*New Idea***Evolution of the seed habit: Is niche construction a missing component?****Ove Eriksson***Department of Ecology, Environment and Plant Sciences, Stockholm University, SE-106 91 Stockholm, Sweden***Abstract**

Evolution of land plants is one of the major transitions in the history of life on Earth. In this process, evolution of seeds constitutes one of the key events, liberating plants from dependence of free external water for fertilization, thus promoting colonization of dry environments and the build-up of terrestrial ecosystems. Previous explanations of evolution of seeds from heterosporous predecessors have been based on a framework of kin and sexual selection theory. Here I suggest that that niche construction is a missing component in these explanations. During colonization of increasingly drier habitats, the heterosporous life cycle was subjected to strong spatial and temporal gradients in water availability. The ancestral condition of separate niches of the sporophyte and female gametophyte generations changed into a situation where the sporophyte generation provided the means by which female gametophytes could develop, in effect ‘constructing’ the recruitment niche for the female gametophyte, attached to the sporophyte. Selection favored modifications in the developmental program, altering the relative timing of fertilization and dispersal. Kin and sexual selection processes could then play out in the context of a plant life cycle where fertilization preceded dispersal, eventually forming the seed habit. Niche construction by the sporophyte removed the ecological independence of the two generations; the sporophyte provided the female gametophyte with a recruitment niche, transforming the biphasic life cycle into a unitary life cycle, and promoted an expansion of the ecological niche zone for land plants, eventually leading to a vegetation covering most parts of the land mass.

Key words: Devonian, heterospory, land plant evolution, pollination, terrestrial ecosystems

Introduction

The origin and evolution of land plants in the Palaeozoic era from the Ordovician (485.4–443.8 Ma) through the Silurian (443.4–419.2 Ma) and Devonian (419.2–358.9 Ma) is one of the major transitions in the history of life on Earth (e.g. Kenrick and Crane 1997, Wellman et al. 2003, Delwiche and Cooper 2015, Edwards and Kenrick 2015). (Time-scale is according to Cohen et al. 2013). Among land plants, the evolution of the seed habit, i.e. a life cycle involving seeds, is one the major events forming not only the currently dominating groups of plants, but also the basis of terrestrial ecosystems as we know them today (Chaloner and Pettitt 1987, DiMichele et al. 1992, Algeo and Scheckler 1998, Taylor et al. 2009). An understanding of the mechanisms behind evolution of the seed habit is thus of great interest.

Land plants evolved from an ancestral lineage of Charophyte algae (Delwiche and Cooper 2015), and the most likely sister group to land plants is the Zygnematophyceae (Wickett et al. 2014). Land plants are characterised by an alternation of generations (Kenrick 1994, Graham and Wilcox 2000, Niklas and Kutcher 2009). In this life cycle, a diploid sporophyte produces haploid spores which after germination develop a haploid gametophyte, producing gametes. Following syngamy, a zygote forms, which after development closes the life cycle by developing a new sporophyte. A conspicuous pattern during land plant evolution is a general trend from gametophyte towards sporophyte dominance (e.g. Bateman and DiMichele 1994, Kenrick and Crane 1997, Kenrick 2018). Early land plants are believed to have had a life cycle where the gametophyte generation was dominating, in the sense of being largest and most long-lived. In extant mosses, the gametophyte generation still dominates, but in lycophytes, horsetails, ferns and seed plants, the

sporophyte generation dominates, in size, life span and complexity.

Living on land implies severe challenges for plants (e.g. Delwiche and Cooper 2015). An essential step in colonization of land was evolution of walled (spore-pollenin coated) spores needed for survival in a terrestrial environment (e.g. Graham and Wilcox 2000). Initially all land plants were homosporous, i.e. the sporophyte produced spores of equal size. In many extant homosporous plants, the gametophytes are capable of producing both female gametes in archegonia and male gametes in antheridia (Taylor et al. 2009, Sessa et al. 2016), but evidence suggests that the earliest gametophytes of land plants were dioecious (Taylor et al. 2005). During the Devonian there was a gradual evolution of spore size towards a dimorphism in some groups, such that spores of these plants became either megaspores or microspores (Chaloner 1967). Although there is a complex relationship between spore size and gender (Jesson and Granock-Jones 2012), it is likely that megaspores produced archegonia, thus acting as females, and microspores produced antheridia, thus acting as males (Taylor et al. 2009).

