0, \ldots, \tau - 1\,, \quad \kappa^-(w, t) \stackrel{\mathrm{def}}{=} f^{-1}(\kappa^+(w, t), w)\,. \tag{7}$$

Thus, the full growth region $\{(k, S, w) \mid u^\sharp(k, w, t) = f(k, w)\} = \{(k, S, w) \mid 0 \le k \le \kappa^-(w, t)\}$ does not depend upon S.

The relationship between thresholds and targets is not straightforward, in the sense that no general inequality exists between $\kappa^+(w, t)$ and $\kappa^-(w, t')$, whatever w, w' in $\mathbb{W}$, even when $w = w'$. As an example, take for growth function $f(k, w) = w\sqrt{k}$ as in (1). Consider a random i.i.d. environment characterized by $\beta \in [0, 1]$, $\mathbb{W} = \{w^-, w^+\} \subset]0, +\infty[$ where $w^- < w^+$, and probability law ρ on $\mathbb{W}$ given by $\rho(\{w^-\}) = p \in]0, 1[$.

Let $m \stackrel{\mathrm{def}}{=} \int w\rho(dw) = pw^- + (1 - p)w^+$. By (11) and (15), we have

$$\kappa^+(w, \tau - 1) = \arg\max_{u \ge 0}[-u + \beta \int_{\mathbb{R}_+} w\sqrt{u}\rho(dw)] = \arg\max_{u \ge 0}[-u + \beta m\sqrt{u}] = \left(\frac{\beta m}{2}\right)^2\,. \tag{8}$$

By (7), we deduce

$$\kappa^-(w, \tau - 1) = [\frac{1}{w}\left(\frac{\beta m}{2}\right)^2]^2\,. \tag{9}$$

Thus, $\kappa^+(w, \tau - 1)/\kappa^-(w, \tau - 1) = [\frac{2w}{\beta m}]^2$. We have $\kappa^+(w^+, \tau - 1)/\kappa^-(w^+, \tau - 1) = [\frac{2w^+}{\beta m}]^2 \ge (2/\beta)^2 \ge 4$ since $w^+ \ge m = pw^- + (1 - p)w^+$ and $0 < \beta \le 1$. On the other hand, $\kappa^+(w^-, \tau - 1)/\kappa^-(w^-, \tau - 1) = [\frac{2w^-}{\beta m}]^2 < 1$ if and only if $\frac{2w^-}{\beta m} < 1$ if and only if $w^+ > \frac{1}{1-p}(\frac{2}{\beta} - p)w^-$.

3.2. Stationary targets and thresholds in constant environments

In a *constant environment*, the sequence $(w_t)_{t=0,\ldots,\tau}$ of environmental factors is both deterministic and constant: $w_t = \overline{w}$, $\forall t = 0, \ldots, \tau$. All β_t are also equal to a fixed $\beta \in [0, 1]$ (except $\beta_\tau = 0$). In this case, one may show that targets and thresholds are stationary ([AC90], or consequence of Proposition 6). Their expressions are[6] (recall also convention in footnote 5):

$$\kappa^+ = \arg\max_{0 \le u}[-u + \beta f(u, \overline{w})] \in [0, +\infty] \quad \text{and} \quad \kappa^- = f^{-1}(\kappa^+, \overline{w}). \tag{10}$$

Moreover, in the constant case, the threshold κ^- is always lower than the target κ^+. Indeed, if $\kappa^+ = +\infty$, then $\kappa^- = +\infty$ too (recall footnote 5). Else, by (10), $\kappa^+ = \arg\max_{0 \le u}[-u + \beta f(u, \overline{w})]$ and thus $-\kappa^+ + \beta f(\kappa^+, \overline{w}) \ge -0 + \beta f(0, \overline{w}) = 0$. Hence, we have $f(\kappa^+, \overline{w}) \ge \beta f(\kappa^+, \overline{w}) \ge \kappa^+$, that is $\kappa^+ \ge \kappa^- = f^{-1}(\kappa^+, \overline{w})$ since f is increasing in its first argument.

3.3. Properties of targets in random i.i.d. environments

A *random i.i.d. environment* is a stationary one in which the fixed stochastic kernel is of the form $\pi(dw' \mid w) = \rho(dw')$ where ρ is a probability law on $\mathbb{W}$. In this case, the sequence $(w_t)_{t=0,\ldots,\tau}$ of environmental factors is i.i.d., with common distribution ρ. This is the case studied by Amir and Cohen. As them, we find that the target does not depend upon w ([AC90], or consequence of formula (39)): $\kappa^+(w, t) = \kappa^+(t)$. However, the thresholds $\kappa^-(w, t) = f^{-1}(\kappa^+(t), w)$ depend upon the environmental factor w by (7).

3.4. Undeterminate growth strategies appear to be generally optimal in random environments

Summing up the above results, optimal strategies of Proposition 2 are characterized by targets (and corresponding thresholds):

- in general stochastic environments, targets and thresholds are functions of time t and, above all, of the environmental factor w;
- in a random i.i.d. environment, the targets only depend upon time t and not upon the environmental factor w; however, the thresholds depend upon both t and w;
- in a constant environment, targets and thresholds are fixed scalars, independent of time t.

We claim that, even if the optimal strategy (6) has a "bang-bang look", the presence of the environmental factor w may induce "undeterminate" growth trajectories. We have the feeling that the dependence of both the value function and the optimal strategy upon the environmental factor w have not been treated with enough care by Amir and Cohen. As a consequence, our conclusion differs from their when they claim in [AC90, p.30] that "any growth strategy is of the "bang-bang" type" and that "the optimal strategy is to keep growing as long as the vegetative body is smaller than $\widetilde{\kappa}(r)$ $[r = 1 - \beta]$ and to switch to reproduction once $\widetilde{\kappa}(r)$ is reached".

We illustrate this on a numerical simulation[7] with growth function $f(k, w) = w\sqrt{k}$ as in (1) and $\alpha = 0$, $\beta = 0.8$, $T = 12$ (corresponding to rebuilding ability within a month). The environmental factor follows an i.i.d. sequence, taking two values 0.15 and 0.65 with equal probability $1/2$. Figure 1 shows two realizations of the environmental factor sequence, giving rise to two optimal control trajectories in Figure 2 and to two optimal vegetative biomass trajectories in Figure 3.

$t = 0$. Consider a plant starting from size k_0 ($k_0 = 0.05$ maintained during the first time interval $[0, 1[$ in Figure 3). If the environmental factor w_0 is such that $k_0 \le \kappa^-(w_0, 0)$, the "plant's first decision" is to grow without reproducing: $k_1 = u_0 = f(k_0, w_0)$. This corresponds to the first time interval $[0, 1[$ in Figure 2.

$t = 1$. Now, the environmental factor takes the value w_1.

---

[6] With the convention that $\arg\max \emptyset = +\infty$.

[7] The numerical simulations are done with the scientific software SCILAB with dedicated programs for stochastic dynamic programming.
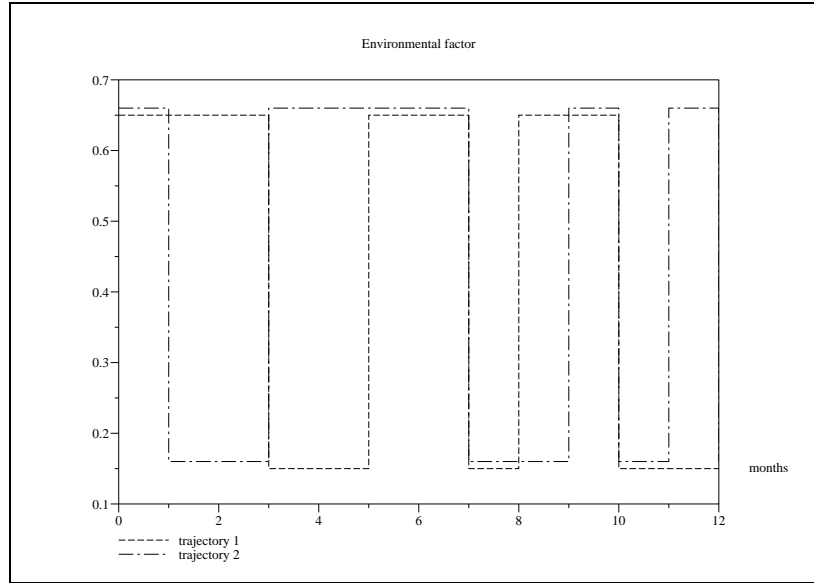
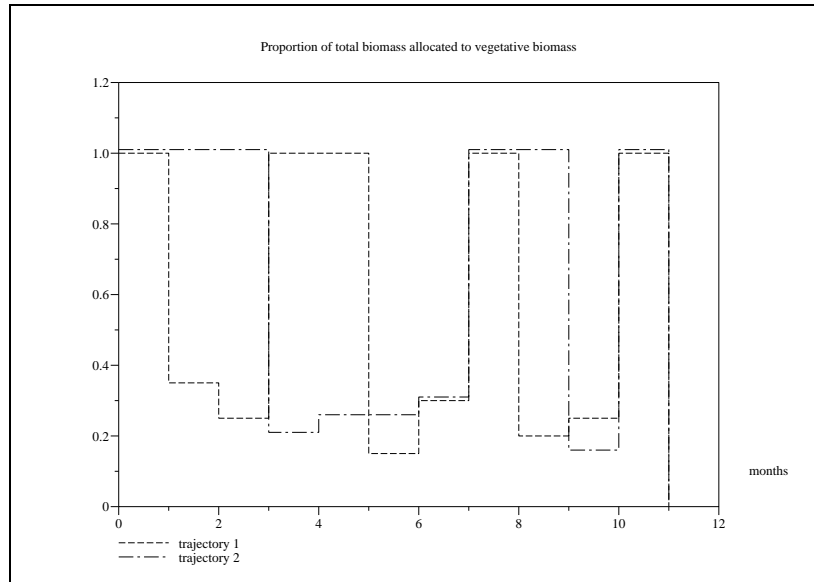**Fig. 1.** *Two realizations of the environmental factor sequence*

Fig. 2. *Proportion of total biomass allocated to vegetative biomass*

- If $k_1 > \kappa^-(w_1, 1)$, the second decision is to grow up to target $k_2 = u_1 = \kappa^+(w_1, 1)$. Since $f(k_1, w_1) > f(\kappa^-(w_1, 1), w_1) = \kappa^+(w_1, 1)$ by definition of $\kappa^-(w_1, 1)$ and, since $k \hookrightarrow f(k, w_1)$ is increasing, the plant produces $f(k_1, w_1) - u_1 = f(k_1, w_1) - \kappa^+(w_1, 1) > 0$ offspring. This corresponds to the trajectory 1 in Figure 2 on the second time interval $[1, 2[$.
- Else, the second decision is growing without reproducing: $k_2 = f(k_1, w_1)$. This corresponds to the trajectory 2 in Figure 2 with 100 % allocation of total biomass to vegetative biomass on the second time interval $[1, 2[$.

