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Evolution of plant reproduction: From fusion and dispersal to interaction and communication

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Based on the existing data concerning the evolution of the sexual reproduction, it is argued that the processes of sex differentiation and interactions play a key role in evolution. From the beginning environment and organism are unified. In a changing dynamic environment life originates and the interaction between life and environment develops from simple to more complex organisms. Sexual reproduction is introduced after the origin of meiosis and is a key process in evolution. The asexual reproduction process prepares to dispersal. Sexual reproduction process adds the genome renewal and the gamete-gamete interaction. Reproduction and dispersal are connected and the process of reproduction has similarities between asexual and sexual reproduction. Unicellular algae develop the physiological and morphological sex differentiation. Sex differentiation is connected with the way of dispersal. The step to multicellular plants introduces cell isolation after meiosis and by the stay on the mother plant within a cell or organ, plant-cell apoplastic interaction originates and by prolonged stay the plant-plant interaction. This stay influences the type of dispersal. A life cycle with alternation of generations and two moments of dispersal permits plants to go on land. In ferns a shift in the moment of sex differentiation to meiospore happens and the stay of the macrospore leads to the seed plants. In water all types of sexual reproduction, interactions and the alternation of generations are prepared and these are used to conquest land. On land the biotic dispersal is realized. The phylogeny of sexual reproduction reveals that the sex differentiation and interaction are the main causes in the evolution of sexual reproduction. Sexual reproduction shows interactions during gamete fusion, between organism and environment and in multicellular plants between organisms. With respect to other types of interaction as in symbiosis or the nutrient chain, interaction is considered as an important action which is based on a persisting cooperation and points to a push during evolution. The push is expressed as communication: the driving force in the evolution. Based on the interactions between organisms and interactions between organisms and the dynamic environment, communication is considered as a driving force leading to the evolution as explained in the development of plant reproduction. Consequences for reproduction, its regulation and the process of evolution are discussed.

Plant reproduction, dispersal, sex differentiation, cell isolation, interaction, phylogeny, evolution, communication

As a result of the comparison of living and extinct organisms and their embryology as well as their appearance in the earth history, it is considered that the origin of life develops in water and thereafter conquests land. From the origin of the cell and prebiotic life, unicellular organisms develop. Subsequently simple multicellular organisms arise and they develop organs with different functions. All these events happen in and are driven by a dynamic environment. In a biotope both environment and organism interact in a continuous changing process leading to a still higher level of complexity. A very important key in the development of life is the origin of the cell division, mitosis with cytokinesis, by which organisms can multiply asexually. Later the meiosis with recombination and formation of four haploid cells pre-

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pares the sexual reproduction with the ability to renew the genome by recombination and after gamete fusion by the complementation of the genomes. Reproduction includes the dispersal of the organism to stay but also to invade a new biotope. Sexual reproduction and dispersal play a key role in the development of life. Plants develop in water from autotrophic prokaryotes to eukaryotic, autotrophic unicellular organisms. From unicellular the multicellular organisms arise by mitosis followed by cell wall contact only, colonies with apoplastic contact, and with cell wall contact and plasmodesmata or pores, the multicellular plants, symplastic contact. The plant autotrophy permits the existence of heterotrophic organisms by oxygen supply and other nutrients and is the primary producer of the nutrient chain. Plant reproduction in water is asexual or sexual and dispersal runs by a unit of dispersal, a spore or zygote respectively, using gravity and water streaming as transport vectors. The life cycle of algae shows a transition of isogamy to oogamy and alternation of generations originates. Land plants inherit the life cycle with alternation of generations and oogamy and use gravity, wind streaming and animals as transport vectors. A common tendency in the development of life is the potency of the diploidy leading to higher levels of differentiation[1].

This paper follows the main events of development of reproduction in water and land, from algae to seed plants[2–5]. Both sexual reproduction and dispersal will be considered as two aspects of the reproduction process. Sexual differentiation is expressed in a physiological and morphological way and the shift of the moment of sex differentiation and influences the dispersal. In multicellular plants the cell isolation after mitosis or meiosis evokes apoplastic interactions after the stay of the cell which has an effect on the type of dispersal. In water most aspects of reproduction are completed and via the life cycle with alternation of generations used during the conquest of land. The lines in the phylogeny of reproduction reveal the sex differentiation and interactions as main processes during the evolution of sexual reproduction. On the base of these interactions and other interactions between organisms and the environment it is postulated that communication can be considered as a driving force during evolution. This other view is discussed with respect to running reproduction research and the evolution.

