


Climate Change during Cretaceous/Paleogene as a Driving Force for the Evolutionary Radiation of Physical Dormancy in Fabaceae

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Abstract: Physical dormancy (PY) due to a water-impermeable seed/fruit coat is one of the characteristic features of many species of Fabaceae; however, the timing and context of the evolution of this trait are poorly understood. In this investigation, fossil and molecular data are used to constrain the timing of the evolution of PY. The phylogenetic reconstruction programs GB-to-TNT and BEAUTi/BEAST are used to create chloroplast gene-based (*rbcl* and *matK*) phylogenies of taxa with well-represented fossil records. PY and non-dormancy are mapped to the terminals of the phylogeny, and ancestral states are reconstructed using parsimony. The initial evolution of PY in Fabaceae is reconstructed to have occurred sometime in the interval between divergence from Polygalaceae (late Campanian) to the diversification of crown-group Fabaceae (late Paleocene) when Fabaceae is known to have undergone multiple whole genome duplication (WGD) events across the Cretaceous/Paleogene (K/Pg) boundary. As in *Nelumbo*, another taxon with PY, Fabaceae may have developed PY in association with climatic change and WGD across the K/Pg boundary. The evolution of PY in association with WGD at the K/Pg boundary is an intriguing hypothesis that requires further investigation.

Keywords: Campanian/Maastrichtian; impermeable seed coat; K/Pg boundary; fossils; whole genome duplication



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1. Introduction

Impermeable seed/fruit coat, i.e., physical dormancy (PY), is only known to occur in several genera of 19 modern-day angiosperm families [1]. In contrast, seeds with physiological dormancy (PD) resulting from the inability of the embryo to elongate either because of the innate constraint or the thick endocarps preventing elongation and/or hormonal imbalance is the most abundant type in spermatophytes [1,2]. Compelling evidence suggests that PY is the most recent form of dormancy and evolved from PD [3,4]. This view is further supported by the fact that a few species have physical and physiological dormancy, i.e., combinational dormancy (PY+PD) [1,5]. Despite the clear recognition of PY more than 100 years ago [6], the evolutionary origins of PY have been largely debated. Several factors claimed to have acted as the selective force behind the evolution of this trait: (1) high temperatures associated with fire episodes [7]; (2) acidic environment in the animal gut during endozoochory [8]; (3) avoiding the risk of catching and dispersing by predators, i.e., the crypsis hypothesis [9,10]; (4) surviving post-dispersal deterioration [11]. However, support for these factors as evolutionary forces behind PY evolution is anecdotal [12–15]. An alternative perspective is that PY evolved as a response to climatic changes such as cooling climate across the K/Pg boundary that occurred during the Cretaceous/Paleogene, presumably due to the K/Pg transition [16,17].

Among those taxa known to have evolved PY during the K/Pg transition is *Nelumbo*, which evolved PY in association with whole genome duplication (WGD) at or near the

K/Pg boundary [18,19]. Indeed, Wu, S. et al. [20] observed in a recent gene ontology analysis that 493 gene families retained duplicated genes from six or more independent WGD's across the K/Pg boundary, including those for abscisic acid (ABA) signaling (i.e., ABA transcription factors) in Fabaceae and other angiosperm taxa, such as *Nelumbo* [21–23]. As with the study by Wu et al. [20], Shi et al. [19] specifically attributed the evolution of seed dormancy in *Nelumbo* to WGD at or near the K/Pg boundary. *N. nucifera* exhibit WGD and the longest-lived seeds (1300 y) known, with seed longevity greater than a millennium [24,25].

PY is a characteristic seed trait of many Fabaceae occurring in all sub-families; however, the timing, context, and evolution of this trait remain enigmatic [1,4]. Fabaceae is known to have exhibited multiple WGD events across the K/Pg boundary [26], and some researchers have demonstrated that it is likely PY evolved in conjunction with WGD in this group [27]. Until recently, the oldest fossils of Fabaceae were regarded to be late Paleocene in age, ca. 58–56 Ma [26,28,29]. The oldest known fossils of Fabaceae were recently discovered to be slightly younger than the K/Pg boundary [29] and late Campanian in age, ca. 73.5 Ma, respectively [30].

