Seed Science Research (2004) **14**, 315–320 DOI: 10.1079/SSR2004185

RESEARCH OPINION

On criteria to use in studies of seed evolution

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Abstract

A critical analysis of different criteria used in investigating seed diversity was made. It is concluded that the most promising way to understand the evolution of seeds is to study not only their morphological features, as used by most workers in the field, but also the physiological diversity of seeds in connection with the taxonomic system of plants, together with their ecological and geographical peculiarities.

Keywords: phylogenetic relationships of seeds, seed dormancy classification, seed evolution, seed morphology, seed physiology

Biographical preface and tribute

Marianna Nikolaeva was born on 23 September 1914 in Ufa, a city just west of the southern Ural Mountains, now the capital of the Republic of Bashkortostan, Russian Federation. Thus, we are celebrating Dr Nikolaeva's 90th birthday with the publication of this tribute. After graduating from high school in 1931, Nikolaeva studied biology at the state university in Leningrad (now St. Petersburg), specializing in geobotany. However, she was attracted to plant physiology, and thus her life-long research has been on the comparative physiology and biochemistry of seed dormancy and germination. Nikolaeva's entire professional career, which began in 1939, was spent at the V.L. Komarov Botanical Institute (St. Petersburg) of the Russian Academy of Sciences. After interruption of her career from 1941 to 1946 by the Second World War, she followed an independent line of research at the Institute and has published more than 100 papers and three books (Nikolaeva, 1967; Nikolaeva *et al*., 1985, 1999), and directed 13 doctoral dissertations. Nikolaeva obtained her PhD degree in 1967, by which time she had published numerous papers on seed dormancy and germination. Since her retirement a number of years ago, she has continued to live in St. Petersburg and publish papers on seed biology, right up until the present time.



Marianna G. Nikolaeva

The title of Nikolaeva's dissertation was *Fiziologiya glubokoga pokoya semyan*, which was translated into English (*Physiology of deep dormancy in seeds*) in 1969. This book is a seminal contribution to seed biology. In

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https://doi.org/10.1079/SSR2004185 Published online by Cambridge University Press

it, she presents the most logical and detailed seed dormancy classification system yet devised, representing each kind of dormancy with a formula. Her system is based on seed internal structure (e.g. underdeveloped versus fully developed embryo); role of seed covering layers (i.e. impermeability to water, mechanical restriction to radicle emergence, presence of chemical inhibitors in imposition of dormancy); and physiological requirements for dormancy-break, including the effects of the plant growth regulator, gibberellic acid. In her comparative method of investigating seed dormancy, she also gave considerable attention to certain taxonomic groups of plants (e.g. *Acer*, *Euonymus*, *Fraxinus*, *Rosaceae*) and more recently to habitat and life-cycle type. Without this broad approach to seed dormancy, Dr Nikolaeva could not have constructed her classification system. Relatively minor revisions of her system were published in 1977 (Nikolaeva, 1977) and 2001 (Nikolaeva, 2001).

Marianna G. Nikolaeva made a major contribution to the evolutionary aspects of seed dormancy in four papers she published in the *Botanicheskii Zhurnal* (Nikolaeva, 1988, 1989a,b, 1990) on the relationship between the kind of seed dormancy and phylogenetic position of large taxa (i.e. classes, subclasses and families *sensu* A. Takhtajan) in both gymnosperms and angiosperms. A summary of the contents of these four papers was published in English in the *Russian Journal of Plant Physiology* (Nikolaeva, 1999).

Without doubt, the research contributions of Marianna G. Nikolaeva have greatly increased our knowledge of the nature of seed dormancy.

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Research Opinion

˘The great diversity of morphological and physiological features of seeds has attracted the attention of seed researchers. A natural desire of botanists is to sort out this diversity and to elucidate the phylogenetic relationships of the different kinds of seeds. However, there are many ways of attempting to do this. Most workers have concentrated on morphological features; some have focused on the outer covers (pericarp and seed coat) and others on internal structures (endosperm and embryo). I will not consider the significance of the outer covers to elucidate pathways of seed evolution. Instead, my aim is to use internal features of seed structure for this purpose.