1 Reproduction process

1.1 Definition

Reproduction enables an organism to multiply and to disperse. There are two types of reproduction: asexual and sexual reproduction. Asexual reproduction runs after mitosis and spores with the same genome and is directed to dispersal. Sexual reproduction depends on meiosis with the crossing-over and recombination and gametes are formed and set free. After the gametes fusion a zygote with a renewed genome is formed and is the unit of dispersal for the new plant. The process is directed to genome renewal and dispersal. Reproduction is the preparation of spore or gametes for dispersal.

1.2 Process

The process leading to asexual reproduction is marked by the following subsequent stages: induction, mitosis with cell isolation, spore differentiation, dispersal and settlement. For sexual reproduction the stages are: induction, meiosis with cell isolation, gamete differentiation, fertilization, dispersal and settlement. Both the asexual and sexual reproduction processes have some similarities in common, especially directed to the preparation of dispersal. In the induction stage factors involved are the photoperiod, temperature, nutrients as exogenous influences, endogenous are the genes, hormones, maturity, condition and biorhythm of the organism. After induction mitosis or meiosis takes place and is followed by cell isolation. During the division cell polarity such as the position of the nucleus and cell organelles is stated. The unicellular organisms are characterized by the continuous cell isolation. In multicellular organisms the cell isolation should be prepared and is considered as a crucial step after mitosis or meiosis leading to interaction. The differentiation stage is directed to preparation of the unit of dispersal for both types of reproduction. For the unit of dispersal it means: the transport, mobile or immobile; the storage of carbohydrates, fats or proteins, to rest and to start the new organism; the protection, by a cell wall and finally the adhesion by glue excretion. For sexual reproduction the differentiation stage realizes the special functions of the gamete: attraction, recognition and fusion. To promote cross fertilization the recognition is involved and selfing is prevented. During fertilization the gametes fuse with their membranes and plasmo- and karyogamy follows, leading to the complementation of the genome and in the new diploid nucleus the sex is determined. After the sex determination the sex differentiation will express the final type of gamete of the organism. The process of sexual reproduction prepares a selective cell-cell interaction. The stages of dispersal include the release of the unit of dispersal. An active transport can be organized by the organism itself. Transfers by vectors are abiotic by gravity and streaming of water or wind, and biotic by animals. Settlement includes the adhesion to the substrate by excretion of glue.

The simplest way of reproduction happens in mobile unicellular plants in water. After induction and mitosis, including complete cell isolation, the mobile spore is complete. In case of sexual reproduction after induction and meiosis equal or isogametes prepared to fertilization are formed. In unicellular plants one gamete can store nutrients and this differentiation leads to an anisogamete. In multicellular plants the reproduction process commonly passes through all stages. The process can run in a special cell or organ, for a spore it is a sporangium, for a gamete, a gametangium. In axial red algae the female pathway of the reproduction process runs endogenous and a haploid cell functions as female gamete. On land the higher fungi, Ascomycetes and Basidiomycetes have a complete endogenous sexual reproduction without gametes. After the dikaryotic phase by plasmogamy, within the organism the nuclei will fuse and form a diploid nucleus which divides by meiosis to form meiospores.

This basal view on reproduction reveals that there are comparable stages in the process of asexual and sexual reproduction. The preparations to dispersal have common characteristics since the differentiation is directed to a vector. The preparation to dispersal runs together with the preparation to a spore or gamete and makes the reproduction process a complex of preparation to dispersal and the renewal after sexual reproduction. This includes also that the reproduction process remains directed to the dynamic external environment, therefore to be considered as an interaction process with the environment. Next to this external interaction there is an internal interaction. Due to the moment of cell isolation in multicellular plants an interaction between the mother plant and the isolated cell is present: plant-cell interaction. In case the isolated cell develops further on the plant, the plant-cell interaction changes into a plant-plant interaction. Plant-cell and plant-plant interactions run via the apoplast in a special organ, a sporangium of gametangium. The apoplast consists of the intercellular space with fluid or gas and cell wall there is no direct cell-cell contact with plasmodesmata as in a symplast.