$t = 2$. Now, the environmental factor takes the value w_2, and the discussion is as above.

Since the thresholds $\kappa^-(w_t, t)$ are always varying, due both to time t and to the stochastic environmental factor w_t, phases of pure growth without reproduction may alternate with phases of mixed growth and
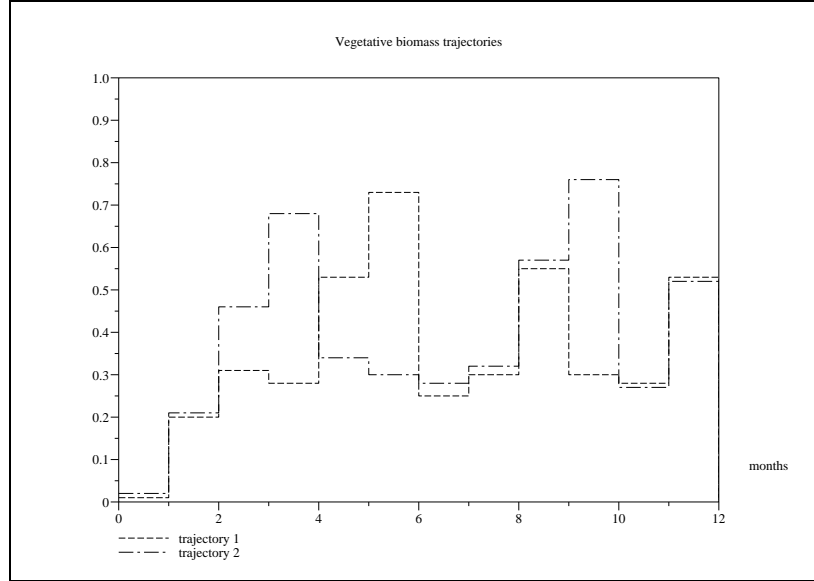
Fig. 3. *Two optimal trajectories*

reproduction (see Figure 2). Contrarily to the constant environment case, following an optimal strategy no longer leads to determinate growth even when maximizing $\mathbb{E}(S_{\tau+1})$. Even in a random i.i.d. environment, the optimal trajectory is *a priori* not "determinate" since the thresholds $\kappa^-(w, t) = f^{-1}(\kappa^+(t), w)$ still depend upon the environmental factor w (see subsection 4.3 for conditions for optimality of determinate growth in random i.i.d. environments).

One may notice on Figure 1 and Figure 2 that full growth occurs when the environmental factor is low. This will be explained in Proposition 9 in relation to the fact that k and w are cooperative factors in the growth function $f(k, w) = w\sqrt{k}$ (i.e. $\frac{\partial^2 f}{\partial k \partial w} \geq 0$).

4. Optimal strategies for "linear maximizers" plants without limitation for rebuilding their vegetative body

In the sequel, we assume that $\alpha = 0$ (see discussion in subsection 2.1).

4.1. Random stationary environments give non increasing thresholds and targets when time goes on

Let us assume that the environment is random stationary, and characterized by $\beta \in [0, 1]$ and stochastic kernel π. Let us introduce[8]

$$
\begin{cases}
\kappa_f^+(w) \overset{\text{def}}{=} \arg\max_{0 \leq u}[-u + \beta \int f(u, w')\pi(dw' \mid w)] = \kappa^+(w, \tau - 1) \in [0, +\infty] \\
\\
\kappa_f^-(w) \overset{\text{def}}{=} \kappa^-(w, \tau - 1) = f^{-1}(\kappa_f^+(w), w).
\end{cases}
\tag{11}
$$

The following result shows that, as time goes on, the thresholds for reproduction are lower and lower, as well as the targets reached.

Proposition 3. *When the environment is random stationary, both thresholds and targets are nonincreasing with time:* $\forall t = 0, \ldots, \tau - 2, \quad \forall w \in \mathbb{W},$

$$
\begin{cases}
\quad\quad\quad\quad \kappa^+(w, t) \geq \kappa^+(w, t + 1) \geq \kappa_f^+(w) = \kappa^+(w, \tau - 1) \\
and \\
\quad\quad\quad\quad \kappa^-(w, t) \geq \kappa^-(w, t + 1) \geq \kappa_f^-(w) = \kappa^-(w, \tau - 1).
\end{cases}
\tag{12}
$$

---

[8] By unicity of the arg max resulting from strict concavity of $u \hookrightarrow f(u, w')$, and recalling conventions in footnotes 5 and 6.

Notice that this result does not mean that a trajectory is nonincreasing, since $\kappa^+(w,t) \geq \kappa^+(w,t+1)$ does not imply that $\kappa^+(w_t,t) \geq \kappa^+(w_{t+1},t+1)$.

We shall now give an example where this decrease is strict, which contradicts the stationary characterization (5) in [AC90, p.22].

Proposition 4. *Let the growth function be* $f(k,w) = w\sqrt{k}$ *as in (1). Let the environment be random i.i.d. characterized by* $\beta \in [0,1]$, $\mathbb{W} = \{w^-, w^+\} \subset]0, +\infty[$ *where* $w^- < w^+$, *and probability law* ρ *on* $\mathbb{W}$ *given by* $\rho(\{w^-\}) = p \in]0,1[$.
If $w^+ > \frac{1}{1-p}(\frac{2}{\beta} - p)w^-$, *the last targets are decreasing:* $\kappa^+(\tau-1) < \kappa^+(\tau-2)$.

4.2. Random stationary environments giving stationary thresholds and targets

Here, we exhibit a condition under which thresholds and targets are stationary in a random stationary environment.

Proposition 5. *Assume that the environment is random stationary and that*

$$\forall w \in \mathbb{W}, \quad \pi(\{w' \mid \kappa_f^+(w') \leq f(\kappa_f^+(w), w')\} \mid w) = 1. \tag{13}$$

Then both thresholds and targets are stationary:

$$\forall t = 0, \ldots, \tau-1, \quad \forall w \in \mathbb{W}, \quad \kappa^+(w,t) = \kappa_f^+(w) \quad and \quad \kappa^-(w,t) = \kappa_f^-(w). \tag{14}$$

Along any optimal trajectory the plant reproduces at all times after having reached maturity. However, there is no fixed size at maturity.

Condition (13) means that, starting from target size $\kappa_f^+(w)$ in environmental state w, the total biomass to allocate under environmental state w' reachable from w is greater than target $\kappa_f^+(w')$.

4.3. Random i.i.d. environments giving stationary thresholds and targets and determinate growth pattern

Consider a random i.i.d. environment characterized by $\beta \in [0,1]$ and probability law ρ on $\mathbb{W}$. Let us define[9]

$$\kappa^+ \stackrel{\text{def}}{=} \arg\max_{0 \leq u}[-u + \beta \int f(u, w')\rho(dw')]. \tag{15}$$

Proposition 6. *Assume that the environment is random i.i.d. and that*

$$\rho(\{w \mid \kappa^+ \leq f(\kappa^+, w)\}) = 1. \tag{16}$$

Then the targets are constant and the thresholds are stationary:

$$\forall t = 0, \ldots, \tau-1, \quad \forall w \in \mathbb{W}, \quad \kappa^+(w,t) = \kappa^+ \quad and \quad \kappa^-(w,t) = f^{-1}(\kappa^+, w). \tag{17}$$

All reachable thresholds are lower than the target: $\rho(\{w \mid \kappa^-(w,t) \leq \kappa^+\}) = 1$. *Along any optimal trajectory the plant reproduces at all times after having reached maturity, and keeps a fixed size* (κ^+) *at maturity.*

The condition (16) means that the maximum total biomass $f(\kappa^+, w)$ for a plant of size κ^+ is no less than κ^+, whatever the environmental factor value. In this case, the optimal pattern is determinate growth, as in constant environments (see subsection 3.2).

This may be seen in Figures 4–5–6 (numerical discretization of vegetative biomass leads to an approximate fixed size at maturity). For the simulations, we have taken the same model as the one used for Figures 2 and 3, except for the values of environmental factor, here 0.15 and 0.35 with equal probability 1/2. Such values satisfy (16).