Palaeobotanical evidence suggests that the seed habit established by the Middle to Late Devonian (387.7–358.9 Ma) (Taylor et al. 2009). It is generally recognized that the most significant adaptive advantage of the seed habit is the removal of a dependence of free external water for completing fertilization (Chaloner and Pettitt 1987, Haig and Westoby 1989, Bateman and DiMichele 1994, Niklas 1997). Although it is possible that seeds originated more than once, the current understanding is that all extant seed plants constitute a monophyletic group (Crane 1985, Hilton and Bateman 2006, Wickett et al. 2014). There is an extensive palaeobotanical literature on the evolution of the seed habit (see reviews in: DiMichele et al. 1989, Bateman and DiMichele 1994, Taylor et al. 2009). A common theme in the early literature is that “...the origin of the seed habit has been viewed as the end of a logical progression that began with homosporous, was followed by various forms of heterosporous, and culminated in the structure termed seed” (Taylor et al. 2009: 508), an idea succinctly encapsulated in the title of a paper by Chaloner and Pettitt (1987): “The inevitable seed”. In contrast to the seed habit, heterosporous evolved several (at least 11) times (Bateman and DiMichele 1994). Thus, as far as known, only one of these heterosporous lineages gave rise to extant seed plants. Chaloner and Pettitt (1987) suggested that the trend towards heterosporous was due to increasing competition, favoring ‘K-selected’ traits, such as an increase in spore size. Selection for increasing food resources in the megaspores, available to the embryo, was then ultimately leading to the evolution of the seed.

During the 1980s and early 1990s, evolution of heterosporous and the seed habit received a renewed attention from students outside the field of palaeobotany. This was because the intricacies of plant life cycles were recognized in the context of kin selection theory (Hamilton 1964, Maynard Smith 1964) and theory of sexual selection (Charnov 1979, Willson 1979, Burley and Willson 1983, Stephenson and Bertin 1983). I henceforth describe this as a ‘conflict paradigm’ for the evolution of the seed habit (cf. ‘conflict hypotheses’, in Friedman et al. 2008: 83). The conflict paradigm is based on the idea that different components of the plant life cycle, such as gametophyte and sporophyte generations, male and female gender, or various kin relations (parent and offspring, siblings) are viewed and analyzed on the premise that each component maximizes its own inclusive fitness (e.g. Haig 1987, 1990, Haig and Wilczek 2006). Thus, there may be evolutionary conflicts between different life cycle components. As several kin-conflicts (at least in extant seed plants) take place within the same integrated plant body, the conflict paradigm also implies that different tissues may have conflicting ‘interests’.

I will here argue that there is a missing component in these explanations of the evolution of the seed habit (explained below), and that a more complete understanding can be provided by involving niche construction theory. Niche construction is a process whereby organisms, through their metabolism, their activities, and their choices, modify their own and/or other species niches (Odling-Smee et al. 2003). A key feature of the niche construction process is that there is a continuous reciprocal interaction between the ‘niche constructing agent’ and the environment, over time changing both the niche constructing agent and the environment. The ‘environment’, constituting the niche, may be abiotic, or composed of other organisms, conspecific or other species. Niche construction theory has been used in many different contexts (e.g. Kendal et al. 2011, Odling-Smee et al. 2013, Scott-Phillips et al. 2014, Laland et al. 2015), but only rarely applied to plant life cycles (Donohue 2005, 2013), although not in relation to evolution of the seed habit.

Crucial steps in the evolution of the seed habit

A seed is a fertilized ovule containing an embryo, where the “seed plant ovule is an indehiscent megasporangium surrounded by one or two sheathing integuments termed the seed coat” (Taylor et al. 2009: 508). The evolution of the seed habit involves several steps. Pettitt (1970) summarized these as: (i) reduction of the number of spores per megasporangium; (ii) retention of the megaspore within the megasporangium; (iii) elaboration of the apex of the megasporangium for

pollen reception; (iv) formation of a maternally derived integument. Bateman and DiMichele (1994: Figure 13) elaborated these steps in more detail, and added: (v) development of a perforated distal chamber on the megasporangium; (vi) retention of the megasporangium on the sporophyte until after pollination and fertilization, and (vii) delivery of male gametes to the megasporangium. Bateman and DiMichele (1994) also stressed that a crucial precondition for evolution of the seed habit was the origin of endospory, i.e., development of the male and female gametophytes within the micro- and megaspores respectively.