2 Reproduction in water

Life develops in water from simple membrane bound nucleic acid containing compartments to prokaryotic unicellular organisms. The membrane system is elaborated and autotrophic bacteria arise and in line of these the multicellular larger Cyanobacteria. By repeated endocytosis, the symbiotic theory, several types of prokaryotic organisms are encapsulated and this is considered as a basis for an eukaryotic plant cell. Asexual reproduction by binary fission is the main way of multiplication, although bacterial plasmids are able to membrane fusion, which happens also in sexual reproduction.

2.1 Asexual reproduction

Asexual reproduction in algae runs by several spore types: unicellular mobile or immobile spores and multicellular immobile fragments, such as propagula. The mobile spores have an active dispersal, immobile spores use water streaming and gravity as vector. Gravity will become the main vector in case the immobile spore enlarges by storage. Next to this effect of cell enlargement on the way of dispersal, the storage enables the spore to a rest and to settle. In some algae the asexual reproduction runs by parthenogenesis and apomixes, the routing towards the dispersal via sexual reproduction is used but there is sporogenesis instead of gametogenesis. Spores can be formed in a sporangium and in this organ the cells become isolated. After complete cell isolation the further development of the cell is governed by the mother plant and the nutrients and signals run via the apoplast and the sporangium opens after ripening of the spore.

2.2 Sexual reproduction

Sexual reproduction in unicellular algae has mobile, enlarged mobile or immobile types of gametes. Equal gametes, isogametes, are recognized by their ability to fuse and one of the most fundamental characteristics is this gamete-gamete interaction. There is physiological sex differentiation after meiosis leading to “+” and “–” gametes. The zygote remains mobile and has active dispersal. In case one of the mobile gametes enlarges by storage, there are unequal or anisogametes both with

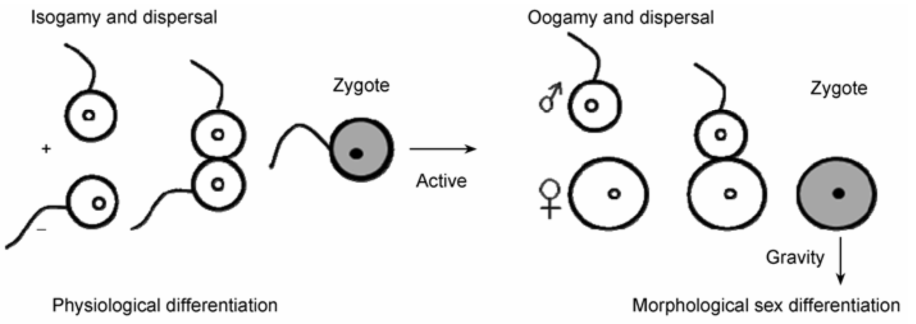

Figure 1 Representation of the basal process of sexual reproduction. Haploid gametes fuse and form a zygote. Depending on the expression of sex differentiation the way of dispersal is directed to gravity.

active dispersal. In this way there is a morphological sex differentiation, a female gamete enlarges by storage and contributes the most to the zygote condition and its dispersal. Commonly this zygote is mobile and has active dispersal. In case the anisogamete becomes immobile an oocyte is formed and will use gravity as dispersal vector. Here again the enlargement of the cell has a direct effect on the way of zygote dispersal. The zygote is able to rest. Figure 1 represents the basic pattern of sexual reproduction and dispersal.

In multicellular algae after meiosis, there is cell isolation to start gametogenesis. The same types of gametes and fusion are formed as in unicellular plants. In some algae there is a special organ in which the gamete develops the gametangium. A gametangium can be a simple cell or more elaborated as is present in the larger algae as *Charales*, and *Fucales*. After meiosis the gametes become isolated from the mother plant and in the gametangium a plant-cell interaction takes place. The mother plant supplies nutrients and probably signals via the apoplast to the differentiating gamete. The differentiation to an oocyte is the result of the enlargement by storage products and has a direct effect on the way of dispersal. After fertilization by oogamy, the zygote uses the gravity as vector and will settle on the substrate.