---

[9] By unicity of the $\arg\max$ resulting from strict concavity of $u \hookrightarrow f(u,w')$ and recalling convention in footnote 6.
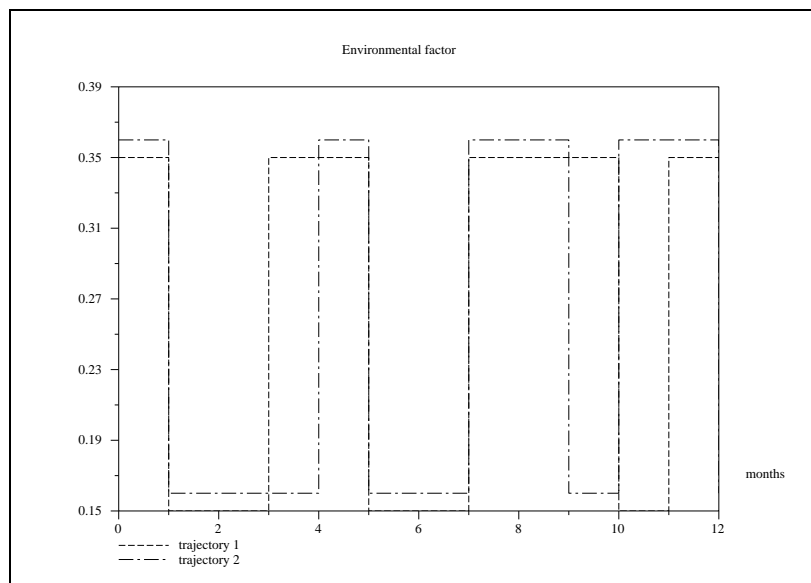
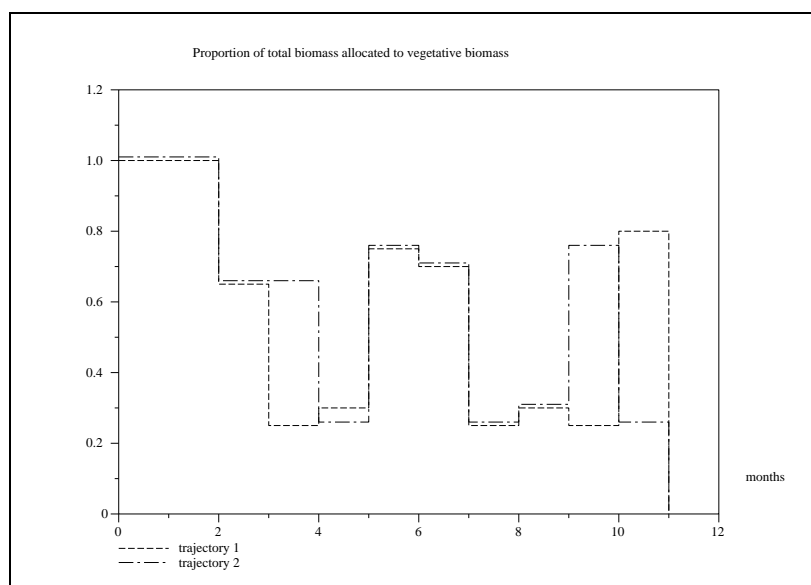**Fig. 4.** *Two realizations of an environmental factor sequence whichs satisfies (16)*

Fig. 5. *Proportion of total biomass allocated to vegetative biomass: approximate determinate growth pattern*

4.4. Stochastically monotonous environments

We assume here that $\mathbb{W}$ is an ordered set.

We say that the stochastic kernel π is *stochastically nondecreasing (resp. nonincreasing)* if the function $w \in \mathbb{W} \hookrightarrow \int \varphi(w')\pi(dw' \mid w)$ is nondecreasing (resp. nonincreasing) for any nondecreasing $\varphi : \mathbb{W} \to \mathbb{R}$ such that the integral is well defined.

Following [AC90], we say that state and environmental factor are *cooperative* if the function f has nondecreasing differences, that is if for all $w_1 \geq w_2$ the function $k \in \mathbb{R}_+ \hookrightarrow f(k, w_1) - f(k, w_2)$ is nondecreasing or, equivalently, if for all $k_1 \geq k_2$ the function $w \in \mathbb{W} \hookrightarrow f(k_1, w) - f(k_2, w)$ is nondecreasing. In the case where small plants are more sensitive to environmental factors than bigger ones, state and environmental factor are *rival* in the sense that the function f has nonincreasing differences.
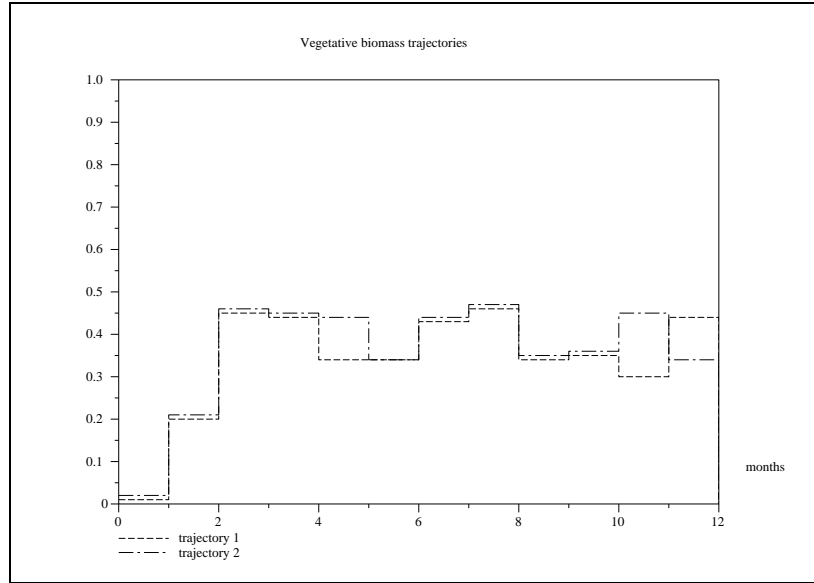
Fig. 6. *Two optimal trajectories: approximate determinate growth pattern*

Notice that, when state and environmental factor are cooperative (resp. rival), then $w \hookrightarrow f(k, w)$ is nondecreasing (resp. nonincreasing) for all k. Indeed, in the cooperative case, f has nondecreasing differences while, on the other hand $f(0, w) = 0$. This gives

$$w_1 \geq w_2 \Rightarrow \forall k \geq 0, \quad f(k, w_1) - f(k, w_2) \geq f(0, w_1) - f(0, w_2) = 0.$$

The rival case is treated in the same way. We have thus proved the following Proposition.

Proposition 7. *When state and environmental factor are cooperative (resp. rival), then $w \hookrightarrow f(k, w)$ is nondecreasing (resp. nonincreasing) for all $k \in \mathbb{R}_+$.*

The following results show the influence of the monotonicity of the stochastic kernel $\pi_{\tau-1}$ on the last targets and thresholds.

Proposition 8.

1. *Assume that state and environmental factor are rival.*
   (a) *If $\pi_{\tau-1}$ is stochastically nondecreasing, then the target $k^+(w, \tau-1)$ is a nonincreasing function of w.*
   (b) *If $\pi_{\tau-1}$ is stochastically nonincreasing, then both the target $k^+(w, \tau-1)$ and the threshold $k^-(w, \tau-1)$ are nondecreasing functions of w.*
2. *Assume that state and environmental factor are cooperative.*
   (a) *If $\pi_{\tau-1}$ is stochastically nondecreasing, then the target $k^+(w, \tau-1)$ is a nondecreasing function of w.*
   (b) *If $\pi_{\tau-1}$ is stochastically nonincreasing, then both the target $k^+(w, \tau-1)$ and the threshold $k^-(w, \tau-1)$ are nonincreasing functions of w.*

When state and environmental factor are cooperative, we shall use the terminology *environmental resource* instead of environmental factor. Thus, for an annual plant in a context where resource are statistically nonincreasing at the penultimate time interval, the plant is more encline to ultimately reproduce when resource are high than when they are low. "High" and "low" may be swapped in the hereabove assertion in case of rival factors. Such a claim cannot be asserted for all previous time intervals and decisions[10].

An easy consequence of Proposition 7 is the following result.

---

[10] Technically, we are not able to prove that supermodularity [Top98] is preserved for the value function at all time intervals in the Proof of Proposition 8.

Proposition 9. *In a random i.i.d. environment, the threshold $\kappa^-(w,t)$ is nonincreasing (resp. nondecreasing) with w when state and environmental factor are cooperative (resp. rival).*

This results from the formula (7) which is here $\kappa^-(w,t) = f^{-1}(\kappa^+(t), w)$ since $\kappa^+(w,t) = \kappa^+(t)$ does not depend upon w in a random i.i.d. environment.

An interesting consequence is the following. Consider a plant in an "unpredictable" environment (random i.i.d.). At the beginning of time interval $[t, t+1[$, assume that the environmental resource is high and that it is optimal to adopt full growth (no offspring). Then, the same holds for all lower environmental resource. In a sense, a plant with a given size is more likely to adopt full growth (no offspring) when environmental resource is low than when it is high. In other words, a plant with a given size is more likely to reproduce when environmental resource is high than when it is low. The opposite holds in case of rival factors.

5. Comparison of "linear maximizers" and "log maximizers"

Under the assumption that state and environmental factor are either cooperative or rival, we prove here that, at the last time interval $\tau - 1$, the domain in which full allocation to growth is optimal for the "log maximizer" is included in the corresponding domain for the "linear maximizer".

In the case of random i.i.d. environments, Amir and Cohen claim such an assertion under a tricky assumption of negative covariance between certain functions of the state process. They also claim that this holds for all time intervals and not only the last one. However, we have doubts on their claim since their characterization of "log maximizer" optimal strategies leads to stationary ones, and we have shown that this does not hold true in general.

Proposition 10. *Assume that $\alpha = 0$, that $\mathbb{W}$ is an interval of $\mathbb{R}$, that f is smooth on $\mathbb{R}_+ \times \mathbb{W}$, that U is smooth, that $\pi_{\tau-1}(dw' \mid w)$ has compact support for all $w \in \mathbb{W}$, and that state and environmental factor are either cooperative (i.e. $\frac{\partial^2 f}{\partial k \partial w} \geq 0$) or rival (i.e. $\frac{\partial^2 f}{\partial k \partial w} \leq 0$). Then, with the notations of Proposition 1 and of Proposition 2, we have:*

$$\forall k \geq 0, \quad \forall S \geq 0, \quad \forall w \in \mathbb{W}, \quad \kappa^+(w, \tau-1) \geq \kappa_U^+(k, S, w, \tau-1). \tag{18}$$

The inequality for the thresholds goes the same way, so that when the "log maximizer" reproduces at the last time interval, so does the "linear maximizer" with the same size.

6. Conclusion

We have studied the impacts of environmental variability on optimal strategies of annual plants, and shown that the presence of the yearly horizon induces nonstationary strategies in general.

Some patterns emerge for a plant i) maximizing the expected value of the annual reproductive yield and ii) able to rebuild completely its vegetative body during a time interval (where environmental conditions are more or less stable). In a constant environment, the plant grows without reproducing as long as its size is less than a fixed threshold; then, in one time interval, it reaches a higher target size and reproduces; it keeps the same size and reproduces till the last time interval where it dies. This pattern is typical of *determinate growth*. In a stochastic environment, targets and thresholds vary with the environmental factor, and targets may be lower than thresholds for some values of the environmental factor. This induces "up and down" trajectories, where a plant may reduce size, and where phases of pure growth without reproduction may alternate with phases of mixed growth and reproduction. When the stochastic environment is stationary, the thresholds for reproduction are lower and lower as time goes on, as well as the targets reached. In some specific cases, stationarity may be optimal, but this is not a general feature. Determinate growth may be optimal in random i.i.d. environments satisfying particular conditions.