Martin (1946) was the first to study the evolutionary relationships of seeds based on their internal structures, and his work is quite often referred to, even today. On the basis of his analysis of the size and shape of seeds and embryos, as well as of the embryo/endosperm storage tissue volume ratio, he formulated a concept of the classification of seed types and their phylogenetic relationships, representing the latter in the form of a so-called 'phylogenetic tree'. One cannot help but appreciate information contained in Martin's work on the main characters of the seed structure of 1287 genera. Without doubt, some of his suggestions on phylogenetic relationships of seeds deserve attention, namely the indication of the seed evolutionary trend of increase in embryo size, and also his placing of the seed type with the rudimentary embryo (according to his terminology, see below) at the base of his phylogenetic tree.

However, it is difficult to agree with Martin's concepts in general. First, he used a formally static approach (i.e. internal structures only) to estimate the values taken as a basis for defining the seed types. In addition, descriptions of the embryos used as the basis for distinguishing the seed types, and their names, are uncertain and quite often controversial. For instance, there is hardly a difference between Martin's rudimentary embryo in seeds of 'medium size or larger' and the embryo in some dwarf (0.3–2.0 mm in length) seeds. In both types of seeds, embryos can be small-globular to ovoid-oblong bodies, with cotyledons developed to varying degrees. In his scheme, Martin includes seeds with rudimentary embryos in the basal type, regardless of their size, and assigns dwarf seeds (with both rudimentary-like and fully developed linear embryos) to the axile type of the subdivision of small seeds. Further, the characteristics of linear embryos are very uncertain. In examples given by Martin (1946), linear embryos vary in different plant species in both size and extent of differentiation, and even in their position in the seed (straight, bent). Other examples may be given. Nevertheless, the factual data on the main features of seed structure of a large number of species determined/compiled by Martin are quite often used at present, and his theoretical concepts are also often accepted. The seed types suggested by Martin are often considered as indisputably established.

However, some works should be mentioned that have continued the efforts to sort out seed diversity on the basis of morphology. Thus, Smirnova (1965) proposed a 'combinative' principle of seed classification, somewhat different from that of Martin. As a basis for this classification, she took the following categories: groups (according to the nature and extent of development of storage tissues – from

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endospermal to embryonal itself), levels (by the ratio of embryo/seed length) and types (complex of features by which to characterize the embryo). The analysis of the phylogenetic distribution of seed types by levels and groups among taxa of flowering plants, in dicotyledons and monocotyledons separately [in accordance with Takhtajan's (1959) plant classification system], led her to an idea of a relative parallelism in the directions of seed evolution. Vyshenskaya (1997) approached the classification of seeds from another angle. In the book *Embryology of flowering plants*, Vyshenskaya suggested a system of seed classification based on embryo morphology, which she considered the most important character of plants. However, in general, her scheme is difficult to use for elucidation of seed evolution.

Of much more interest is the recent work by Forbis *et al*. (2002) devoted to the problem of 'evolution of embryo size'. Like others, they accepted the ratio of embryo and seed size as a key characteristic of seeds. However, in doing so, they took as an index of this ratio the 'generalized least squares' (GLS), instead of linear sizes. These authors analysed the relations of GLS values to the taxonomic position of plants (1222 genera in 179 families) using the phylogenetic system of Soltis *et al.* (1997, 2000). Their results demonstrated that the GLS value increased from 'primitive' taxa toward evolutionarily advanced ones. It must be emphasized that Forbis *et al.* (2002) did not restrict their work to the aforementioned morphological characteristics, but considered the problem of seed evolution in a much broader context, including accounts of physiological and ecological features of the seeds. They also used the results of research by Grushvitskii (1967), Baskin and Baskin (1998) and Nikolaeva (1999), i.e. works that are important milestones in that they are the beginning of a new way to study evolutionary processes of seeds. Undoubtedly, we must expand on these works in detail.