2.3 Alternation of generations

Algae have a life cycle with iso-, aniso, or oogamy and from the zygote the new plant develops. The life cycle of multicellular plants has two moments of a unicellular stage: the isolated meiotic cell, the onset for the gametogenesis, and the zygote after fertilization, the onset for the new plant. In case in such a life cycle the unicellular meiospore also develops to a plant, there are two plants within one life cycle, this is called a life cycle with alternation of generations. In such a life cycle each unicellular stage forms a multicellular organism. The cycle has two plants with a haploid and subsequently a diploid genome: the haplont and the diplont. Each organism is adapted to its environment and has its own way of dispersal. There is a difference in function between the haplont and diplont. Only the haplont is able to form the gametes and is called the gametophyte and after the fertilization the zygospore is formed. The diplont makes after meiosis the meiospores and therefore called the sporophyte. Alternation of generations permits the plant to multiply the periods of dispersal and to change the way of dispersal within one life cycle. In some algae there is one period with small mobile meiospores with active dispersal and another one by an enlarged immobile zygote with gravity dispersal. These extended periods and ways of dispersal make it possible to invade another type of biotope. Both plants, the gametophyte and sporophyte can have the same form, but there are life cycles in which the plants differ in form. Both plants can have the same functions but only the gametophyte produces gametes and the sporophyte meiospores. In some algae the sporophyte and gametophyte differ in form and function. The life cycle with alternation of generations permits also a shift of the moment of sex differentiation, which begins during the meiospore formation. The meiospores are similar but have physiological sex differentiation. In algae are several types of life cycles with alternation of generations. On the sporophyte the meiospores develop, but in case the physiological sex differentiation takes place and + and - meiospores are formed, one will develop a male gametophyte and another one the female gametophyte. The sex differentiation begins on the sporophyte so the sex differentiation shifts to an earlier moment in the life cycle. A next step in the life cycle is the stay and further development of the oocyte on the gametophyte. As example in *Laminaria sp.* the oocyte will stay on the ga-

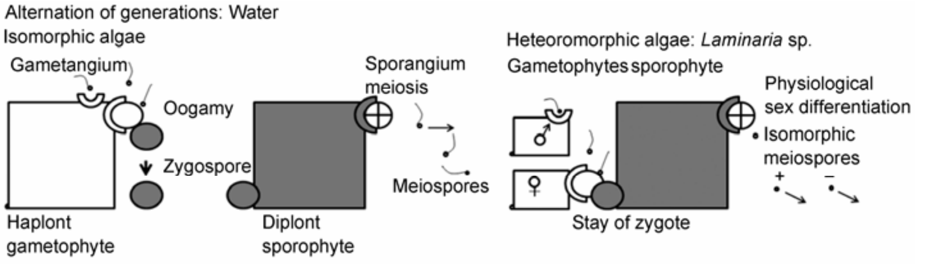

Figure 2 Alternation of generations, each unicellular stage forms an organism. In isomorphic algae sex differentiation takes place on the gametophyte. Heteromorphic algae with alternation of generations have physiological sex differentiation of the meiospores on the sporophyte and the stay of the zygote on the gametophyte.

metophyte after fertilization and on the female gametophyte the new sporophyte develops. Such stay of the zygote and its further development on the female gametophyte result in a plant-plant interaction via the apoplast. The settlement of the sporophyte is determined by the + meiospore which forms the female gametophyte. Figure 2 represents the life cycle with alternation of generations of isomorphic and heteromorphic algae.

2.4 From water to land

In water the ways of sexual reproduction and ways of dispersal are prepared to conquest land. From unicellular plants, with isogamy and sex differentiation leading to anisogamy and oogamy, the multicellular plants develop. The origin of an oocyte and oogamy has a consequence of the gravity dispersal of the zygote. On multicellular plants after meiotic division an isolated cell originates and some algae develop a simple gametangium in which the nutrient supply and signals from the mother plant run via the apoplast to the isolated gamete: plant-cell interaction. In case the zygote develops further to a plant in the gametangium, the plant-plant interaction follows the plant-cell interaction. The way of dispersal is active or uses water streaming and gravity. The alternation of generations permits the plant to different moments of dispersal and the invasion in another biotope. After the origin of multicellular algae the sequences in key moments of sexual reproduction towards land are: gametangium formation, meiosis, sex differentiation, cell isolation, plant-cell to plant-plant interaction, oogamy, zygote dispersal by gravity and origin of a life cycle with alternation of generations.

3 Reproduction on land

Land plants inherit the life cycle with alternation of generations, the way of asexual and sexual reproduction by oogamy as prepared in water[6]. The dispersal becomes directed to the land conditions.