For the impact of monotonicity and for the case of "log maximizers", we are only able to provide results for the optimal strategy at the last time interval. We were not able to propagate the property of supermodularity by backward induction. This problem still has to be attacked.

Thus, most of the mathematical analysis developed in this paper is made possible by the following assumptions: absence of density-dependence effects in the model, linear fitness criterion, no lower bound else

than zero constraining the control. In biological terms, this amounts to study plants in large population, with little competition, with variability within year, and with "rebuilding ability". Abandoning these assumptions lead to serious mathematical difficulties. We illustrate in Figures 7-8-9-10 what may happen when we prevent the plant from rebuilding completely its vegetative body during every time interval. Three cases are presented ($\alpha = 0$, $\alpha = 0.9$, $\alpha = 1$) with numerical simulations of optimal state, control and fitness trajectories[11]. We observe that, when the plant can rebuild, vegetative biomass is more variable and fitness is greater.
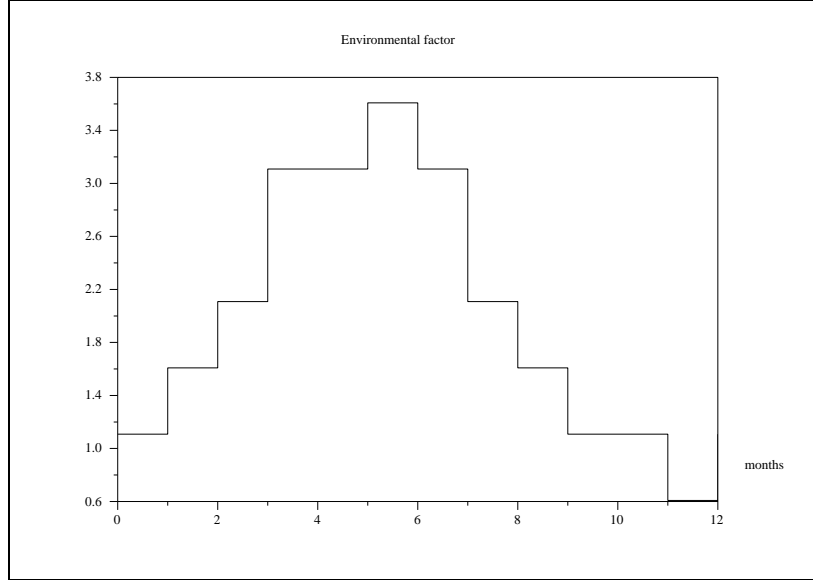

Fig. 7. *Common environmental factor trajectory*

A. Appendix

A.1. A few useful results

The proofs of the two following lemmas are technical and will be omitted.

Lemma 1. *Let $\phi : [0, +\infty[\to \mathbb{R}$ be continuous and concave. Let us define (recall convention in footnote 6)*

$$u^+ \stackrel{\text{def}}{=} \inf \quad \arg \max_{0 \leq u < +\infty} \phi(u) \in [0, +\infty].\tag{19}$$

Thus, u^+ is the infimum of the set of maximizers of ϕ on $[0, +\infty]$. Then

1. ϕ is increasing on $[0, u^+]$ and nonincreasing on $[u^+, +\infty[$;
2. for all $y \in [0, +\infty[$,

$$\inf \quad \arg \max_{0 \leq u \leq y} \phi(u) = \min(y, u^+).\tag{20}$$

---

[11] Growth function is $f(k, w) = w\sqrt{k}$ with $\beta = 0.9$, $T = 12$. The environmental factor does not follow an i.i.d. sequence, but follows more or less a sinusoid.
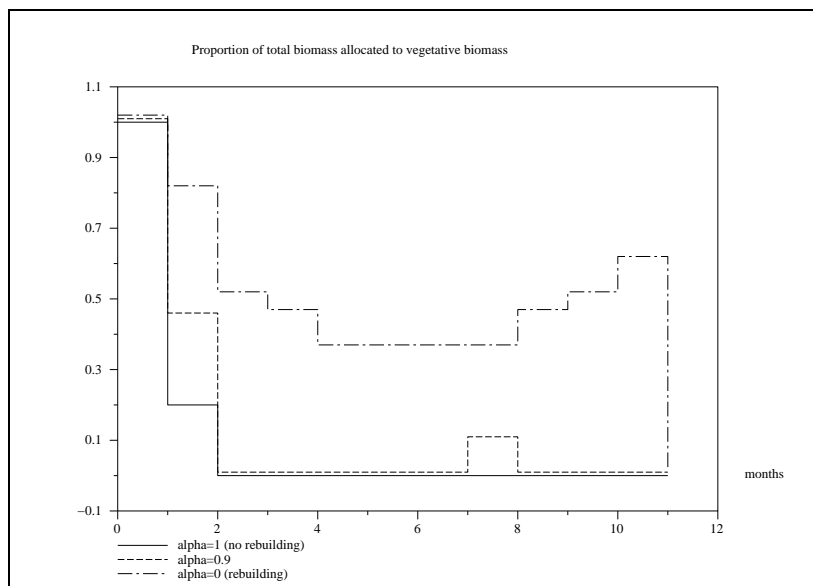
Fig. 8. *Optimal proportions of total biomass allocated to vegetative biomass in three cases*
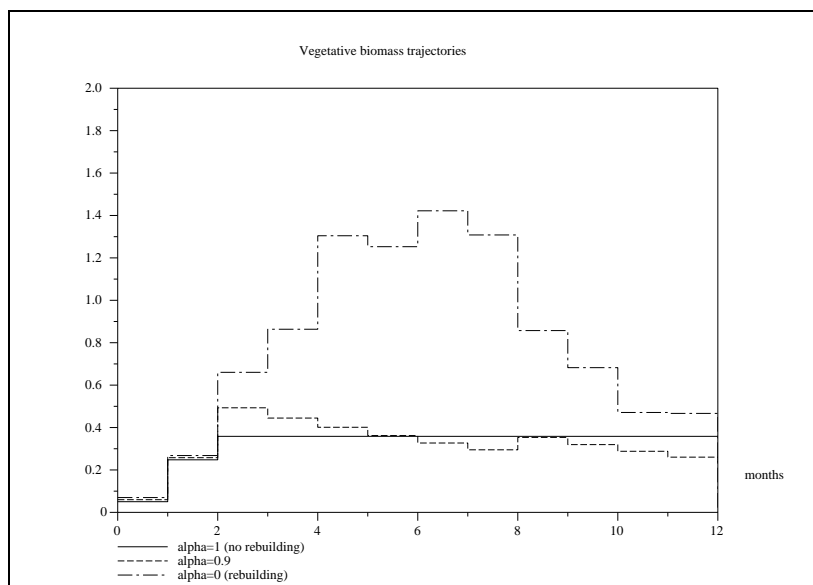
Fig. 9. *Optimal trajectories of vegetative biomass in three cases*

3. for all $0 \le y' \le y < +\infty$,

$$\inf \quad \arg\max_{0 \le u \le y} \phi(u) = \max(y', \min(y, u^+)).$$ (21)

If ϕ is strictly concave, we can suppress the $\inf$ in the $\arg\max$.

Lemma 2. *Let $z \in]0, +\infty[$ and $\phi : [0, z[\to \mathbb{R}$ be concave and continuous. Let us define*

$$u^+ \overset{\mathrm{def}}{=} \inf \quad \arg\max_{0 \le u < z} \phi(u) \in [0, z] \quad (\text{with the convention that} \quad \inf \emptyset = z).$$ (22)

Then

1. ϕ is increasing on $[0, u^+]$ and nonincreasing on $[u^+, z[$;

Fig. 10. *Optimal fitness trajectories in three cases*

2. for all $y \in [0, z[$, (20) holds true;

3. for all $0 \le y' \le y < +\infty$, (21) holds true.

If ϕ is strictly concave, we can suppress the inf *in the* arg max.

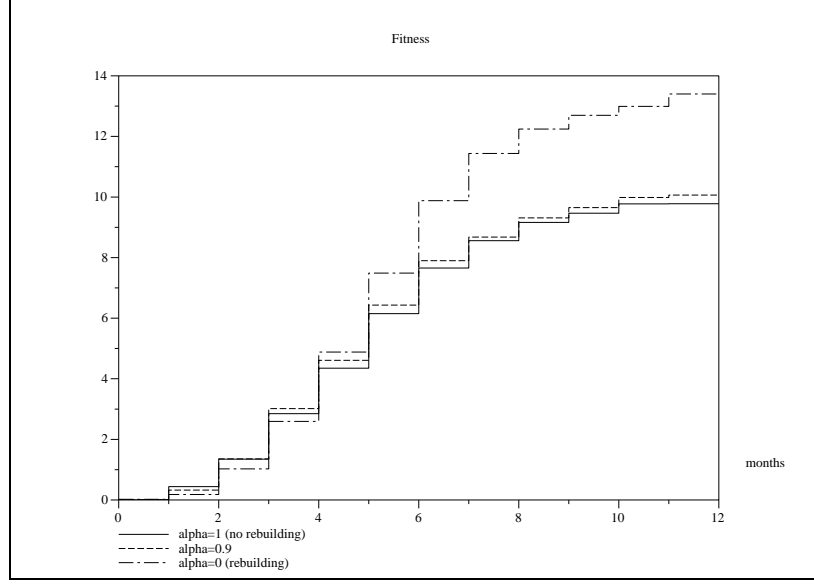**Lemma 3.** *Let $\mathcal{D} \subset \mathbb{R}$, let $g : \mathcal{D} \to \mathbb{R}$ and $h : \mathcal{D} \to \mathbb{R}$. Assume that the following arg max exist and are unique:*

$$u_g^\sharp \stackrel{\mathrm{def}}{=} \arg\max_{u \in \mathcal{D}} g(u) \quad and \quad u_h^\sharp \stackrel{\mathrm{def}}{=} \arg\max_{u \in \mathcal{D}} h(u).$$

If $h - g$ is nondecreasing on $\mathcal{D}$, then $u_g^\sharp \le u_h^\sharp$.

