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INTERACTIONS WITH THE ENVIRONMENT DURING PLANT SEXUAL REPRODUCTION AND DISPERSAL
CONSEQUENCES FOR THE CONCEPT OF SEXUAL REPRODUCTION AND LIFE

MICHIEL T.M. WILLEMSE*

Laboratory of Plant Cytology and Morphology, Wageningen University, Arboretumlaan 4, 6703 BD Wageningen, The Netherlands

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The interaction between seed plants and animals during pollination and fruit and seed dispersal is well known, and marks the sexual reproduction process. During the history of the plant kingdom, the development of sexual reproduction has been governed by changes in the environment of the plant, together with the increasing complexity of organisms. The interactions between gametes and the environment are prepared during gametogenesis, and therefore reproduction and dispersal are related from the beginning. The dynamic environment should be considered as an interactive partner. The more intensive interactions in multicellular organisms make the interaction in seed plants far more complex. Sexual reproduction plays a key role in the progress of the interaction between the dynamic environment and the biosphere. Sexual reproduction embodies the renewal and dispersal of organisms. This means that the interactions between organisms and their environment are not only an essential element of sexual reproduction but also a characteristic of life, based on the unity of organism and environment. The driving force of the increasing complexity of life is the dynamic environment and the persisting organism.

Key words: Pollination, sexual reproduction, environment, interaction.

SEXUAL REPRODUCTION AND INTERACTION

The process of sexual reproduction is a sequence of events that depend on interactions. In water, gametes have to be prepared for fusion, and the zygote has to be dispersed. On land, the seed plant, a sporophyte, develops and cooperates with the male and female gametophytes, resulting in the production of pollen and an embryo sac. Pollen dispersal is dependent on environmental vectors. After pollination there is again an interaction between gametophyte and sporophyte, leading to cross-pollination and fertilization. The development of the seed, the new sporophyte, also depends on the regulation and nutrition of the former sporophyte, and prepares for dispersal in the environment. Thus, in seed plants there is strong interaction between the sporophyte, gametophytes and the environment.

A well-known interaction with the environment is pollination and fruit and seed dispersal. Pollination scenarios reveal a sequence of interplay between plants and animals. Such interplay can occur between a plant and one specialized animal, but most plants have a wider range of pollination vectors. Seed and fruit dispersal can also involve specialists or generalists. Next to biotic pollination and seed and fruit dispersal, there are abiotic vectors such as gravity, wind or water. Both pollination and fruit and seed dispersal are very complex interactions between the biotic and abiotic environments.

Pollination or dispersal can be observed easily, but how does this interplay originate and develop? Attempts at an answer should point to the history of interaction between the organism and its environment.

This essay addresses the interactions between the organism and the environment during the development of sexual reproduction. Interaction is considered as a characteristic of life, based on the unity of organism and environment.

SEXUAL REPRODUCTION AND HISTORY

Sexual reproduction is a complex process in the plant kingdom. Originally, sexual reproduction developed in an aqueous environment. The conquest of the land added many other types of environments which invited organisms to form biotopes. Since the environment changes continuously, the diversity of orga- nisms increases, as does the variety of reproduction mechanisms.

*e-mail: MTM.Willemse@hccnet.nl

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Prokaryotes have asexual reproduction by simple cell fission. This means cell duplication with complete cell isolation. Each new cell starts its life cycle. Cell fusion followed by gene transfer is well known in bacteria. Cell fusion is a very basic process which also occurs in sexual reproduction in eukaryotes.

Eukaryotes reproduce asexually by cell division, that is, mitosis with complete cytokinesis to isolate the cell. Next, eukaryotes develop sexual reproduction. The diploid cell or diplont produces, after meiosis, an isolated haploid cell, the gamete, with the ability to fuse. Two gametes fuse to form a zygote, a renewed cell for dispersal of the new organism. The rate of renewal of the organism is enhanced by cross-fertilization. Unicellular algae represent the basic pattern of the process of sexual reproduction.