3.1 Asexual reproduction

Asexual reproduction runs by spores, transported by wind. Spores are small and have a thick pigmented cell wall protecting against light and desiccation and have a metabolism persisting drought and cold. Multicellular spores or specialized organs such as gemmae are mainly transported by gravity or water and settle and germinate. In some ferns root buds, stolons, vivipary or fragmentation are present. In seed plants nodal cells organize structures such as axial buds, bulbils, or they have vivipary. On land most asexual units of dispersal are immobile and active dispersal is rare. In multicellular organized structures the external covering protects the unit of dispersal. Most of the structures have storage and are able to rest, to settle and germinate. In seed plants apomixis happens frequently. Apomixis is the only asexual way of reproduction by using the interplay of the sporophyte with the biotic vectors.

3.2 Sexual reproduction

In the sexual reproduction of early land plants, with alternation of generations and plant-plant interactions, gametes are formed in gametangia and the oocyte will stay and develop to a sporophyte after fertilization. The oogamy needs water because of the mobile male gamete. The dispersal runs by immobile meiospores which use the streaming of wind and gradually by gravity.

In the life cycle of mosses the main autotrophic plant is the gametophyte with some protection against water loss and a simple transport- and strength system. After fertilization the sporophyte develops connected with the gametophyte and functions in meiospore production and dispersal. The capsule is elevated and by drought and wind the meiospores are set free. In exceptional cases there is biotic dispersal by dung flies as in *Splanchnum.sp.* In contrast with the mosses, the fern sporophyte is the well differentiated autotrophic plant.

3.3 Ferns

In ferns the autotrophic gametophyte functions are gradually restricted to mainly gametes formation and realization of fertilization which depends on the presence of free water. The sporophyte develops to an autotrophic plant, well protected against water loss, with storage and a good transport and strength system and cares for meiospore dispersal. The ferns are considered as the first land plants preceding the seed plants because the sporophyte is the main autotrophic plant in the life cycle as in seed plants. The life cycle of homosporic ferns has small autotrophic gametophytes with simple gametangia, the antheridia with mobile male gametes and archegonia with one oocyte. The fertilization needs water and the zygote is not dispersed but develops on the gametophyte to a large autotrophic plant. This sporophyte develops sporangia to develop and disperse meiospores. Meiospores are small and use mainly the wind dispersal but will fall down by gravity. In the *Equisetales*, the physiological sex differentiation leads to equal meiospores to form a male or a female gametophyte. This means a shift in the moments of sex differentiation during meiosporogenesis on the sporophyte. The dispersal of these isospores happens joined together by the elaters to avoid a too long distance between the spores. Heterosporic ferns have morphological sex differentiation and form enlarged female meiospores, macrospores and small male meiospores, microspores. The difference is also expressed in the difference in the volume of the sporangia. The sporophyte supplies nutrients and signals via apoplastic plant-cell interaction to the developing spores. The microspore remains small and is dispersed by wind and will fall down by gravity. The macrospore gets extra nutrient supply and stores nutrients and enlarges. After set free of the macrospore the enlargement by storage evokes transport by gravity. Since after fertilization the new sporophyte will develop on the small autotrophic female gametophyte, the macrospore determines the new place in a biotope for this fern. In fact there is a risk in the dispersal of the wind transported microspore and gravity transported macrospore. The microspore will germinate and form the microgametophyte which produces mobile male gametes to swim to the oocyte in an archegonium developed on the female gametophyte from the macrospore. Although there are attractants produced by the female gametophyte, the distance influences the action of the signal and can be too long and no fertilization occurs. In *Hydropterides* with heterospory and dispersal on land or in water the distance between the micro- and macrospores is reduced by several types for a collective dispersal, such as strands or hooks. Remarkable are their more elaborated sporangia around the microspores and macrospores.

3.4 Seed plants

The extinct seed ferns are the next step towards seed plants[7]. The important feature of seed ferns is the stay of the macrospore on the sporophyte in a macrosporangium. This stay means the continuation of the plant-plant interaction after the fertilization to form a seed as unit of dispersal. There is again a risk to realize fertilization. The first aspect is to direct a microspore dispersed by wind towards the female gametophyte with oocyte which is positioned on the plant above the ground level. A second aspect is the need of water to let swim the mobile male gamete. In ferns the abiotic way of dispersal by sex differentiated spores plays an important role[8]. With the origin of seed ferns the changes in the dynamic environment are also caused by the presence of animals. The shift of the moment of sex differentiation with the physiological sex differentiation and the morphological sex differentiation with the stay and development of the macrospore on the sporophyte are the main events to develop the seed dispersal.