The structures listed above all make up important features of the seed habit. However, as remarked by Chaloner and Pettitt (1987) and DiMichele et al. (1989), one of these steps is the most essential feature of the seed habit, namely the timing of dispersal in relation to timing of fertilization. In free-sporing heterosporous life cycles, dispersal of megaspores takes place before fertilization. In seed plants, dispersal takes place after fertilization (and development of an embryo). The rationale for choosing this as the most essential feature of the seed habit is that this feature, and only this, definitely liberates plant life cycles from the dependence of free external water for completing the life cycle.

A closer look at the ‘conflict paradigm’ and evolution of the seed habit

A relevant starting point is Haig and Westoby (1988) who discussed the evolution of heterospory, a generally assumed precondition for the evolution of the seed habit (Chaloner and Pettitt 1987, Haig and Westoby 1989, Bateman and DiMichele 1994). Haig and Westoby (1988) suggested that a gradual increase in spore size (as described by Chaloner 1967) implied that, at some point, the costs of producing larger spores reached a limit where it was cheaper to produce small but exclusively male spores. A subsequent divergence in spore size followed. In accordance with ‘Bateman’s principle’ (Bateman 1948) - female fitness is limited by resources and male fitness is limited by the number of eggs fertilized - the two size types of spores were ultimately associated with female function (megaspores) and male function (microspores), respectively. The outcome was that the sporophyte, controlling resource allocation to the spores, produced large female spores (megaspores) and small male spores (microspores).

As mentioned above, the conflict paradigm is based on the idea that different parts of the plant life cycle, or different tissues, depending of their genetic composition and relatedness, maximize their own inclusive fitness and thus potentially have conflicting ‘interests’. Two early papers deal specifically with structures that are part of the maternal sporophyte of seed plants. Westoby and Rice (1982) suggested that the adaptive advantage

of the maternally derived integument is not only (as previously thought) to protect the embryo, but is mainly due to the integument’s function to control the mother’s resource allocation to the embryo, based on the mother’s assessment of the embryo’s vigour. Hence, there is a potential conflict between the mother and different embryos. Furthermore, Queller (1983) suggested that the double fertilization in angiosperms (that produce an endosperm where, in most angiosperms, 2/3 of the genome is maternal) has a similar adaptive advantage for the mother to control resource allocation to the embryo. Thus, both structures (integument, endosperm) are functioning to secure maternal control over resources to embryo development. Studies of angiosperm female gametophytes and endosperm provide empirical support for these hypotheses (e.g. Friedman et al. 2008, Wu et al. 2013).

Haig and Westoby (1989) made a thorough examination of evolution of the seed habit, including a whole suite of its defining features, focusing on the retention of a single megaspore in the megasporangium (see also Haig 1986), the evolution of integuments, and the evolution of features promoting ‘microspore capture’ (pollination). In their model, pollination played a key role (see also DiMichele et al. 1989). Inter-male competition promoted an increasingly effective pollination, in turn affecting features related to microspore (pollen) capture and formation of microspore haustorial tubes (pollen tubes). Various features of the maternal sporophyte were modified in association with pollination, such as adapting the megasporangium apex for pollen reception, and maternal control over resource provisioning to the embryo.

However, development of integument, endosperm and effective pollination all concern features that presume that a megasporangium with a developed female gametophyte, and, after fertilization, an embryo (i.e. what is to become a seed), retained on the maternal sporophyte, is already in place. Accordingly, none of the above-mentioned explanations bears directly on the question why, in the first place, the megasporangium was retained on the sporophyte until after fertilization, thereby effecting the altered timing between fertilization and dispersal. Thus, even though the conflict paradigm indeed may have explanatory power for evolution of integument, endosperm and various features related to pollination, it does not contribute to explain the crucial altering of timing between fertilization and dispersal. As stressed above, this feature is a most essential step in evolution of the seed habit, as it enables the completion of the life cycle without the aid of external water (Chaloner and Pettitt 1987).