Surprisingly, the timing and context of the evolution of PY in relation to these fossil lineages remain equivocal. Here, we used fossil records and molecular data to constrain the timing of the evolution of PY. Previously, molecular phylogenetics has been used in evolutionary studies of plants and plant structure evolution [31–33]. In particular, parsimony and Bayesian phylogenetic analyses of the plastid *matK* and *trnL* intron sequences have been used to show the early branching of the papilionoid clade. However, the application of these methods for seed traits is only recently gaining momentum [34,35]. Thus, the important objective of this work is to unequivocally place the evolution of PY in the context of the evolutionary radiation across the K/Pg boundary by using Fabaceae as a model family. In doing so, we articulate that climate drying during and following the Cretaceous/Paleogene acted as the driving force for the radiation of PY.

2. Methods and Materials

Ribulose-1, 5-biphosphate carboxylate/oxygenase large subunit (*rbcL*), and maturase K (*matK*) chloroplast gene sequences for taxa with fossil records were drawn from GenBank, as these gene sequences have previously been used to investigate phylogenetic relationships among Fabaceae with fossil records (Supplementary Table S1, [28,36]). Sequences were aligned using Muscle v. 3.8.31 [37] and subsequently manually checked for alignment. Genbank-to-Tree Analysis Using New Technology [38,39] was used to create FASTA files, which were dually uploaded in Bayesian Evolutionary Analysis Utility (BEAUTi) and Bayesian Evolutionary Analysis Sampling Trees (BEAST), v. 2.6.5 [40] and TNT v. 1.5 [39]. As divergence time estimates for major clades in the Fabaceae are well constrained by previous investigations [26,28,36,41], this investigation did not incorporate these priors into phylogenetic reconstruction and divergence time estimation. Markov chain Monte Carlo (MCMC) chain length was set at 20,000,000 (10% burn-in) based on Tracer v. 1.7.2 [42] results. The program Tree Annotator [42] was used to create a maximum clade credibility tree, with burn-in and posterior probability established from analyzing the results of Tracer v. 1.7.2. PY and ND or PD were mapped to terminal taxa in the maximum clade credibility tree by creating a separate character matrix and reconstructing ancestral states using parsimony in Mesquite v. 3.61 [43]. Phylogenetic analysis also was performed using TNT, and PY and ND or PD were subsequently mapped to the molecular phylogeny by appending an additional character to the molecular dataset. Taxa with fossil records known to exhibit ND (water-permeable) seeds include Polygalaceae, *Diploptropis*, *Machaerium*, and *Tipuana* [1,44]. PY has been well demonstrated in the other lineages [1,45–47].

3. Data and Results

ND occurred in some lineages of Fabaceae with fossil records, including *Diplotropis*, *Machaerium*, and *Tipuana*, during the Cenozoic (Figures 1 and 2). On the basis of the fossil record, the divergence between Fabaceae and Polygalaceae occurred during the late Campanian with a subsequent, late Paleocene diversification. When mapped onto the molecular phylogeny of lineages with well-preserved fossil records, PY evolved once during this temporal interval, when Fabaceae is known to have undergone one or more WGD events in multiple angiosperm lineages across the K/Pg boundary (Figures 1 and 2). The evolution of PY is bracketed by two probable WGD events.