3.5 Gymnosperms

In gymnosperms the transfer of the microspores towards the female gametangium and the arrival of the mobile male gamete become elaborated. Like the stay on the sporophyte of the macrospore and the development to a macrogametophyte in a sporangium, now called the ovule also the microspore stays on the sporophyte and develops to a microgametophyte in a sporangium, called the anther. The plant-cell interaction of the meiospore is transferred in the plant-plant interaction and both gametophytes become heterotrophic. The anther releases the microgametophyte, called pollen. The sporangia with male and female gametophytes are positioned on scales in different cones. Small pollens are dispersed by wind and able to stay long in the air by upwards transport. Occasionally as in *Ephedra.sp.* is the pollination by animals attracted by yellow color of the flower and shining drop in the micropyle of the ovule. The construction of the female cone enhances a directed pick up of the wind dispersed pollen to the micropyle of an ovule. Here the pollen forms a tube towards the micro-gametophyte with an archegonium and large oocyte. In the tube mobile (*Ginkgo* sp., *Cycadales*) or immobile male gametes (other gymnosperms) are formed. The pollen tube releases the spermatozoids in *Ginkgo sp.* and the *Cycadales* in water of the archegonial chamber. In the other gymnosperms the male gamete is transferred in the cytoplasm of the pollen tube. After oogamy the zygote develops to an embryo and the surrounding tissues of the female gametophyte form the haploid endosperm. Exceptional is the loss of the formation of a real oocyte in *Welwitschia sp*. and *Gnetum* sp.[9]. Embryo and endosperm are surrounded by a macrospore wall and several protection layers of the macrosporangium and this compose the seed. The seed will be transported by gravity and sometimes wings are present to give some delay in their fall down. Exceptional is the biotic transport of the colored seeds with a red arillus as in *Taxus sp*. or *Ephedra sp.* In *Gnetum sp*. and *Ephedra sp*. double fertilization takes place[10] and two embryos are formed. Gymnosperms prepare the interplay of the plant with the biotic vector.

3.6 Angiosperms

In angiosperms the covering and nutrition of the gametophyte, the influence on the function on sexual reproduction and development of the biotic dispersal are the main events all realized by the sporophyte. By the prolonged nutrient supply of the sporophyte most of the gametophyte functions are taken over. In the micro-gametophyte the antheridium is not elaborated but restricted to the formation of a simple cell producing two male gametes. The formation of a real female gamete with storage is absent and an egg cell initial remains[11]. The female gametophyte is now fully dependent on the sporophyte and the formation of endosperm becomes dependent on fertilization. The result is that the female gametophyte is equipped partly with highly differentiated cells, two synergids, the central cell with diploid nucleus and antipodals and the egg cell initial. The further development of the egg cell initial to an embryo and the central cell to endosperm depends on double fertilization. In fact, the female gametophyte runs only the attraction of the pollen tube and transport of the male gametes for double fertilization. The role of the sporophyte is the nutrition by the plant-plant interaction of the gametophytes and after fertilization of the embryo and endosperm. The recognition system to promote cross fertilization is taken over by the sporophyte. In plants several pollen recognition systems are developed and the incompatibility is expressed in the flower pistil to promote the cross fertilization. Exception is the ovular incompatibility which runs between the gametophytes. The most expressed function of the angiosperm sporophyte is the preparation and realization of the biotic dispersal of pollens and seeds by the development of a flower. This interaction with the environment leads to a specialized wind flower and animal flower and in very specialized interactions to a flower animal as in orchids. Biotic pollination and seed dispersal evoke the flower with animal attraction and nutrition. With respect to the biotic dispersal the flower determines the pollination route for the animal in which the nectar gland is the main target to reach and the anther will be passed during the visit. The sporophyte organizes the release of the seed offering nutrients by the formation of a fruit which are exposed, colored and smelt (Figure 3).