One may say that the conflict paradigm is ‘retrospective’ in the sense that it focuses on the adaptive functions and fine-tuning of structures that presume that the change in timing between fertilization

and dispersal has already been established. Some fossil evidence indeed suggests that adaptations for receiving pollen by the megasporangium were not present in the earliest seeds (Galtier and Rowe 1989, Gerrienne et al. 2004). In order to solve this potential dilemma, Haig and Westoby (1989: 224) proposed the following: “Occasionally, a microspore would have settled near a megaspore that was still attached to its parent sporophyte. Fertilization would have been in the interests of both spores, because neither could be guaranteed fertilization at a subsequent encounter. Thus, a minority of fertilizations would have been the result of encounters which occurred before megaspore dispersal. An obligate pollination system could have evolved by such encounters gradually replacing encounters occurring after dispersal as the major cause of fertilization.”

Accordingly, the process leading to the seed habit was initiated by a chance event. Natural selection thereafter operated on genetic variation somehow affecting the likelihood that sporophytes retained megaspores attached to them, and, driven by inter-male competition among microspores for reaching these retained megasporangia, the seed habit evolved. However, a question is: what were the conditions that at some point led these ‘occasional events’ to become a developmental program for megaspore retention on the sporophyte. It is here, I argue, that niche construction enters as a plausible mechanism.

Niche construction: a missing component in the evolution of the seed habit

The mechanism I propose concerns a change in the relative timing of fertilization and dispersal. In contrast to their heterosporous ancestors, in seed plants the female gametophyte is retained on the sporophyte, and dispersal occurs after fertilization and development of an embryo. This could be seen as an example of what Gould (1977) termed ‘heterochrony’, a relative change in timing of developmental events during ontogeny (DiMichele et al. 1989). This term is however merely descriptive. To suggest a mechanism for such an altered timing of ontogenetic events, one may start by a remark made by Bateman and DiMichele (1994: 391): “The biphasic life history of embryophytic plants permits the conspecific sporophyte and gametophyte to have independent ecological preferences and fates, albeit linked by a shared genome.” A free-sporing heterosporous plant potentially has two separate niches, one for the sporophyte and one for the gametophyte, perhaps even three, if one considers the possibility that the male and female gametophytes have different habitat requirements. However, as successful fertilization requires close proximity of male and female gametophytes, it seems likely that both gametophytes

occupy the same ecological niche. Given the importance of free water for successful fertilization, it seems reasonable to assume that abundant free water is the essential environmental factor defining their niche. Despite endosporic gametophyte development, external water is needed for fertilization and thus water is the most likely cue for initiating spore germination and development of the gametophytes.

For plants with a life cycle composed of two alternating generations, a fundamental question is how they can maintain two separate ontogenetic development programs. Some recent studies have shed light on this question (Friedman 2013). Sakakibara et al. (2013) identified a genetic mechanism controlling suppression of gametophyte ontogeny, and concluded that the same genetic ‘toolkit’ was used to control expression of both sporophyte and gametophyte generations. They suggested that this toolkit most likely was present already in the ancestors of land plants (see also Bowman et al. 2016). Also other genes regulating gametophyte-sporophyte transitions have been identified, and, furthermore, the expression of these regulatory genes are controlled epigenetically (Horst et al. 2016, Horst and Reski 2016). The importance of epigenetic mechanisms for regulation of gene expression is increasingly recognized (e.g. Laland et al. 2015), and evidence suggests that environmental factors such as temperature, light and nutrition may influence epigenetic mechanisms, which can be transmitted across generations (Skinner 2015).

It is likely that the gene regulatory toolkit controlling development of the sporophyte and gametophyte generations is also involved in controlling *when* the female gametophyte develops (relative to other life cycle events, for example dispersal), and that there may be heritable variation in the expression of these genes. Referring again to the concept of heterochrony (Gould 1977), one may envisage that retention of the female gametophyte on the sporophyte until after fertilization can be achieved either by (i) delaying megaspore release and dispersal in relation to a fixed timing of development of the female gametophyte and (after fertilization) an embryo, or by (ii) advancing development of the female gametophyte and embryo in relation to a fixed timing of release and dispersal. The result would be the same. A question is what would initiate such a change in the developmental timing?