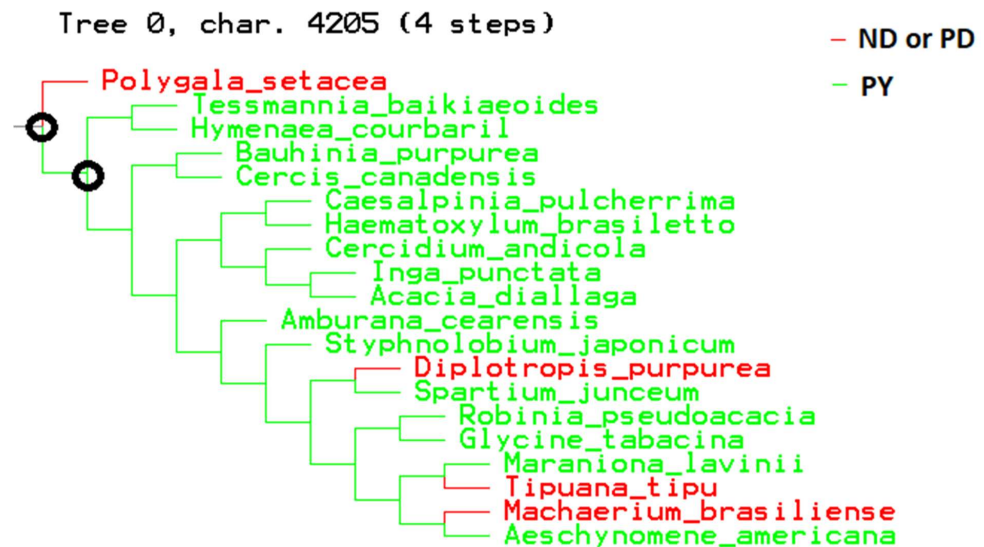


Figure 1. Strict consensus tree produced using TNT v. 1.5 with seed dormancy traits [non-dormancy (ND) or physiological dormancy (PD) and physical dormancy (PY)] mapped to terminals. Circles indicate putative whole genome duplication events from Koenen et al. [26,41]. Note that divergence between Polygalaceae (ND) [1] and Fabaceae (predominately PY) is estimated to have occurred in the Campanian/Maastrichtian on the basis of previous investigations [26,28,36,41].

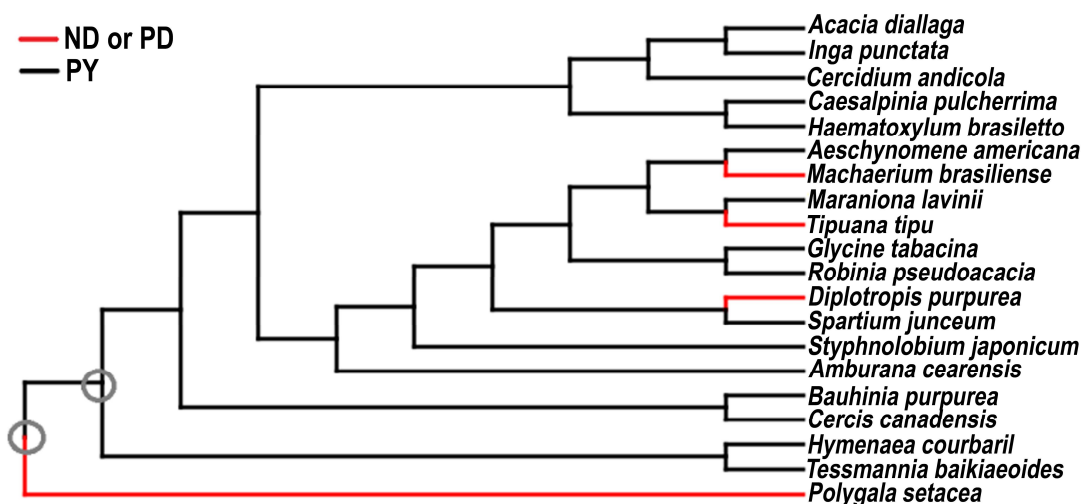


Figure 2. Maximum clade credibility tree generated using BEAUTi and BEAST v. 2.6.5 with seed dormancy traits [non-dormancy (ND)] or [physiological dormancy (PD) and physical dormancy (PY)] mapped to terminals. Circles indicate putative whole genome duplication events from Koenen et al. [26,41]. Note that divergence between Polygalaceae (ND) [1] and Fabaceae (predominately PY) is estimated to have occurred in the Campanian/Maastrichtian on the basis of previous investigations [26,28,36,41].

4. Discussion

Despite the lack of strong evidence for WGD at the base of every clade, several present-day Fabaceae species are relicts of polyploidy [48,49]. However, several lines of evidence indicate that polyploidy events in Fabaceae possibly led to the evolution of the complex modern symbiotic rhizobial nodule and radiation of sub-families near the K/Pg boundary [50]. A recent study by Koenen et al. [41] revealed that multiple WGD events occurred in Fabaceae at or near the K/Pg boundary, which is when PY is projected to have evolved in this family (Figures 1 and 2). These results agree with the contemporary perspective that PY evolved in conjunction with WGD in Fabaceae [27].