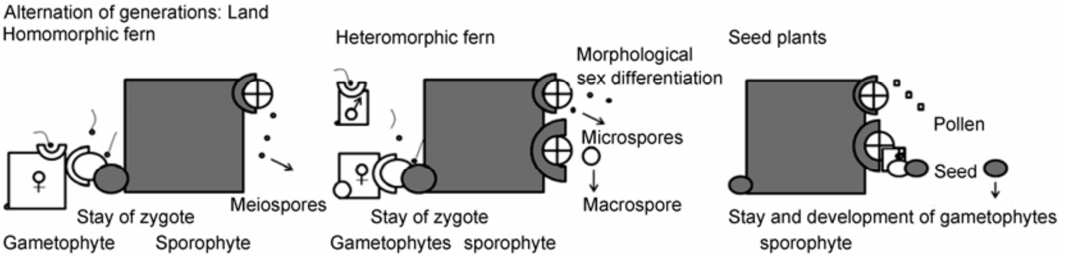

Figure 3 Alternation of generations on land of homosporic ferns with meiospore dispersal and heteromorphic ferns with macrospore dispersal. The shift of the sex differentiation to the sporophyte leads to micro- and macrospores. In gymnosperms: the meiospores stay and develop on the sporophyte to pollen and embryo sac and after fertilization the seed is formed and dispersed by gravity.

3.7 Events on land

From the homosporic ferns the first change is the shift in the moment and physiological sex differentiation leading to two different types of meiospores[12,13]. In heterosporic ferns the macrospore expresses the sex differentiation by its enlargement and determines the way of dispersal by gravity and the settlement of the new plant. The microspore dispersal is by wind and gravity. In seed ferns the macrospore will stay and develop the sporophyte on the plant and the dispersal is by the seed, using gravity. In gymnosperms the female and male gametophytes develop on the plant. The transport of the male gamete and way of fertilization show the transition to a water independent reproduction. In angiosperms the sporophyte dominates and cares for the gametophyte and embryo. The sporophyte develops an intensive interaction with the environment by the flower, the organ for pollination and seed dispersal both functions also directed to biotic vectors.

4 Reproduction: interaction and regulation

The reproduction process is marked by the plant-cell to plant-plant interaction and plant-environment interaction. The plant-cell interaction originates in multicellular plants after cell isolation by mitosis or meiosis. Nutrition via apoplastic transport is supplied by the mother plant together with signals to regulate the development of the isolated cell to spore or gamete to realize dispersal. The plant-cell interaction is followed by the plant-plant interaction in case the meiospore develops and divides during its stay on the plant. In plants a special organ the sporangium or gametangium can be the place of this interaction. From water to land and also in a life cycle with alternation of generations the plant-plant interaction is common. On land the nutrient supply and regulation by the sporophyte of the gametophyte becomes more expressed. In seed plants the whole process from cells to new plants is realized on the sporophyte together with the preparation to a unit of dispersal, the seed. In this relation the sporophyte becomes dominant and takes over some functions of the gametophyte together with the elaboration of the biotic dispersal. The plant-environment interaction is a progression of the process of the dynamic development of the environment. The interaction is expressed in the adaptation to the environment. From the beginning plant life in water is influenced by gravity, light and temperature and the plant acts and reacts on these influences. The plant-environment interaction with respect to reproduction and dispersal becomes clear in unicellular algae after the storage of one of the gametes which results in the use of gravity in its dispersal. In water it has a consequence that the unit of dispersal will fit to the substrate. On land such enlargement is repeated in the formation of the macrospore after the shift of the sex differentiation. This results in the unit of dispersal of the macrospore. The interplay of the sporophyte with the environment becomes very intensive in seed plants. The development of the plants on land is followed by the appearance of heterotrophic organisms which need plants as primary producers. So an intensive contact based on the nutrient supply begins. Plant parts as leaves, stem or root parts are used. On the other hand the plant starts to offer nutrients as carbohydrates and proteins present in the extra floral or floral nectaries. The flower attracts by odor, color, and shape the then present insects and small animals and guides them to offer nutrients as nectar, pollen or fats to realize cross pollination. This is a first step to a localized nutrient source on the plant to get cross fertilization. Later the connection with larger animals is realized by the formation of the fruit, a second nutrient source offered by seed plants to get biotic dispersal[8]. The interplay with the dynamic biotic environment is mainly elaborated by the angiosperm sporophyte. In the flower the interaction is expressed in the attraction, pollination and nutrient supply. For plant reproduction the flower promotes cross fertilization and abiotic and biotic dispersal. The sequence of all types of interactions can be easily demonstrated in the flower bud, open flower and fruit. Figure 4 summarizes the sequence of plant-cell, plant-plant and plant-environment interactions of angiosperms.