Proof. Let $u_g^\sharp \in \mathcal{D}_g$. For any $u \in] - \infty, u_g^\sharp[\cap\mathcal{D}$, we have, on the one hand, $g(u) < g(u_g^\sharp)$ by definition of $u_g^\sharp$ and, on the other hand, $(h - g)(u) \le (h - g)(u_g^\sharp)$ since $h - g$ is nondecreasing. Thus, summing both inequalities, we obtain that $u \in] - \infty, u_g^\sharp[\cap\mathcal{D} \Rightarrow h(u) < h(u_g^\sharp)$. We conclude that $u_h^\sharp \in [u_g^\sharp, +\infty[$.

A.2. Properties of the stochastic dynamic programming operator (general case)

Let $\beta \in [0, 1]$. Let π be a stochastic kernel on a Borel set $\mathbb{W}$ with σ-algebra $\mathcal{W}$. For technical reasons, we assume that π satisfies the Feller property: for all continuous function $V : \mathbb{R}_+ \times \mathbb{W} \to \mathbb{R}$, the function $(k, w) \hookrightarrow \int V(k, w')\pi(dw' \mid w)$ takes finite values and is continuous. Let $f : \mathbb{R}_+ \times \mathbb{W} \to \mathbb{R}$ satisfy the assumptions in paragraph 2.3. Let $U : \mathrm{Dom}(U) \to \mathbb{R}$ be a increasing continuous concave function.

Proposition 11. *Let $W : \mathbb{R}_+ \times \mathrm{Dom}(U) \times \mathbb{W} \to \mathbb{R}$ be continuous. Define $P_U W : \mathbb{R}_+ \times \mathrm{Dom}(U) \times \mathbb{W} \to \mathbb{R}$ by*

$$P_U W(k, S, w) \stackrel{\mathrm{def}}{=} \sup_{\alpha k \le u \le f(k,w)} [(1 - \beta)U(S + f(k, w) - u) + \beta \int W(u, S + f(k, w) - u, w')\pi(dw' \mid w)]. \quad (23)$$

1. The function $P_U W$ takes finite values and is continuous.

2. If $S \hookrightarrow W(k, S, w)$ is nondecreasing, then $S \hookrightarrow P_U W(k, S, w)$ is nondecreasing.

3. If $S \hookrightarrow W(k, S, w)$ is nondecreasing and if $(k, S) \hookrightarrow W(k, S, w)$ is concave, then $(k, S) \hookrightarrow P_U W(k, S, w)$ is concave.

Proof. 1. The expression between brackets in (23) is continuous in (u, k, S, w) (by the Feller property of π), and so is the growth function f. By a consequence of results on marginals functions (see [Aub82, Th. 3, p. 70]), the function $P_U W$ takes finite values and is continuous.

2. Easy proof.

3. Since $f(k, w)$ is concave in k, so is the function $(k, S, u) \hookrightarrow S + f(k, w) - u$. Since $W(k, S, w)$ is concave in (k, S) and $W(k, S, w)$ is nondecreasing in S, direct calculation shows that the function $(k, S, u) \hookrightarrow W(u, S + f(k, w) - u, w')$ is also concave for all w'. Obviously, so is also $(k, S, u) \hookrightarrow \int W(u, S + f(k, w) - u, w')\pi(dw' \mid w)$. In the same vein, the function $(k, S, u) \hookrightarrow U(S + f(k, w) - u)$ is concave. Now, the set $\{(k, u), \alpha k \leq u \leq f(k, w)\}$ is convex as the intersection of two convex sets. Thus, by a well known result on the maximum on one variable in a convex set of a jointly concave function ([Roc70]), the function $(k, S) \hookrightarrow \sup_{\alpha k \leq u \leq f(k, w)}[(1 - \beta)U(S + f(k, w) - u) + \beta \int W(u, S + f(k, w) - u, w')\pi(dw' \mid w)]$ is concave.

A.3. Properties of the stochastic dynamic programming operator (linear fitness case)

Let $V : \mathbb{R}_+ \times \mathbb{W} \to \mathbb{R}_+$

1. be continuous and satisfy $V(0, w) = 0$;
2. be such that, for all $w \in \mathbb{W}$, the function $k \in \mathbb{R}_+ \hookrightarrow V(k, w)$ is strictly concave.

Let $Q_f V : \mathbb{R}_+ \times \mathbb{W} \to \mathbb{R}_+$ be defined by

$$Q_f V(k, w) \overset{\text{def}}{=} \sup_{\alpha k \leq u \leq f(k, w)} \left(f(k, w) - u + \beta \int V(u, w')\pi(dw' \mid w) \right). \tag{24}$$

We also define the following $\arg\max$ (recall convention in footnote 6), unique by strict concavity of $k \in \mathbb{R}_+ \hookrightarrow f(k, w)$ and $k \in \mathbb{R}_+ \hookrightarrow V(k, w)$, together with pre-image by f (recall convention in footnote 5):

$$\begin{cases} \kappa_f^+(w) \overset{\text{def}}{=} \arg\max_{0 \leq u}[-u + \beta \int f(u, w')\pi(dw' \mid w)] \in \mathbb{R}_+ \cup \{+\infty\} \\ \\ \kappa_V^+(w) \overset{\text{def}}{=} \arg\max_{0 \leq u}[-u + \beta \int V(u, w')\pi(dw' \mid w)] \in \mathbb{R}_+ \cup \{+\infty\} \\ \\ k_V^-(w) \overset{\text{def}}{=} f^{-1}(k_V^+(w), w) \end{cases} \tag{25}$$

Proposition 12. *The function $Q_f V : \mathbb{R}_+ \times \mathbb{W} \to \mathbb{R}_+$*

1. is continuous and satisfies $Q_f V(0, w) = 0$, for all $w \in \mathbb{W}$;
2. is such that, for all $w \in \mathbb{W}$, the function $k \in \mathbb{R}_+ \hookrightarrow Q_f V(k, w) - f(k, w)$ is concave;
3. is such that, for all $w \in \mathbb{W}$, the function $k \in \mathbb{R}_+ \hookrightarrow Q_f V(k, w)$ is strictly concave.

Proof. 1. Continuity of $Q_f V$ is a consequence of results on marginals functions (see [Aub82, Th. 3, p. 70]). Since $f(0, w) = V(0, w) = 0$, we have

$$Q_f V(0, w) = \sup_{\alpha \times 0 \leq u \leq f(0, w)} \left(f(0, w) - u + \beta \int V(u, w')\pi(dw' \mid w) \right) = \beta \int V(0, w')\pi(dw' \mid w) = 0.$$

2. By (24), we may write

$$Q_f V(k, w) = f(k, w) + \sup_{\alpha k \leq u \leq f(k, w)} \left(-u + \beta \int V(u, w')\pi(dw' \mid w) \right). \tag{26}$$

Since, for all $w \in \mathbb{W}$, the function $k \in \mathbb{R}_+ \hookrightarrow V(k, w)$ is concave, then so is also the function $u \in \mathbb{R}_+ \hookrightarrow -u + \beta \int V(u, w')\pi(dw' \mid w)$. Now, the set $\{(k, u) \in \mathbb{R}_+ \times \mathbb{R}_+ | \alpha k \leq u \leq f(k, w)\}$ is convex for all $w \in \mathbb{W}$. Thus, the function $k \in \mathbb{R}_+ \hookrightarrow \sup_{\alpha k \leq u \leq f(k, w)} \left(-u + \beta \int V(u, w')\pi(dw' \mid w) \right)$ is concave, as the maximum on one variable in a convex set of a jointly concave function ([Roc70]).

3. The function $k \in \mathbb{R}_+ \hookrightarrow Q_f V(k, w)$ is the sum of the strictly concave function $k \hookrightarrow f(k, w)$ and of the concave function $k \in \mathbb{R}_+ \hookrightarrow Q_f V(k, w) - f(k, w)$: it is thus strictly concave.

A.4. Properties of the stochastic dynamic programming operator (linear fitness case) when $\alpha = 0$

We assume that $\alpha = 0$ in this whole subsection.

Proposition 13. *For all $w \in \mathbb{W}$, the function $k \in \mathbb{R}_+ \hookrightarrow Q_f V(k, w) - f(k, w)$ is nondecreasing.*

Proof. By (26), $Q_f V(k, w) - f(k, w) = \sup_{\alpha k \leq u \leq f(k,w)} \left(-u + \beta \int V(u, w')\pi(dw' \mid w) \right)$ is nondecreasing in k since the function $k \in \mathbb{R}_+ \hookrightarrow f(k, w)$ is increasing.

Lemma 4. *For all $w \in \mathbb{W}$, define:*

$$\forall u \in \mathbb{R}_+ , \quad \psi_w(u) \stackrel{\text{def}}{=} \int [Q_f V(u, w') - f(u, w')]\pi(dw' \mid w) . \tag{27}$$

Then ψ_w is nondecreasing. Moreover, ψ_w is constant on $[\kappa_f^+(w), +\infty[$ if

$$\forall w \in \mathbb{W} , \quad \kappa_V^+(w) \leq \kappa_f^+(w) \quad \text{and} \quad \pi(\{w' \mid \kappa_f^+(w) < \kappa_f^-(w')\} \mid w) = 0 . \tag{28}$$

Proof. Since $u \in [0, +\infty[\hookrightarrow Q_f V(u, w') - f(u, w')$ is nonincreasing, for all $w' \in \mathbb{W}$, by Proposition 12, the function ψ_w is nondecreasing on $[0, +\infty[$.