In the plant kingdom, algae have visible gametes and even simple organs to produce these cells. Gametes are set free in water and are able to fuse. After fertilization, dispersal by a zygote or spore occurs in conjunction with abiotic factors such as gravity, water and wind, but seldom with biotic factors. The increase in storage of one of the gametes is the first change in the sexual reproduction system leading to oogamy. This female gamete is set free or can stay on the mother plant in a simple sexual organ. Important is the introduction of alternation of generations, the ability to generate more than one organism in one life cycle, as in some algae and mosses and ferns. Such organisms use each one-cellular stage – the haploid cell after meiosis, the zygote after gamete fusion – to form a new organism. The haploid cell forms the gametophyte and the zygote the sporophyte. Mosses and ferns need an aqueous environment for the mobile male gamete to swim to the oocyte in the archegonium present on the gametophyte. After fertilization, the zygote develops the sporophyte for spore dispersal, with the help of the gametophyte. Seed plants hide their gametes and organs but expose additional sex characteristics by means of the flower. Wind or animals are the main factors for pollen transfer, and seed dispersal occurs mainly by gravity, wind and animals.

The transition in the plant kingdom from water to land, and from a unicellular organism to a cormophyte, lays the foundations of a history. Sexual plant reproduction is a dynamic process, leading to cell fusion and renewal of the organism, involving several mechanisms. Continuous changes of environment or the dynamism of the environment are a driving force to develop new biotopes.

SEXUAL REPRODUCTION AND ENVIRONMENT

UNICELLULAR ORGANISMS

The main features of sexual reproduction in a unicellular organism are the preparation of a haploid cell by meiosis and the ability to fuse. When two isomorphic cells fuse to form a zygote as a unit of dispersal, and this zygote immediately undergoes a meiosis, it becomes very difficult to distinguish the haploid cells as vegetative cells or sexual + and – gametes. This manner of sexual reproduction, isogamy, is the most basic type.

The origin of sexual reproduction includes not only the onset of meiosis leading to the formation of an isolated haploid cell able to fuse, but also preparation of the dispersal of the renewed zygote. From its origin the sexual reproduction process is related to environmental conditions. Gamete movement, gamete attraction and zygote dispersal are clear examples.

A factor oriented on outside events is the gamete's ability to move in water. During gametogenesis a mobile male cell and an immobile female cell can be formed. This has consequences for the position of the female cell in water, and may influence both the manner of approach of the male gamete and the manner of dispersal of the zygote.

The gamete is set free in the environment and should reach its partner. This is realized by attraction by the partner or, without attraction, by the production of a high number of gametes. The probability of fusion is enhanced if the timing and location of sexual cell release facilitates close contact between gametes.

The zygote is a free cell and should reach a good place by dispersal. Zygote dispersal takes place in water, as a mobile cell by flagella or as an immobile one by water streaming or circulation. If the zygote needs extra stored food to germinate, one of the gametes will be enlarged, called the female. Such differentiation is related to the onset of germination, but has also an effect on the manner of dispersal: gravity has a great influence, and an enlarged cell will have a different position in the environment than a smaller one. A large immobile zygote will sink to the bottom in an aqueous environment.

The preparation of a gamete to fuse and disperse means that gametogenesis is a developmental process oriented on further events outside the plant in the surrounding environment. For algae, mosses and ferns, the surrounding environment is water.

The sexual reproduction process also requires the organism to prepare for interplay with the surroundings. Sexual reproduction and dispersal are connected to each other from the beginning. Studies of the sexual reproduction process are generally focused on gametogenesis and the fusion to form a zygote, but too little on the preparation for its dispersal. During gametogenesis the preparation for dispersal already takes place.

