Supplementary file "Theoretical considerations on the Gompertzian timecourse of the anomalous germination"

Article title: **Anomalous germination of dormant dehulled red rice seeds provides a new perspective to study the transition from dormancy to germination and to unravel the role of the caryopsis coat in seed dormancy**

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Theoretical considerations explaining why the timecourse of the anomalous germination follows a Gompertz distribution

The basic rationale for observing a Gompertz distribution is that failure of a given system, or function, is dependent on one or more essential components that undergo a “wearing-out” process in which the risk of failure increases progressively (Abernethy 1979). The wearing-out of each component would stem from the wearing-out of its constituent elements (Abernethy 1979). According to the reliability theory, the key feature for a Gompertz distribution to display is that these elements be irreplaceable and highly redundant, that is, there be an initial large excess in the number of elements acting in parallel with respect to the minimum number that would be required for the involved component to perform its function (Gavrilov and Gavrilova 2001; Kirkwood 2015). This initially masks the effect of a linearly increasing number of failures for the elements of the involved component, which continues to perform its function (except for those unfortunate instances wherein redundancy is quickly overcome by many concomitant elementary failures). In this way, a growing number of non-decisive elementary failures can accumulate, and, over time, this will result in an exponentially increasing probability that the last failure in an initially redundant cluster of elements will be decisive, bringing about the system failure (Kirkwood 2015). Redundancy therefore minimizes the probabilities of early system failures and renders system failures much more spread over time.

A central role for redundancy depletion in determining the probability of failure of a functional system has been further advocated by Milne (2008), who made explicit a series of logical assumptions able to explain the ageing pattern described by the Gompertz function, as well as some deviations from it. Among such assumptions, the basic model of Milne (2008) requires that: (i)- the burden of a biological function (performed by a system component) is distributed evenly across the component’s redundant capacity (a capacity that exceeds normal demand), so that the burden per unitary element of redundancy is inversely proportional to the total redundancy; (ii)- for each element, the probability of failure in the presence of a constant risk (i.e., a fairly constant intensity in the use of the component) is linearly dependent on use, and therefore it is constant over time; this implies that (iii)- the probability of failure of each one element can be described by a half-life; thus, (iv)- within each component, redundancy declines in a linear and largely invariable fashion with time; (v)- since the functional burden per unit of redundancy is inversely proportional to total redundancy, half-life is assumed to vary, during the system life, in direct proportion to the actual redundancy (as the intensity in the use of the component is not constant, but rather it increases with time); (vi)- component (and therefore function) failure is dependent upon the failure of the remaining elements to bear the whole burden of the biological function, not directly upon element-specific failure; (vii)- the rate of function failure is therefore obtained as a compounding of a constant element-specific failure by a constantly decreasing number of elements; thus that, (viii)- an exponentially rising function failure is a natural consequence of linearly declining redundancy. In a more complex form that incorporates biological variation, the model of Milne (2008) shows to be quite robust to both within-individual and inter-individual heterogeneity. Heterogeneity is assumed to be distributed either normally or log-normally, depending on the parameter. The distributions of the values (or of the logarithm of the values) are centred around a mean value which is characteristic of each individual, and then around a mean value which is characteristic of the population or species of which they are a part, for heterogeneity within individuals and for heterogeneity between the mean values of individuals, respectively (Milne 2008).