Assume that (28) holds true. Since $k \in [0, +\infty[\hookrightarrow f(k, w')$ is increasing, we deduce from $\kappa_V^+(w') \leq \kappa_f^+(w')$ and (11) that $\kappa_V^-(w') \leq \kappa_f^-(w')$. Now, let $w \in \mathbb{W}$ be fixed. As a consequence, we have

$$\forall u \geq \kappa_f^+(w) , \quad 0 \leq \int \mathbf{1}_{[0,\kappa_V^-(w')[}(u)\pi(dw' \mid w)$$

$$\leq \int \mathbf{1}_{[0,\kappa_f^-(w')[}(u)\pi(dw' \mid w) \quad \text{since} \quad \kappa_V^-(w') \leq \kappa_f^-(w')$$

$$\leq \int \mathbf{1}_{[0,\kappa_f^-(w')[}(\kappa_f^+(w))\pi(dw' \mid w) \quad \text{since} \quad \mathbf{1}_{[0,\kappa_f^-(w')[} \text{ is a nonincreasing function}$$

$$= \int_{\{w' \mid \kappa_f^+(w) < \kappa_f^-(w')\}} \pi(dw' \mid w) = 0 \quad \text{by assumption.}$$

This may also be written as $\forall u \geq \kappa_f^+(w) , \quad \mathbf{1}_{[0,\kappa_V^-(w')[}(u) = 0 \quad \pi(dw' \mid w) - a.s.$, or also as

$$\forall u \geq \kappa_f^+(w) , \quad \mathbf{1}_{[\kappa_V^-(w'),+\infty[}(u) = 1 \quad \pi(dw' \mid w) - a.s. \tag{29}$$

Thus

$$\forall u \geq \kappa_f^+(w) , \quad \psi_w(u) = \int [Q_f V(u, w') - f(u, w')]\pi(dw' \mid w)$$

$$= \int \mathbf{1}_{]\kappa_V^-(w'),+\infty[}(u)[Q_f V(u, w') - f(u, w')]\pi(dw' \mid w) \quad \text{by (29)}$$

$$= \int \pi(dw' \mid w)\mathbf{1}_{]\kappa_V^-(w'),+\infty[}(u) \int [-\kappa_V^+(w') + \beta \int V(\kappa_V^+(w'), w'')\pi(dw'' \mid w')]$$

$$\text{by (24) and by definition (25) of} \quad \kappa_V^-(w')$$

$$= \int \pi(dw' \mid w) \int [-\kappa_V^+(w') + \beta \int V(\kappa_V^+(w'), w'')\pi(dw'' \mid w')] \quad \text{by (29)}$$

and thus $\psi_w(u)$ does not depend upon $u \geq \kappa_f^+(w)$.

Proposition 14. *The following* $\arg\max$ *(recall convention in footnote 6) is unique*

$$\kappa^+_{Q_f V}(w) \stackrel{\mathrm{def}}{=} \arg\max_{0 \le u}[-u + \beta \int Q_f V(u, w')\pi(dw' \mid w)] \in [0, +\infty] \tag{30}$$

and we have, for all $w \in \mathbb{W}$,

$$\kappa^+_f(w) \le \kappa^+_{Q_f V}(w). \tag{31}$$

Proof. Unicity of the $\arg\max$ results from by strict concavity of $u \hookrightarrow Q_f V(u, w')$. To compare the $\arg\max$ in (25) and in (30), we shall make use of Lemma 3. Let w be fixed and let us introduce

$$\mathcal{D} = [0, +\infty[, \quad g(u) = -u + \beta \int f(u, w')\pi(dw' \mid w), \quad h(u) = -u + \beta \int Q_f V(u, w')\pi(dw' \mid w).$$

The difference $h(u) - g(u) = \beta \int [Q_f V(u, w') - f(u, w')]\pi(dw' \mid w) = \beta \psi_w(u)$ is a nondecreasing function of u by Lemma 4. Thus inequality (31) holds by Lemma 3 since

$$\kappa^+_f(w) = \arg\max_{u \in \mathcal{D}} g(u) \le \kappa^+_{Q_f V}(w) = \arg\max_{u \in \mathcal{D}} h(u).$$

Lemma 5. *Assume that (13) holds true. Then* $\forall w \in \mathbb{W}, \quad \kappa^+_{Q_f V}(w) = \kappa^+_f(w).$

Proof. To the difference of the previous proof, we swap the definitions of g and h:

$$\mathcal{D} = [0, +\infty[, \quad h(u) = -u + \beta \int f(u, w')\pi(dw' \mid w), \quad g(u) = -u + \beta \int Q_f V(u, w')\pi(dw' \mid w).$$

The difference $h(u) - g(u) = -\beta\psi_w(u)$ is constant on $[\kappa^+_f(w), +\infty[$ by Lemma 4. Since $\kappa^+_f(w) = \arg\max_{u \in \mathcal{D}} h(u)$, we may apply Lemma 3 to get $\kappa^+_{Q_f V}(w) = \arg\max_{u \in \mathcal{D}} g(u) \le \kappa^+_f(w) = \arg\max_{u \in \mathcal{D}} h(u)$. Since, by Proposition 14, we know that $\kappa^+_f(w) \le \kappa^+_{Q_f V}(w)$, we get the desired result $\kappa^+_f(w) = \kappa^+_{Q_f V}(w)$.

A.5. Proof of Proposition 1

Proof. It is well known that optimal strategies of (3) may be deduced from the following backward stochastic dynamic programming equation ([Ber00]):

$$\begin{cases} W(k, S, w, \tau + 1) = U(S) \\[2mm] W(k, S, w, t) = \sup_{\alpha k \le u \le f(k, w)} (\ (1 - \beta_t) \int W(0, S + f(k, w) - u, w', t + 1)\pi_t(dw' \mid w) \\[2mm] \qquad\qquad\qquad\qquad + \beta_t \int W(u, S + f(k, w) - u, w', t + 1)\pi_t(dw' \mid w) \ ). \end{cases} \tag{32}$$

This reflects the dynamics described in paragraph 2.1, in particular the fact that the plant allocates first $S + f(k, w) - u$ to reproduction, then is submitted to a death risk with probability $1 - \beta_t$.

Since $f(0, w) = 0$, it may readily be proved that $\forall t = 0, \ldots, \tau + 1, \quad W(0, S, w, t) = U(S)$, so that the above equations give

$$\begin{cases} W(k, S, w, \tau + 1) = U(S) \\[2mm] W(k, S, w, t) = \sup_{\alpha k \le u \le f(k, w)} (\ (1 - \beta_t)U(S + f(k, w) - u) + \\[2mm] \qquad\qquad\qquad\qquad \beta_t \int W(u, S + f(k, w) - u, w', t + 1)\pi_t(dw' \mid w) \ ). \end{cases} \tag{33}$$

The function $(k, S) \hookrightarrow W(k, S, w, \tau + 1) = U(S)$ is concave (recall that U is concave) and the function $S \hookrightarrow W(k, S, w, \tau + 1) = U(S)$ is nondecreasing (recall that U is nondecreasing). By Proposition 11, it may thus readily be proved by backward induction that $(k, S) \hookrightarrow W(k, S, w, t)$ is concave and that $S \hookrightarrow W(k, S, w, t)$ is nondecreasing, for $t \in \{0, \ldots, \tau + 1\}$.

Thus, for any $t \in \{0, \ldots, \tau\}$, $w \in \mathbb{W}$ and $z > 0$, the following function ϕ is also concave:

$$\phi : u \in [0, z[\, \hookrightarrow (1 - \beta_t)U(z - u) + \beta_t \int W(u, z - u, w', t + 1)\pi_t(dw' \mid w) \,. \tag{34}$$

We define $\widetilde{\kappa}_U^+(z, w, t)$ as the infimum of the set of maximizers (Lemma 2 applied to ϕ):

$$\widetilde{\kappa}_U^+(z, w, t) \overset{\text{def}}{=} \inf \quad \arg \max_{0 \leq u \leq z} (1 - \beta_t)U(z - u) + \beta_t \int W(u, z - u, w', t + 1)\pi_t(dw' \mid w) \,. \tag{35}$$

Since an optimal strategy $u^\sharp(k, S, w, t)$ is any element of the above $\arg \max$ where z is replaced by $f(k, w)$, Lemma 1 enables us to conclude on (4), once we have introduced (recall conventions in footnotes 5 and 6)

$$\kappa_U^+(k, S, w, t) \overset{\text{def}}{=} \widetilde{\kappa}_U^+(S + f(k, w), w, t) \quad \text{and} \quad \kappa_U^-(k, S, w, t) \overset{\text{def}}{=} f^{-1}(\kappa_U^+(k, S, w, t), w) \,. \tag{36}$$

Since U is increasing, we have in particular

$$\widetilde{\kappa}_U^+(z, w, \tau) \overset{\text{def}}{=} \inf \quad \arg \max_{0 \leq u \leq z} (1 - \beta_\tau)U(z - u) + \beta_\tau \int U(z - u)\pi_\tau(dw' \mid w) = 0$$

so that $u^\sharp(k, S, w, \tau) = 0$.

A.6. Proof of Proposition 2

Proof. We may easily see by backward induction on (33) that

$$W(k, S, w, t) = S + V(k, w, t) \tag{37}$$

where $V(k, w, \tau + 1) = 0$ by (32), and

$$\forall t = 0, \ldots, \tau \,, \quad V(k, w, t) = \sup_{\alpha k \leq u \leq f(k, w)} \left(f(k, w) - u + \beta_t \int V(u, w', t + 1)\pi_t(dw' \mid w) \right) \,. \tag{38}$$

Since $V(k, w, \tau + 1) = 0$, we have

$$\begin{cases} V(k, w, \tau) = \sup_{\alpha k \leq u \leq f(k, w)} (f(k, w) - u) = f(k, w) - \alpha k \\ u^\sharp(k, w, \tau) = \arg \max_{\alpha k \leq u \leq f(k, w)} (f(k, w) - u) = \alpha k \,. \end{cases}$$

By Proposition 12, we know that the function $k \in [0, +\infty[\, \hookrightarrow V(k, w, t)$ is strictly concave for $t = 0, \ldots, \tau$ and for all $w \in \mathbb{W}$. Then the function $u \in [0, +\infty[\, \hookrightarrow \int V(u, w', t + 1)\pi(dw' \mid w)$ is also strictly concave for $t = 0, \ldots, \tau$. Thus, by unicity (by strict concavity of $u \hookrightarrow V(u, w', t + 1)$) of the $\arg \max$ (recall convention in footnote 6), let

$$\kappa^+(w, t) \overset{\text{def}}{=} \arg \max_{0 \leq u}[-u + \beta_t \int V(u, w', t + 1)\pi_t(dw' \mid w)] \in [0, +\infty] \,. \tag{39}$$