The process of sexual reproduction involves the interplay between two gametes as partners, but the interplay with its surrounding environment, water for example, is crucial. In this view, sexual reproduction is completed by two gametes in tandem with the environment. There is interaction of each sex cell with the water environment, and interaction between the gametes. In

fact there are three components cooperating in sexual reproduction: two gametes and one environment, interplay between three partners. After fertilization, two partners interact: the zygote and the environment.

Interaction with the environment during gamete fusion and zygote dispersal marks the sexual reproduction process. The environment should be considered a partner.

MULTICELLULAR ORGANISMS

Multicellular organisms gain a higher level of differentiation and express different functions. In some algae, mosses and ferns, one of the expressions of such higher differentiation is the formation of a sexual organ on the plant, in which sex differentiation becomes visible. Such an organ is made to release or to receive gametes, and is equipped to interact with the water environment. Organs can make mobile male gametes (spermatozoids), immobile male gametes (spermatia), or one or more immobile female gametes (oocytes).

In some algae, all mosses and ferns, a free oocyte can remain, even after oogamy, in the sex organ on the mother plant. In fact, the mother plant prepares an organ to develop each of the gametes for fusion and dispersal. In algae such an organ is the oogonium, whereas in ferns and mosses it is the archegonium. Retention of the sex organ on the mother plant means a change in the environment of the oocyte. The oocyte is an isolated cell in the sex organ, and is surrounded by a water film. The spermatozoid has to swim towards the sex organ containing the oocyte and attracting the male gamete. The interaction process in water remains the same for both gametes. Mosses and ferns also need water for fertilization, but the zygote formed remains on the mother plant in the archegonium. With the help of the surrounding tissues of the mother plant, the zygote develops the sporophyte to function in spore dispersal.

In the aqueous environment, autotrophy and heterotrophy develop through the emergence of the prokaryotes, plants and animals; the plants participate as producer and nutrient source, the animals as consumers. The use of nutrients is the earliest interaction with the environment shown by animals. The use of animals for spore dispersal is rare. A positive interaction in spore dispersal is illustrated by the relationship between red algae and the Crustacea that eat them. Mosses have an exceptional level of cooperation with insects. The open yellow sporangium of Splachnaceae, growing on dung, attracts flies by color. The flies land on the sporangium and eat and disperse the moss spores to the dung.

A nice example of the response to the dynamic environment is the ability to generate alternation of generations, as in some algae and in mosses, ferns and seed plants. The development of sporophyte and gametophyte promotes the separation of different functions of the organism, and organisms' ability to live in different environments.

The history of the earth is characterized by dynamic development of the environment, offering new biotopes. If organisms fit into or explore the environment, they should have the ability to interact with it. This means that the dynamic environment elicits changes in organisms. Environment and organism interact, and both cause new conditions such as an increasing level of oxygen or the appearance or disappearance of organisms. The dynamic environment is a driving force in the development of the biosphere. Sexual reproduction plays a key role in this cooperative process.

SEED PLANTS

The seed plants that conquered the land were characterized by multicellular construction, a higher level of differentiation, oogamy, and alternation of generations. All these elements are already developed in algae (Willemse, 1985, 2003), and all involve interplay with the dynamic abiotic and biotic environments. To stay on land, seed plants intensified the development of gametophytes on the sporophyte in the flower bud. The water environment for fertilization gradually would be lost. In pollen and diaspore dispersal, a complex interaction between environment and seed plant would develop.

Seed plants on land, in biotic and abiotic environments, began to offer a localized nutrient source, with carbohydrates, some proteins and lipids, such as in nectaries. With the appearance of the sexual organ from a generative apex on the plant axis and the combination with nectaries, the plant could direct animals, in early periods the insects, to consume the nutrients. In gymnosperms, a special construction of the cone is adapted for wind pollination. The gymnosperm *Ephedra* sp. attracts and feed flies with a shining pollination droplet in combination with the yellow color of the cone (Bino et al., 1985). In angiosperms, the odor, form and color attract and permit animals to pollinate. The nectary, and also pollen and oil in the open flower, offer nutrients to animals, mainly insects. The nectary is located together with the anther and stigma in a pollination route promoting cross-pollination. A small number of angiosperms use wind as the main pollination vector. The interaction with animals for seed dispersal became elaborated in a more recent period with the involvement of larger animals (van der Pijl, 1982). Here, the ripe fruit attracts with its odor, color and form, and offers nutrients. Most angiosperms disperse fruit and seeds by wind, gravity and sometimes water. In seed plants, pollination and dispersal are a further elaboration of the interaction with the dynamic environment.