Grushvitskii presented his ideas on the role of embryo underdevelopment in the evolution of flowering plants in a paper published in 1967, but in more detail in one published in 1961. According to his view, the term 'rudimentary embryo' in Martin's sense was uncertain. In cases of incomplete development of the embryo, he suggested the term 'underdeveloped' be used when possible, with an indication of the stage where the development stopped. He showed that the most essential property of seeds with an underdeveloped embryo is not so much its small size, as compared to the endosperm, but its continuing development after seed ripening and separation from the parent plant; during that time, its size and shape change considerably. Then, Grushvitskii distinguished a special group of seeds with an underdeveloped embryo of secondary origin, i.e. with a reduced embryo, and suggested the name 'rudimentary' for this case. Unlike seeds with an underdeveloped embryo, those with a rudimentary embryo (*sensu* Grushvitskii) are typical of plants with a special biology (saprophytic, parasitic and epiphytic). They are characterized by small size of both the embryo and the seed itself, and their germination takes place without any additional development of the embryo. Grushvitskii used the phylogenetic system of Takhtajan (1959) and showed that seeds with underdeveloped embryos are typical mostly of primitive plants,while seeds with a reduced (i.e. rudimentary, *sensu* Grushvitskii) embryo occur in a number of evolutionarily advanced taxa. Thus, he was the first to consider the evolution of seeds in the context of the taxonomic system of the plants themselves.

A question of the evolutionary significance of germination conditions, in particular the phenomenon of seed dormancy, has attracted the special attention of researchers. As data accumulate, it becomes clear that dormancy is determined by both morphological and physiological properties of seeds. Thus, both of these characters should be used in investigations of evolutionary changes in seeds. Obviously, it is first necessary to know the diversity of the kinds of seed dormancy. Nikolaeva (1967, 1977) distinguished dormancy types on the basis of causes of dormancy, and the conditions required to break it. She suggested a concept of three groups of the seed dormancy types: exogenous, endogenous and combined. Dormancy of seeds in the first group is connected with properties of their outer covers. The second group, endogenous dormancy, includes morphological dormancy (the cause of which is embryo underdevelopment), levels of physiological dormancy (non-deep, intermediate and deep) related to a special physiological state of the embryo and levels of morphophysiological dormancy, where delay of development is determined by a combination of embryo underdevelopment and physiological causes. The group of combined dormancy comprises numerous cases of combinations of exogenous and endogenous causes. Later on, this classification was improved and supplemented by Baskin and Baskin (1998) and Nikolaeva (2001). Thus, they significantly extended the concepts of physiological and morphophysiological seed dormancy, and distinguished two types of non-deep physiological dormancy, one broken by cold and the other by warm temperatures.

Using data from the literature and their own data, Baskin and Baskin (1998) outlined the evolution of seeds of both gymnosperms and angiosperms. They used as indices, first, embryo types, *sensu* Martin (from rudimentary to linear and then to more developed forms), and secondly, kinds of seed dormancy, from morphological to physiological and lack of dormancy. Their scheme related time of appearance and evolution of physiological seed dormancy to conditions of plant habitats. A

https://doi.org/10.1079/SSR2004185 Published online by Cambridge University Press

simplified version is represented as a table by Nikolaeva (2001). It follows from the table that, in regions with a temperate climate, the flora has formed under cold conditions, and as a result, most plants have types of physiological dormancy that differ in depth, and are broken under the influence of cold. In contrast, in hotter regions, species have evolved with another type of dormancy, i.e. non-deep physiological, which is broken under the effect of high temperatures.

A matter of interest is the recent paper by Baskin and Baskin (2004) 'A classification system for seed dormancy' in which they revised the Nikolaeva classification to some extent. The views of the hierarchical layers of the kind of dormancy suggested in the paper are very promising. The detailed consideration of the nature of different types of non-deep physiological dormancy is also of great importance. Besides, their exclusion of mechanical and chemical dormancy from the Nikolaeva classification scheme is probably correct. However, I believe it hardly correct to use the seeds of *Arabidopsis* and those of other species of cultivated plants as models to investigate the mechanism of physiological dormancy. These species, widely used in a number of works, are considered as having seeds with non-deep physiological dormancy. However, as the Baskins themselves have shown, non-deep physiological dormancy is very labile and, moreover, exists in different types. Besides, it must be emphasized that the results of these studies cannot be used to understand the nature of intermediate or deep physiological dormancy.