In the context of the anomalous germination, it is proposed that: (i)- the burden of biological function is the expansion force of the turgid embryo; (ii)- the component performing this biological function is the caryopsis coat, which has a capability to contain the embryo that exceeds ordinary embryo thrust; (iii)- the caryopsis coat is constituted by a very large number of cellulose microfibrils that share the burden of embryo turgor, more or less equitably (i.e., the burden distribution does not need to be exactly even across its redundant capacity); (iv)- individual microfibrils can fail (actually, it is the anchoring of the microfibril to the cellulose-hemicellulose network that should fail, since cellulose microfibrils have a high tensile strength and hemicelluloses are more prone to ageing and degradation; Geitmann 2010; Azwa *et al.* 2013), but not all simultaneously, because of random differences in microfibril (or microfibril-anchoring) load-bearing capacities and/or in the distribution of the load among microfibrils, and/or because of the ageing of the microfibrils (or of the hemicellulose network) due to chemical/biochemical degradation (i.e., there is a random distribution of load-bearing failures over time for the microfibrils of each caryopsis); thus, (v)- the microfibrils represent the redundant elements whose probability of failure, in the presence of a constant turgor, is more or less constant over time; (vi)- at each time, the full failure of the caryopsis coat is dependent upon the failure of the remaining upholding microfibrils to bear the burden of embryo turgor; therefore, (vii)- for every caryopsis, the rate of coat failure is obtained as a compounding of a microfibril-specific failure rate by a decreasing number of upholding microfibrils (redundancy); hence, (viii)- an exponentially rising failure of the caryopsis coat with time is a natural consequence of a microfibril-specific failure rate that results in a declining number of upholding microfibrils, and therefore in a depletion of redundancy in the embryo-constraining function, which culminates in the collapse of the caryopsis coat; (ix)- germination follows.

An initial random distribution of upholding capabilities and/or of loads among the microfibrils of each caryopsis will produce a wide distribution of load-bearing failures over time by summing up with a random distribution of ageing effects on the microfibrils due to chemical/biochemical degradation. The latter, either due to seed metabolism or to the occasional microflora, is hard to consider as a stand-alone cause of generalized microfibril failure, since almost the whole distribution of germination times is essentially observed within each Petri dish, and it would be difficult to explain why degradation should be so widely heterogeneous among the caryopses in the same dish. On the other hand, an inborn, random distribution of elementary upholding capabilities among microfibrils statistically determines an average upholding capability for each caryopsis that is still randomly distributed among the different caryopses, though the distribution of such averages has a much smaller variance (typically, according to the square root of the number of constituent elements, i.e., microfibrils). So, a random distribution of load-bearing failures over time among coat microfibrils in each caryopsis would translate into a non-uniform distribution of the average load-bearing capacity of the microfibrils among caryopses. Assuming a uniform turgor among caryopses, differences in the average, or modal, load-bearing capacity of the coat microfibrils among caryopses will therefore produce a Gompertz distribution. The same is true if the average, or modal, load-bearing capacity of the microfibrils is uniform among caryopses but the embryo turgor is normally distributed among caryopses. Both cases might even apply at the same time.

Ultimately, what characterizes the observed distribution of germination times turns out to be the gradual failure of microfibrils that increases the load on the remaining upholding ones and thereby increases their probability of failure. In other words, there is a gradual loss of redundancy. In this context, redundancy should be intended as the ratio between the total load-bearing capacity of microfibrils and the embryo turgor thrust within each caryopsis. What, then, makes the observed

distribution a sigmoid is a relatively wide distribution of average load-bearing failures among caryopses (supposedly consequent to a relatively wide distribution of the average load-bearing capacities and/or of embryo thrust among caryopses): only a very few caryopses initially have a low redundancy (this can even mean an high, ordinary number of microfibrils, but with only a small excess of the total load-bearing capacity with respect to a large embryo turgor thrust) and therefore there are only very few initial failures; but, with time, the depletion of redundancy hits an increasing proportion of the caryopses and therefore the failure rate increases and becomes large. When most caryopses have germinated, the cumulative distribution shows a slowing down in approaching the upper limit (100% germination) because, even if the failure rate of the caryopsis coats in the remaining caryopses continues to increase, the strong reduction in the number of ungerminated caryopses overcomes the effect of the increasing failure rate. It remains to be ascertained whether the observed Gompertz distribution is actually due to an inborn distribution of upholding capabilities and/or loads among the microfibrils of each caryopsis, which both can generate a distribution of load-bearing failures over time. The roles of a distribution of embryo thrusts among caryopses and of ageing (wearing-out, degradation) of the microfibrils, should be established as well.

From a physiological point of view, the interesting feature is that the theoretical considerations adopted above to explain why the timecourse of the anomalous germination follows a Gompertz distribution, are entirely based on the mechanical properties of the caryopsis coat, and specifically upon the gradual depletion of its redundant capability to withstand embryo turgor. This supports that what actually causes and shapes the anomalous germination of red rice dormant seeds is indeed the mechanical failure of the coats.

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