The life of seed plants on land also changed the environment of the male and female gametes. To become independent of free water, the cytoplasm in the pollen tube and synergid provides the pathway for

transport of the generative cell and, after division, of the immobile male gametes. Gymnosperms have an egg cell fixed in a large gametophyte, which is surrounded by the mother plant. Angiosperms have an initial cell as the egg cell (Favre-Duchartre, 1984) fixed in a small gametophyte surrounded by the mother plant. Complete differentiation into a mobile male gamete and a large egg cell and large gametophyte is interrupted in angiosperms.

Seed plants intensify the interaction between sporophyte and gametophyte and with the environment. The sporophyte takes over many functions of the gametophyte, and the gametophyte gains a high level of differentiation. The dynamic environment on land leads to intensive interaction between plants and animals. The gradual development of the exosphere interacts with the gradual development of the biosphere. The continuation and intensification of interaction between organism and environment occur via reproduction. Sexual reproduction has the potential for renewal of the organism through changes in the genome and through dispersal, to achieve modifications and adaptations in cooperation with the dynamic environment. Sexual reproduction is renewal and dispersal.

SEXUAL REPRODUCTION AND THE DYNAMIC UNITY OF ORGANISM AND ENVIRONMENT

Since the origin of sexual reproduction, the interaction with the environment is conspicuous. Organisms interact with each other because they are part of the same environment. Sexual reproduction results in a renewed organism, which is able to persist in a dynamic environment in continuous contact with the biotic and abiotic environments. Increasing variety of environments leads to higher diversity of organisms and a higher level of interaction. Interaction is an essential element in the process of reproduction and maintenance. From the origin of life there has been interaction between organism and environment. This leads to the statement that interaction should be added to the series of functions that characterizes what we call 'life,' such as assimilation, respiration, movement and reproduction. A prerequisite of this interaction is the ability to communicate, which is also valuable for the other life characteristics.

The process of sexual reproduction plays a key role in the continuation of life and the persistence of the organism. Changes in biotope conditions meant that the organism had to change to persist. The more complex the environment, the more complex should be the organism and therefore the more intense the interaction. Such dependence expresses the unity of organism and environment.

The difference between the organism and the environment is clear; nevertheless, organisms have a dynamic interaction with the environment and both are dependent on each other. Even a unicellular organism has characteristics with respect to the environment, such as cell polarity, expressed, for example, in the position of the chloroplast in photosynthesis, the eyespot in orientation, or the flagella in movement. Some unicellular algae have a diurnal rhythm expressed in their position in the water. Moreover, a unicellular organism uses the environment for oxygen, nutrients and transport. Pollination and diaspore dispersal illustrate the interaction between plant and environment with animals on land. Fascinating examples of the cooperation between animal and plant in pollination and diaspore dispersal are reflected in the composition of the angiosperm inflorescence and flower.

The interaction between organism and environment from the origin of life includes the potency of communication of life, based on the unity and divesity between organism and environment. The abilities to assimilate, to respire, to move, to reproduce and to interact, all characteristics of life, reflect this communication. The answer to the origin of the interactions during pollination and seed and fruit dispersal is that interaction is a characteristic of life.

The dynamic unity between organism and environment is a prerequisite for the maintenance of life. The dynamic environment and the persistence of organisms are the driving forces behind the increasing complexity of life.

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