Our finding that PY evolved near the K/Pg boundaries is concordant with previous investigations, such as those which link the evolution of PY in *Nelumbo* with WGD at the K/Pg boundary [19]. On the basis of the fossil record, the oldest fossils of Fabaceae appeared ~73.5 Ma [30] with subsequent radiation of crown Fabaceae by ~58–56 Ma [26,28]. Lavin et al. (2005) gave the following lineages as well constrained by the fossil record: (1) the *Cercis* clade (ca. 34 Ma), represented by *Cercis/Bauhinia*, (2) the *Hymenaea/Tessmania* clade (ca. 34 Ma), (3) the *Mezoneuron* clade (ca. 34 Ma), represented by *Caesalpinia/Haematoxylon*, (4) the *Acacia* clade (ca. 15 Ma), represented by *Acacia* and *Inga/Mimosa*, (5) the *Papilionoideae* clade (ca. 55 Ma), represented by *Amburana/Cercidium/Glycine*, (6) the *Stypholobium* clade (ca. 40 Ma), (7) the *Diploptropis* clade (ca. 56 Ma), represented by *Diploptropis/Spartium*, (8) the *Machaerium* clade (ca. 40 Ma), represented by *Aeschynomene/Machaerium*, (9) the *Tipuana* clade (ca. 10 Ma), represented by *Tipuana/Maraniona*, and (10) the *Robinia* clade (ca. 34 Ma), represented by *Robinia/Coursetia*. Additional constraints discussed by Bello et al. [36] include a Campanian/Maastrichtian divergence between Polygalaceae and Fabaceae, coupled with additions to the oldest fossil records of the latter [29,30]. Detailed discussions of the morphological apomorphies that support the recognition of these lineages in the fossil record, which is beyond the scope of this paper, can be found elsewhere [36,51]. During this time, WGD events occurred at or near the K/Pg boundary with perhaps one pan-legume WGD occurring on the stem separating Polygalaceae from crown Fabaceae [26].

Lyson et al. [29] speculated that the evolution and diversification of Fabaceae were associated with endozoochory by mammals, a perspective shared by Huegele and Manchester [52]. This inference appears to support the contention of Temple, S.A. [8] that PY evolved in response to the acidic environment associated with wind endozoochory by mammals; however, these results are contested by the earlier evolution of Fabaceae, which is now known to have preceded the post-K/Pg radiation of mammals [30].

Contemporary K/Pg asteroid impact models predict a multi-year episode of drastically reduced precipitation and sub-freezing conditions associated with sunlight-blocking aerosols produced by the Chicxulub impact [53–56]. Previously linked to the differential survival of plants with varying seed strategies, e.g., recalcitrant vs. orthodox seeds [57] as discussed by an emerging literature [34,35], these K/Pg climate models suggest that PY may have permitted the survival or post-K/Pg diversification of Fabaceae, as has already been postulated for *Nelumbo* [19,34,35]. If this perspective is correct, then PY may represent an exaptation (Sensu [58]) for plant survival across the K/Pg boundary, as climate-related dormancy has similarly been linked to fortuitous survival across the K/Pg boundary in diatoms [59]. This perspective differs from that of other researchers, who have posited that the evolution of root nodules associated with WGD may have permitted the survival and diversification of Fabaceae across the K/Pg boundary [60,61] but is consistent with the contemporary perspective of Van de Peer, Y. et al. [62], who suggested seed dormancy and ABA signaling were traits selected among vascular plants during the K/Pg transition.