Then, by the definition of $\widetilde{\kappa}_U^+(z, w, t)$ in (35) when $U(S) = S$, we have

$$\widetilde{\kappa}_U^+(z, w, t) = \arg \max_{0 \leq u \leq z} [(1 - \beta_t)(z - u) + \beta_t((z - u) + \int V(u, w', t + 1)\pi_t(dw' \mid w))]$$

$$= \arg \max_{0 \leq u \leq z} [-u + \beta_t \int V(u, w', t + 1)\pi_t(dw' \mid w)] = \min(z, \kappa^+(w, t)) \quad \text{by Lemma 1.} \tag{40}$$

Thus,

$$
\begin{aligned}
k \leq \kappa_U^-(S, w, t) &\iff f(k, w) \leq \kappa_U^+(S, w, t) \quad \text{by equation (36)} \\
&\iff f(k, w) \leq \widetilde{\kappa}_U^+(S + f(k, w), w, t) \quad \text{by equation (36)} \\
&\iff f(k, w) \leq \min(S + f(k, w), \kappa^+(w, t)) \quad \text{by equation (40)} \\
&\iff f(k, w) \leq \kappa^+(w, t) \\
&\qquad \text{since} \quad a \leq b \iff a \leq \min(S + a, b) \quad (\text{recall that} \quad S \geq 0) \\
&\iff k \leq \kappa^-(w, t) \quad \text{if we define} \quad \kappa^-(w, t) \quad \text{by (7)}.
\end{aligned}
$$

Now, we have obtained thus *an* optimal strategy. It is in fact *the* optimal strategy since $\arg\max_{\alpha k \leq u \leq z}[-u + \beta_t \int V(u, w', t+1)\pi_t(dw' \mid w)]$ is reduced to a single element, by strict concavity.

A.7. Proof of Proposition 3

Proof. For $t = 0, \ldots, \tau$, we have $V(k, w, t-1) = (Q_f V(., t))(k, w)$ with the notation (24), so that $\kappa^+(w, t) \geq \kappa_f^+(w)$ by (31). By (39), we have that

$$
\kappa^+(w, t) = \arg\max_{0 \leq u}[-u + \beta \int V(u, w', t+1)\pi(dw' \mid w)] \tag{41}
$$

and, by Lemma 3, $\kappa^+(w, t-1) \geq \kappa^+(w, t)$ holds true if the following statement (H_t) holds true:

$$
(H_t) \quad k \hookrightarrow V(k, w, t) - V(k, w, t+1) \quad \text{is nondecreasing.} \tag{42}
$$

We shall prove by backward induction that $(H_0), \ldots, (H_{\tau-1})$ hold true.

$(H_{\tau-1})$ is true. Indeed, on the one hand, $V(k, w, \tau) = f(k, w)$ and thus $\kappa^+(w, \tau-1) = \kappa_f^+(w)$ by (11). On the other hand, we have $V(k, w, \tau-1) = (Q_f V(., \tau))(k, w) = (Q_f f)(k, w)$ with the notation (24). Then, by Proposition 12, we know that $k \hookrightarrow V(k, w, \tau-1) - V(k, w, \tau) = (Q_f f - f)(k, w)$ is nondecreasing.

Assume now that (H_t) holds true. By (39) and (38), we have

$$
V(k, w, t-1) = \begin{cases} \beta \int V(f(k, w), w', t)\pi(dw'|w) & \text{if} \quad k \leq \kappa^-(w, t-1) \\ f(k, w) - \kappa^+(w, t-1) + \beta \int V(\kappa^+(w, t-1), w', t)\pi(dw'|w) & \text{if} \quad k \geq \kappa^-(w, t-1). \end{cases}
$$

Then, since $\kappa^+(w, t-1) \geq \kappa^+(w, t)$ as a consequence of (H_t), we have

$$
V(k, w, t-1) - V(k, w, t) = \begin{cases} \beta \int [V(f(k, w), w', t) - V(f(k, w), w', t+1)]\pi(dw'|w) & \text{if } k \in [0, \kappa^-(w, t)] \\ \beta \int V(f(k, w), w', t)\pi(dw'|w) - f(k, w) - \mu(w, t) & \text{if } k \in [\kappa^-(w, t), \kappa^-(w, t-1)] \\ \mu(w, t-1) - \mu(w, t) & \text{if } k \in [\kappa^-(w, t-1), +\infty[\end{cases}
$$

where $\mu(w, t) \stackrel{\text{def}}{=} -\kappa^+(w, t) + \beta \int V(\kappa^+(w, t+1), w', t)\pi(dw'|w)$. Now

1. $[V(f(k, w), w', t) - V(f(k, w), w', t+1)]$ is nondecreasing in k, so that $V(k, w, t-1) - V(k, w, t)$ is nondecreasing in $k \in [0, \kappa^-(w, t)]$;
2. $-u + \beta \int V(u, w', t)\pi(dw'|w)$ is nondecreasing in $u \in [0, \kappa^+(w, t-1)]$, so that $\beta \int V(f(k, w), w', t)\pi(dw'|w) - f(k, w)$ is nondecreasing in $k \in [0, \kappa^-(w, t-1)]$;
3. $V(k, w, t-1) - V(k, w, t) = \mu(w, t) - \mu(w, t+1)$ is constant in $k \in [\kappa^-(w, t-1), +\infty[$.

In consequence, $V(k, w, t-1) - V(k, w, t)$ is continuous in k and nondecreasing on three consecutive intervals: it is thus nondecreasing and (H_{t-1}) holds true.

A.8. Proof of Proposition 5

Proof. The proof is by backward induction. We have $\kappa^+(w, \tau - 1) = \kappa_f^+(w)$ and $\kappa^-(w, \tau - 1) = \kappa_f^-(w)$ by (11).

Assume now that $\kappa^+(w, t+1) = \kappa_f^+(w)$. With the notation (24), we have $V(k, w, t) = (Q_f V(., t+1))(k, w)$. Then $\kappa^+(w, t) = \kappa_f^+(w)$ is a straightforward consequence of Lemma 5, and equality $\kappa^-(w, t) = \kappa_f^-(w)$ follows from (7). By applying the optimal strategy (6), once reproduction starts we have (almost surely), due to condition (13):

$$k_{t+1} = \kappa^+(w_t, t) = \kappa_f^+(w_t) \geq \kappa_f^-(w_{t+1}) = \kappa^-(w_{t+1}, t+1) \, .$$

Thus, (almost surely) whatever the realizations $(w_0, \ldots, w_\tau)$, the plant reproduces at all times after having reached maturity since $k_{t+1} \geq \kappa^-(w_{t+1}, t+1)$. However, there is no fixed size at maturity since $k_{t+1} = \kappa_f^+(w_t)$ is generally random.

A.9. Proof of Proposition 6

Proof. This is a straightforward application of Proposition 5 since (16) is the translation of (13) when environment is random i.i.d.

As in Proposition 5, the plant reproduces at all times after having reached maturity. But here, there is a fixed size at maturity since $k_{t+1} = \kappa^+$ is deterministic.

By condition (16), we have that, ρ-almost surely in w, $f(\kappa^+, w) \geq \kappa^+ = f(\kappa^-(w, t), w)$. Thus, $\kappa^+ \geq \kappa^-(w, t)$ since f is increasing in its first argument.

A.10. Proof of Proposition 8

We simply prove Proposition 8 in the cooperative case, the rival case being similar.

Proof. Assume that the stochastic kernel $\pi_{\tau-1}$ is stochastically nondecreasing.

Since state and environmental factor are cooperative, f has nondecreasing differences: for all $k_1 \geq k_2$ the function $w \in \mathbb{W} \hookrightarrow f(k_1, w) - f(k_2, w)$ is nondecreasing Thus, the function $w \hookrightarrow \int f(k_1, w')\pi(dw' \mid w) - \int f(k_2, w')\pi_{\tau-1}(dw' \mid w)$ is nondecreasing since the stochastic kernel $\pi_{\tau-1}$ is stochastically nondecreasing. In other words, $(u, w) \hookrightarrow \int f(u, w')\pi_{\tau-1}(dw' \mid w)$ has nondecreasing differences.

Let $w_1 > w_2$. Let us adopt notations of Lemma 3 with

$$\mathcal{D} = [0, +\infty[\, , \quad g(u) = -u + \beta_{\tau-1} \int f(u, w')\pi_{\tau-1}(dw' \mid w_2) \, , \quad h(u) = -u + \beta_{\tau-1} \int f(u, w')\pi_{\tau-1}(dw' \mid w_1) \, .$$

Since $(u, w) \hookrightarrow \int f(u, w')\pi_{\tau-1}(dw' \mid w)$ has nondecreasing differences,

$$(h - g)(u) = \beta_{\tau-1}[\int f(u, w')\pi_{\tau-1}(dw' \mid w_1) - \int f(u, w')\pi_{\tau-1}(dw' \mid w_2)]$$

is nondecreasing. Thus, by

$$\kappa^+(w, \tau - 1) = \arg\max_{0 \leq u}[-u + \beta_{\tau-1} \int f(u, w')\pi_{\tau-1}(dw' \mid w)] \in [0, +\infty] \, .$$

and Lemma 3, the target $\kappa^+(w, \tau - 1)$ is a nondecreasing function of w since

$$\kappa^+(w_1, \tau - 1) = \arg\max_{0 \leq u} g(u) \leq \kappa^+(w_2, \tau - 1) = \arg\max_{0 \leq u} h(u) \, .$$

If the stochastic kernel $\pi_{\tau-1}$ is stochastically nonincreasing, then we prove in the same way that the target $\kappa^+(w, \tau - 1)$ is a nonincreasing function of w. But, in this case, we can also prove that the threshold $\kappa^-(w, \tau - 1)$ is a nonincreasing function of w.