A transition implying that the female gametophyte generation was ‘internalized’ in the sporophyte (paving the way for fertilization before dispersal), would lead to a functionally unitary individual (Bateman and DiMichele 1994), i.e. the former independent generations, gametophyte and sporophyte, acting ecologically as two different species, become functionally united. This would equal a transition towards a more complex integrated biological structure.

Figure 1. A schematic illustration of the model for evolution of the seed habit. See the text for an explanation of the steps included in the model.

Inspired by the seminal book *The Major Transitions in Evolution* (Maynard Smith and Szathmáry 1997), Kikvidze and Callaway (2009) argued that such transitions, i.e. the emergence of new complex biological structures (such as cells, multicellular organisms etc) are due to positive interactions. With positive interactions, Kikvidze and Callaway implied interactions that were beneficial to both (all) structures that were involved and become merged into a higher order biological structure.

Based on these considerations I suggest the following model for evolution of the seed habit (Figure 1):

- (1) Assume that there is an environmental cue for megaspore germination, i.e. development of the female gametophyte, and that this cue is water availability. Considering the dependence of free water for successful fertilization, this is highly likely. Thus, external water is the environmental factor initiating the expression of genes regulating the developmental program of the female gametophyte.
- (2) Assume that there are strong local ecological gradients in water availability. These gradients could be either spatial or temporal, i.e. seasonally dry environments. The latter may be most likely, since heterosporous plants were associated with fluvial

habitats. In a situation of water stress, the most reliably available water obtainable by a megaspore is associated with the maternal sporophyte. This ecological situation would be analogous to what is commonly found in strongly arid environments, where ‘nurse plants’ facilitate recruitment, both for conspecifics and for other species (e.g. Armas et al. 2011, Pugnaire et al. 2011). In effect, this means that the recruitment niche for the megaspore is constrained to the sporophyte.

- (3) This situation can be described as the sporophyte ‘constructs’ the recruitment niche for the female gametophyte, although this effect initially is an indirect consequence of the strong gradients in water availability. If the recruitment niche in this way is constructed by the sporophyte, there will be an advantage both for the female gametophyte and for the sporophyte to further promote construction of the recruitment niche for the female gametophyte. The reciprocal niche construction process would then further augment changes in the expression of genes in the toolkit for regulating the alternation of the gametophyte and sporophyte generation, promoting the development of the female gametophyte attached to the sporophyte. This implies a positive interaction between the two generations enabling development of an integrated (more complex) structure where the

female gametophyte is internalized in the sporophyte. This step is conceptually similar to what was suggested by Donohue (2013) as ‘developmental niche construction’, meaning that cued developmental transitions determine the environment experienced by subsequent life stages.

- (4) The advent of these early ‘pre-seeds’ enabled completion of the life cycle in drier habitats. In addition, this life cycle has the advantage of reducing the time between dispersal and recruitment of a new sporophyte, since fertilization is already completed. This may have conferred seed plants a competitive advantage in exploiting temporally occurring periods with water availability in seasonally dry habitats. Combined, these advantages led to an expansion/shift of the niche for the sporophytes, i.e. an expansion into a new niche zone characterized by drier soils, where selection further refined the seed habit. As this new niche zone became occupied, the initial dominance of facilitation effects (positive interactions between sporophyte and gametophyte generations) successively were replaced by antagonistic interactions among components of the plant life cycle, leading to refinements such as integumentation, development of endosperm, and a functional pollination system, as suggested by the conflict paradigm.

The model implies that although the conflict paradigm explains several features of the seed habit, it is rather the removal of conflicts that is the key issue for the initial step leading to the seed habit. The structural modifications initially driven by niche construction, i.e. a reciprocal positive feedback between a sporophyte-driven change in the recruitment niche for the female gametophyte, the fitness of the female gametophyte, and the fitness of the sporophyte, provided the arena where kin and sexual conflicts could be played out.

Discussion

A difference between a niche construction model and a ‘standard evolutionary model’ is that niche construction implies that species do not just adapt to an external environment, but also ‘construct’ (at least partly) the environment (Odling-Smee et al. 2003, Laland et al. 2015), i.e. there is a continuous reciprocal interaction between the niche constructing agent and the environment. The model suggested above implies that the sporophyte constructed the niche for the female gametophyte, and thus promoted fitness of both the sporophyte and the gametophyte. As the process continued, the niche constructing agents (i.e. seed plants) were able to expand into new niche space, represented by increasingly dry habitats, further enhancing the process.