Whilst linking the evolutionary traits, particularly the ones like impermeable coats with the specific time frame, is an obscene paradox, numerous traits have been considered to evolve during Cretaceous, which favored the early diversification of angiosperms [63,64]. Despite the unsettled debate about the evolution of angiosperms, growing evidence points the origin to Upper Triassic (350 mya) and radiations occurring throughout the Jurassic

and particularly Lower Cretaceous about 80–60 mya [65,66]. Climate data available prior to the K/Pg event suggest that the cool and wetter climate prevailed from the inception of angiosperms favored desiccation-sensitive, i.e., recalcitrant, seeds. Such climatic conditions were present in the Western Interior of North America during the late Maastriichtian. Fossil records and climatic data indicate that prior to the K/pg event ancestors of modern-day rainforest species belonging to families Annonaceae, Arecaceae, Meliaceae, and Myristicaceae were common until Paleocene-Eocene [67,68], during which the climate warmed 5–7 °C, resulting in species diversification, specifically the wide colonization of Fabaceae [69,70].

The recent finding of the oldest Fabaceae fossil from the Olmos Formation undoubtedly extends the radiation of this family to the Cretaceous. The climate of the Olmos Formation during the Cretaceous appears to be wet with rare aridity or drought [71], plausibly favoring a water-permeable coat. Subsequent movement of Fabaceae species to dry forests or climate becoming drier might possibly have led to the evolution of water-impermeable coats. This is in agreement with Rubio de Casas et al. [72] who showed that Fabaceae species in wetter regions were large and non-dormant, seasonally dry climates impose pressure to develop impermeable coats. Multiple WGDs in Fabaceae species explain the possible evolution of impermeable coats independently in some species and subsequently lost. Support for this view comes from Lavin et al. (2005), as those authors showed that most of the lineages with fossil records available come from tropical dry forests (also see above). In the conceptual model proposed by Van Staden et al. [16] for the evolution of impermeable seed coats in Fabaceae, the ancestral legumes had water permeable coats with the non-dormant embryo, which gave rise to two independent traits due to increasing in aridity: (1) development of pleurogram and PY and (2) development of hilum and PY. The oldest fossil record with explicit features (i.e., a palisade layer in the endocarp) showing the possibility of PY comes from 43 Ma extinct fossil records of extinct *Rhus rooseae* (Anacardiaceae) [73]. Furthermore, fossil records of orders of all 18 families in which PY occur are exceptionally restricted to the Cretaceous or early Paleogene [74,75], implying a strong association between dry (and hot) climate and evolution of PY [19,76], but this warrants further study from the WGD perspective [19,62]. In any case, the association of WGD and the evolution of PY in the context of climatic factors at the K/Pg boundary in at least two lineages of vascular plants (Fabaceae and *Nelumbo*) suggests a convergent evolution or a congruent pattern of vascular plant evolution across the K/Pg boundary and a general role for WGD in plant macroevolution, i.e., as an exaptation for fortuitous survival during the K/Pg impact winter [59], which has generally been lacking [77,78].

Is there any other fossil evidence for the proliferation of plant lineages that have undergone WGD at the K/Pg boundary? Lomax et al. [77] suggested that this was not the case, countering the results of numerous genomic studies [60,62,79]. However, it is important to note that at least two stem representatives of polyploid crown genera, including *Stenochlaena* (Blechnaceae) [80,81] and *Cyclocarya* (Juglandaceae) [82], are known to have emerged immediately above the K/Pg boundary in the strata of western North America [29,34,83]. Examples of duplicated genes retained across the K/Pg boundary in both Fabaceae and *Stenochlaena* include chalcone isomerase (*chi1/2*) genes, which also function in seed coat traits and other stress-related factors [84–87]. Clearly, this is a topic worth further investigation.

5. Conclusions

The timing and context of the evolution of PY in Fabaceae have remained enigmatic. Mapping the evolution of this trait onto a molecular phylogeny of taxa with well-preserved fossil records indicates that PY evolved sometime between the divergence of Fabaceae from Polygalaceae (late Campanian) and prior to the diversification of crown Fabaceae (late Paleocene), an interval of time that overlaps with an episode of multiple putative WGD events in Fabaceae and other angiosperm families. This appears to parallel the pattern observed in another taxon, *Nelumbo*, which also appears to have evolved PY in association

with WGD and the K/Pg transition. Additional studies are needed to determine whether this pattern is congruent with that observed among other lineages of vascular plants.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/seeds2030023/s1>, Table S1. Muscle v. 3.8.31- aligned *rbcL* and *matK* GenBank chloroplast gene sequences for lineages with a fossil record (based on Lavin et al. [28]).

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