By (7), we have $\kappa^+(w, \tau - 1) = f(\kappa^-(w, \tau - 1), w)$ for all w. Letting $w_1 \geq w_2$, we have $f(\kappa^-(w_1, \tau - 1), w_1) = \kappa^+(w_1, \tau-1) \leq \kappa^+(w_2, \tau-1) = f(\kappa^-(w_2, \tau-1), w_2)$ since the target $\kappa^+(w, \tau-1)$ is a nonincreasing function of w. By Proposition 7, we deduce that

$$f(\kappa^-(w_2, \tau - 1), w_1) \geq f(\kappa^-(w_2, \tau - 1), w_2) \geq f(\kappa^-(w_1, \tau - 1), w_1) \, .$$

This gives $\kappa^-(w_2, \tau - 1) \geq \kappa^-(w_1, \tau - 1)$ since $k \hookrightarrow f(k, w_1)$ is increasing. Thus, we have proved that both the target $\kappa^+(w, \tau - 1)$ and the threshold $\kappa^-(w, \tau - 1)$ are nonincreasing functions of w.

A.11. Proof of Proposition 4

Proof. Let $m \overset{\text{def}}{=} \int w\rho(dw) = pw^- + (1-p)w^+$. By (8) and (9), we have

$$\kappa_f^+ = \kappa^+(\tau - 1) = \left(\frac{\beta m}{2}\right)^2 \quad \text{and} \quad \kappa_f^-(w) = \kappa^-(w, \tau - 1) = [\frac{1}{w}\left(\frac{\beta m}{2}\right)^2]^2. \tag{43}$$

By Proposition 3 and (39), we know that

$$\kappa^+(\tau - 2) = \arg\max_{u \geq 0}[-u + \beta(pV_{\tau-1}(u, w^-) + (1-p)V_{\tau-1}(u, w^+))] \geq \kappa_f^+ = \kappa^+(\tau - 1). \tag{44}$$

If $\kappa^+(\tau - 2) = +\infty$, the proof ends since $\kappa^+(\tau - 2) = +\infty > \kappa_f^+ = \left(\frac{\beta m}{2}\right)^2$. We thus assume from now on that $\kappa^+(\tau - 2) < +\infty$. By (38), we have $V_\tau(k, w) = f(k, w) = w\sqrt{k}$ and

$$V_{\tau-1}(k, w) = \sup_{0 \leq u \leq w\sqrt{k}} (w\sqrt{k} - u + \beta m\sqrt{u}) = \begin{cases} \beta m(w\sqrt{k})^{1/2} & \text{if} \quad w\sqrt{k} \leq \kappa_f^+ \\ w\sqrt{k} + \left(\frac{\beta m}{4}\right)^2 & \text{if} \quad w\sqrt{k} \geq \kappa_f^+ . \end{cases}$$

The following function

$$\varphi(k) \overset{\text{def}}{=} p\frac{V_{\tau-1}}{\partial k}(k, w^-) + (1-p)\frac{V_{\tau-1}}{\partial k}(k, w^+)$$

is decreasing since $k \hookrightarrow V_{\tau-1}(k, w)$ is strictly concave by Proposition 12. By definition of $\kappa^+(\tau - 2)$ in (44), we have that $-1 + \beta\varphi(\kappa^+(\tau - 2)) = 0$. We compute

$$\frac{\partial V_{\tau-1}}{\partial k}(k, w) = \begin{cases} \frac{1}{4}\beta m w^{1/2} k^{-3/4} & \text{if} \quad k \leq \kappa^-(w, \tau - 1) \\ \frac{1}{2}wk^{-1/2} & \text{if} \quad k \geq \kappa^-(w, \tau - 1) . \end{cases}$$

From the computations made right after equation (9), recall that $\kappa^+(w, \tau - 1)/\kappa^-(w, \tau - 1) = [\frac{2w}{\beta m}]^2$. We deduce that $\kappa^+(\tau - 1) \geq \kappa^-(w^+, \tau - 1)$ and that $\kappa^+(w^-, \tau - 1) < \kappa^-(w^-, \tau - 1)$ since the assumption $w^+ > \frac{1}{1-p}(\frac{2}{\beta} - p)w^-$ is equivalent to $0 < \frac{2w^-}{\beta m} < 1$. In consequence

$$\begin{aligned} -1 + \beta\varphi(\kappa_f^+) &= -1 + \beta[p\frac{1}{4}\beta m(w^-)^{1/2}(\kappa_f^+)^{-3/4} + (1-p)\frac{1}{2}w^+(\kappa_f^+)^{-1/2}] \\ &= -1 + \beta[\frac{p}{2}(\frac{\beta m}{2})^{-1/2}(w^-)^{1/2} + \frac{(1-p)w^+}{\beta m}] \quad \text{by (43)} \\ &= -1 + \beta\frac{p}{2}(\frac{2w^-}{\beta m})^{1/2} + (1-p)\frac{w^+}{m} \\ &= -1 + \frac{(1-p)w^+ + pw^-}{m} + p[\frac{\beta}{2}(\frac{2w^-}{\beta m})^{1/2} - \frac{w^-}{m}] \\ &= p\frac{\beta}{2}[(\frac{2w^-}{\beta m})^{1/2} - \frac{2w^-}{\beta m}] \quad \text{by definition of} \quad m \\ &> 0 \quad \text{since} \quad 0 < \frac{2w^-}{\beta m} < 1 \\ &= -1 + \beta\varphi(\kappa^+(\tau - 2)) . \end{aligned}$$

Recalling that φ is decreasing, we conclude that $\kappa_f^+ = \kappa^+(\tau - 1) < \kappa^+(\tau - 2)$.

A.12. Proof of Proposition 10

Proof. With the notations of the proof of Proposition 1, we just have to prove that $\widetilde{\kappa}_U^+(z, w, \tau - 1)$ given by (35) is less or equal than $\kappa_f^+(w)$ given by (11).

Let $w \in \mathbb{W}$ and $z \geq 0$ be fixed. $\widetilde{\kappa}_U^+(z, w, \tau - 1)$ achieves the maximum of the concave function $u \hookrightarrow (1 - \beta_{\tau-1})U(z - u) + \beta_{\tau-1} \int U(z - u + f(u, w'))\pi_{\tau-1}(dw' \mid w)$ on $[0, z]$. If $\widetilde{\kappa}_U^+(z, w, \tau - 1) = 0$, the proof ends. Else, $\phi_U(\widetilde{\kappa}_U^+(z, w, \tau - 1)) \geq 0$ by the Euler condition, where

$$\phi_U(u) \stackrel{\text{def}}{=} -(1 - \beta_{\tau-1})U'(z - u) + \beta_{\tau-1} \int (-1 + \frac{\partial f}{\partial k}(u, w'))U'(z - u + f(u, w'))\pi_{\tau-1}(dw' \mid w).$$

The differentiation under the integral is made possible by smoothness of all functions and by the assumption that $\pi_{\tau-1}(dw' \mid w)$ has compact support for all $w \in \mathbb{W}$. We have

$$\phi_U(u) = \int [-(1 - \beta_{\tau-1})U'(z - u) + \beta_{\tau-1}(-1 + \frac{\partial f}{\partial k}(u, w'))U'(z - u + f(u, w'))]\pi_{\tau-1}(dw' \mid w)$$

$$= \int [(\beta_{\tau-1}\frac{\partial f}{\partial k}(u, w') - 1)U'(z - u + f(u, w')) + (1 - \beta_{\tau-1}) \underbrace{(U'(z - u + f(u, w')) - U'(z - u))}_{\leq 0}]\pi_{\tau-1}(dw' \mid w)$$

$$\leq \int [(\beta_{\tau-1}\frac{\partial f}{\partial k}(u, w') - 1)U'(z - u + f(u, w'))\pi_{\tau-1}(dw' \mid w)$$

since $f(u, w') \geq 0$ and U' is nonincreasing. Thus, $\phi_U(\kappa_f^+(w)) \leq \int a(w')b(w')\pi_{\tau-1}(dw' \mid w)$ where

1. on the one hand, $a(w') \stackrel{\text{def}}{=} (\beta_{\tau-1}\frac{\partial f}{\partial k}(\kappa_f^+(w), w') - 1)$ is nondecreasing when $\frac{\partial^2 f}{\partial k \partial w} \geq 0$ (and is nondecreasing when $\frac{\partial^2 f}{\partial k \partial w} \leq 0$);

2. on the other hand, $b(w') \stackrel{\text{def}}{=} U'(z - \kappa_f^+(w) + f(\kappa_f^+(w), w')) > 0$ is nonincreasing when $\frac{\partial^2 f}{\partial k \partial w} \geq 0$ since then $w' \hookrightarrow f(k, w')$ is nondecreasing by Proposition 7 and U' is nonincreasing; it is nondecreasing when $\frac{\partial^2 f}{\partial k \partial w} \leq 0$.

We shall prove that $\int a(w')b(w')\pi_{\tau-1}(dw' \mid w) \leq 0$. If $a(w') < 0$ for all w', this is clear since $b(w') > 0$. Else, by continuity of a (recall that f is smooth), there exists $\overline{w} \in \mathbb{W}$ such that $a(\overline{w}) = 0$. We have $a(w')(b(w') - b(\overline{w})) = (a(w') - a(\overline{w}))(b(w') - b(\overline{w})) \leq 0$, since, either the function a is nondecreasing and the function b is nonincreasing or the opposite. Thus,

$$\int a(w')b(w')\pi_{\tau-1}(dw' \mid w) \leq b(\overline{w}) \int a(w')\pi_{\tau-1}(dw' \mid w).$$

By the Euler condition for $\kappa_f^+(w)$ (arg max of a concave function on $[0, +\infty[$), we have

$$\int a(w')\pi_{\tau-1}(dw' \mid w) = \int (\beta_{\tau-1}\frac{\partial f}{\partial k}(\kappa_f^+(w), w') - 1)\pi_{\tau-1}(dw' \mid w) \leq 0.$$

Thus, we have

$$\phi_U(\kappa_f^+(w)) \leq \int a(w')b(w')\pi_{\tau-1}(dw' \mid w) \leq b(\overline{w}) \int a(w')\pi_{\tau-1}(dw' \mid w) \leq 0.$$

On the other hand, we have $\phi_U(\widetilde{\kappa}_U^+(z, w, \tau - 1)) \geq 0$. As a consequence, $\phi_U(\widetilde{\kappa}_U^+(z, w, \tau - 1)) \geq \phi_U(\kappa_f^+(w))$. Now, ϕ_U is nonincreasing as the derivative of a concave function. This implies that $\widetilde{\kappa}_U^+(z, w, \tau-1) \leq \kappa_f^+(w) = \kappa^+(w, \tau - 1)$.

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