The model is based on the assumption that there was an environmental impetus initiating the process, namely strong local, spatial and temporal ecological gradients in water availability. During the Middle and Late Devonian, there was a general transformation of terrestrial ecosystems resulting in a diversification of habitat conditions (DiMichele et al. 1992, Joachimski et al. 2009, Gibling and Davies 2012). Land plants evolved an increasingly diverse range of life forms and, in particular, the evolution of leaves and roots, and the tree habit (arborescence) had major impacts on terrestrial ecosystems, influencing soil formation, hydrology and climate (Algeo and Scheckler 1998, Morris et al. 2015). Tree-dominated vegetation, deep rooting, accumulation of litter and litter degradation created well-drained soil conditions and ecological gradients, including well-drained dry habitats subjected to periodic disturbance (DiMichele et al. 1992, Morris et al. 2015). Thus, the environmental setting during Middle and Late Devonian included the conditions assumed in the model.

Furthermore, when the seed habit had evolved, the possession of seeds functioned as a ‘preadaptation’ (*sensu* DiMichele et al. 1987: 167) for promoting colonization of dry habitats. A corollary of the model is that the seed habit was both a result of (initial) gradients of water availability, a beneficiary of these gradients, and a promoter of ecological gradients due to vegetation on dry soils. During this process, and as new niche zones were filled, the initial dominance of positive interactions between sporophyte and gametophyte generations gave way to a dominance of antagonistic interactions among components of the plant life cycle, as suggested by the conflict paradigm. In turn, this would have spurred a diversification in features of seed plants: “...the ecological fabric of the Late Devonian/Lower Carboniferous selective landscape” (DiMichele et al. 1989: 8).

The suggested model assumes that the genomic toolkit for internalizing ‘the other’ of the alternating generations was already present early in land plant evolution (cf. Bowman et al. 2016, Kenrick 2018). One may recall that such an internalization occurs in bryophytes, but in these plants it is the gametophyte that constructs and provides the environment for development of the sporophyte. What was needed for sporophytes to internalize gametophytes, was an environmental trigger and a mechanism of change. The trigger was environmental stress (drought) and the mechanism was niche construction (by the sporophyte) of a local environment suitable for the development of the female gametophyte within the sporophyte plant body. Microspores disperse randomly (it can be assumed), wherefore some microspores of course landed also on megaspores still attached to sporophytes. This is similar to the suggestion by Haig and Westoby (1989), but with one crucial element added - niche construction

by the sporophyte, enabling the female gametophyte to remain attached to the sporophyte and eventually leading to an altering of the developmental programs of the sporophyte and gametophyte generations. This niche construction removed the ecological independence of the two generations; the sporophyte provided the female gametophyte with a recruitment niche, transforming the biphasic life cycle into a unitary life cycle, and promoted an expansion of the ecological niche zone for land plants, eventually leading to a vegetation covering most parts of the land mass.

Is it possible to test this model? In a recent paper, Rothwell et al. (2014) reviewed and argued for an approach combining recent advances in developmental biology with palaeobiology, to “...infer mechanism by which plant form and development have evolved” (Rothwell et al. 2014: 899). The suggested approach is to combine and correlate identification of regulatory pathways with fossil evidence, and they gave a number of examples concerned with evolution of wood, leaves, and water-conducting tissues (e.g. Xu et al. 2014). Kenrick (2018) discusses a similar approach for studies of the evolution of land plant life cycles. One way forward may be a close examination of the genomic mechanisms behind the development and timing of retention and dispersal of megaspores in extant heterosporous plants, such as *Selaginella*, a genus with a wide range of ecological relationships to water availability (e.g. Korall and Kenrick 2004). A question would be whether external factors, for example drought, could influence the epigenetic mechanisms controlling the expression of genes regulating the timing of dispersal vs. development of the female gametophyte. Given the tools now available in molecular biology, the ultimate test would be to investigate whether it is possible to induce the first steps towards transforming *Selaginella* into a seed plant.

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