Along with this, Baskin and Baskin (1998) and Nikolaeva (1999, 2001) made a detailed analysis of kinds of seed dormancy in different taxa of both gymnosperms and angiosperms, using the systems of Takhtajan (1980, 1986, 1987). Their research makes it possible to trace, with different degrees of confidence, the paths of seed evolution. They showed that properties of seeds, including the phenomenon of dormancy, are related to a great degree to the taxonomic position of plants. With this, it should be noticed that, according to Nikolaeva's data, seed characteristics change in the same direction in gymnosperms and angiosperms, and also within the orders of angiosperms. Thus, embryo underdevelopment, and morphological and morphophysiological dormancy, are mainly typical of primitive taxa, i.e. in subclasses *Magnoliidae* and *Ranunculidae* of angiospermous dicotyledons, in the subclass *Arecidae* of angiospermous monocotyledons and in the families *Ginkgoaceae*, *Podocarpaceae* and *Taxaceae* of gymnosperms. In contrast, typically the most evolutionary advanced taxa mainly have seeds with fully developed embryos and lacking dormancy, or have physiological dormancy, which is more often of the non-deep level. Among dicotyledons, this is typical of subclasses *Caryophyllidae* and *Hamamelidae* and of the family *Asteraceae* of subclass *Asteridae*. Within monocotyledons, this kind of dormancy is observed in the family *Poaceae* (subclass *Liliidae*). The same types of seeds (fully developed embryo, lacking dormancy or having non-deep dormancy) are typical of the most advanced taxa of gymnosperms (families *Pinaceae*, *Taxodiaceae* and some others). No doubt, peculiarities of seeds inherent to representatives of higher taxa were developed a long time ago.

Unfortunately, due attention has not been paid to the problem of causes of differences in seed properties among plants within smaller taxa. This can be explained partly by scarcity of such information, as well as by peculiarities of infrageneric taxonomy. Only recently have more and more data appeared about seed properties within minor taxa, such as genus and species, and the conditions of the origin of these properties (see Nikolaeva *et al*., 1985; Baskin and Baskin, 1998). Obviously, to reveal phylogenetic relationships in development of seed peculiarities, i.e. to trace initial stages of their evolutionary process, it is necessary to compare the seed features with both taxonomic position of the plants and the ecological conditions of their habitats, as illustrated by the following examples.

Using published and original data, Nikolaeva analysed seed features of species of the genus *Fraxinus*; distinctions in seed peculiarities in different *Fraxinus* species are related to both their taxonomic position and geographical distribution (Steinbauer, 1937; Asakawa, 1956; Nikolaeva, 1958, 1967). Species of the genus *Pinus* are another example of the effect of geographical conditions of plant habitats on seed properties. A detailed analysis of data from the book *Seeds of woody plants in the United States* (Schopmeyer, 1974) has shown that most species occurring in comparatively mild climates (e.g. the plains of southern North America), as well as in areas of lower altitude (e.g. in Mediterranean countries), are characterized by small seeds and non-deep physiological dormancy. In contrast, 17 of 21 species (about 80%) of those occurring in northern regions and areas of high altitude form large seeds with deep dormancy (Nikolaeva, 1990). Recently, the study of seeds of 94 species of *Allium* by Specht and Keller (1997) has shown that species in the subgenera *Allium* and *Rhiziridium* are characterized by seeds germinating in warm conditions (at 16°C or 26°C). In contrast, cold (*c*. 5°C) is necessary for germination of seeds of species in the subgenus *Melanocrommium*. These examples show that seed germination conditions for different species within the same genus are related to both their taxonomic position and geographical and ecological conditions of their habitats.

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Dependence of seed properties on plant environment is obvious even for plants of the same species. For example, some plants in the family *Fabaceae* form seeds with water-impermeable seed coats. The percentage of 'hard' seeds in certain species varies considerably, depending on the environmental conditions of the mother plant during seed ripening (Poptsov, 1976). Seeds of *Fraxinus excelsior* are characterized by an underdeveloped embryo and morphophysiological dormancy. However, size of the seed and the embryo, as well as depth of dormancy, depend on the locality of plant occurrence (Nikolaeva and Vorob'eva, 1978).

An even more striking example of the effects of environment is *Pinus brutia* (Skordilis and Thanos, 1995). This endemic pine occurs in the Mediterranean region, mainly on islands in the Aegean Sea. However, despite relatively small distances between the islands (about 600 km maximum), they differ considerably in climate. Seeds of *P. brutia* on the southern islands, in particular on Crete, are smaller and germinate at a wide range of temperatures (5–25°C), although most successfully (up to 80–90%) at 10–20°C. In contrast, seeds of plants on the northern islands are somewhat larger and require other conditions for germination: seeds from Thasos Island germinate at a narrower range of temperatures (15–25°C) and more successfully (60–80%) at 18–22°C. Further, cold stratification at 2–4°C only somewhat accelerates germination of the southern seeds, while 1 month of stratification of the seeds from Thasos caused an increase in germination percentage at 15°C, and accelerated it at 20°C. Seeds from Soufli, the nearest locality to Thasos, practically do not germinate at all without cold stratification for at least 2–3 months. These data illustrate a remarkable correspondence of seed properties to habitat conditions.

It follows from the above statements that attempts to elucidate seed diversity based only on morphological peculiarities, and especially on any one character, such as on the inner structure of mature seeds, do not provide comprehension of the dynamics of seed evolution. Much more effective are studies devoted to a wide range of both morphological and physiological seed properties. Moreover, analysis must be performed on the relation of these properties to the taxonomic position of plants and to the effects of ecological and geographical conditions of their habitats.

Data accumulated to date allow us to propose the main ways of evolution of seed properties. First of all, they provide evidence that seed properties are related in a broad sense to the phylogenetic position of the plant. The underdeveloped (small, but differentiated) embryo should be regarded as the most ancient phenomenon, and is typical of seeds of plants from the most primitive taxa, mainly from tropical areas. However, it also occurs in evolutionarily advanced taxa. On the other hand, the presence of undifferentiated embryos in mature seeds is considered to be a derived condition, and it occurs in species with a special biology, such as parasites, saprophytes or epiphytes (Teryokhin, 2001).

A certain parallelism can be traced in the changes of seed properties in plants of higher taxa, such as angiosperms and gymnosperms, or monocotyledons and dicotyledons. Along with this, it is obvious that the environment exerts much effect on seed peculiarities. This is especially clear for lower taxa (genus, species). For this reason, research into the environmental effects on the process of seed evolution is of special interest.

In conclusion, studies of seed diversity based on consideration of only their internal structures do not promote understanding of phylogenetic relationships and evolutionary trends. Approaches that deal with both morphological and physiological characteristics, including dormancy, as well as the taxonomy and ecological conditions of their habitat, are more likely to clarify evolutionary relationships among seeds.

Acknowledgements

Jerry and Carol Baskin thank Maria Doussi and Costas Thanos (University of Athens, Greece) for translating from Russian to English certain information from the article entitled 'Marianna Georgievna Nikolaeva – celebration and dates' by L.M. Pozdova, E.N. Polyakova and M.V. Razumova, published in *Botanicheskii Zhurnal* **79**, 118–127 (1994). The editor gratefully expresses his appreciation to J.M.B. and C.C.B. for their patience and valiant efforts to bring this project to fruition. Happy Birthday, Dr Nikolaeva!

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Received 27 June 2004
accepted after revision 30 August 2004
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https://doi.org/10.1079/SSR2004185 Published online by Cambridge University Press