The use of attraction and guiding, to offer the nutrients and to promote cross fertilization as well as the advertising connected with fruit dispersal is very striking. It points to a kind of intensive relationship with the diversity of the animal world. The receipt of external stimuli and to react on them shows the dynamic interaction with the environment. Such interplay of the plant resulting in a response of attraction and nutrient offer gives the plant an active role in the dynamic environment. Such position includes that the interplay between plant and environment is a mutual activity. To understand such interaction the sensitivity of the plant to gravity, light, temperature and seasons can explain the

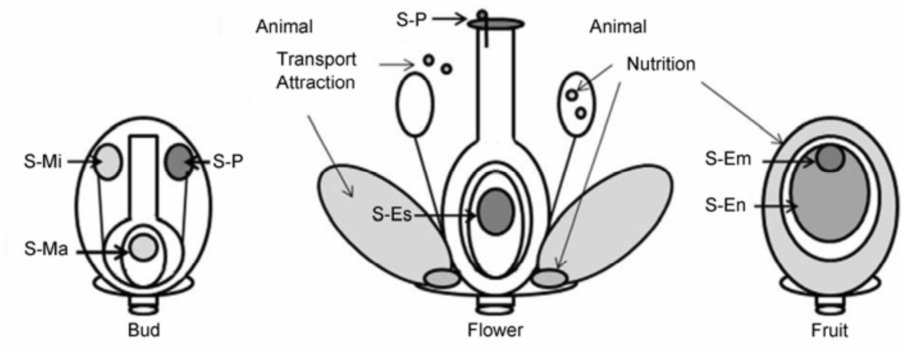

Figure 4 Interactions during reproduction and dispersal in angiosperm flower. The interaction is presented in different shaded areas indicating plant-cell: light shaded, plant-plant: dark shaded and plant-environment: middle shaded and thin arrows. S, Sporophyte; Mi, microspore; Ma, macrospore; Es, embryo sac; Em, embryo; En, endosperm. Explanation of e.g. S-Mi means: Sporophyte-Microspore interaction, a plant-cell interaction.

way along the interplay runs. With respect to the diversity of interactions with the environment, it should be postulated that the presence and production of numerous secondary plant products, non-volatile as well as volatile, can play also a role in the plant-environment interaction. Examples are the volatile defense reaction on damage[14] and the non-volatile strigolactones excreted by roots to find parasites or symbiontic fungi[15].

5 Phylogeny of sexual reproduction

The phylogeny of reproduction and dispersal is based on the process of reproduction which develops together with the dynamic changes in the environment. From the beginning there is a plant-environment interaction. The process of reproduction prepares to dispersal and in case of sexual reproduction to genome renewal and complementation by gamete fusion. In multicellular plants the cell isolation leads to plant-cell and the stay of the zygote on the plant to plant-plant interaction. To conquest the land, the development of a life cycle with the alternation of generations is crucial, partly because it has two moments of dispersal. During the development of reproduction from water to land several lines can be followed.

5.1 Asexual reproduction

The line in asexual reproduction shows the change in way of dispersal from water to wind streaming. On land the meiospore dispersal turns to gravity dispersal by the origin of a macrospore. The simple sporangium of the algae becomes more complex due to its function in active meiospore dispersal. There is a preference on land to use the multicellular units of dispersal. The tendency of asexual reproduction is the use of the spore, multicellular structures and apomixis in water and again on land. Based on the ways of asexual reproduction present in water there are no new possibilities added.

5.2 Sexual reproduction

During the development of sexual reproduction, there are a lot of changes following the row from water to land; from algae to angiosperms are several lines to recognize. Figure 5 summarizes the main events of the sexual reproduction and dispersal from water to land.

5.2.1 Sexual reproduction and dispersal from water to land

The line of the increase in the sporophytic dominance is expressed in an increase of different functions and interactions with the environment. In a life cycle with alternation of generations this results in a dominance of the sporophyte with the takeover of functions of the gametophyte such as autotrophy and recognition. With respect to the environment the sporophytic interaction results in an offer of nutrients to realize cross fertilization and the pollen and seed dispersal. This progress in levels of differentiation is governed by the diploid of an organism, a common tendency expressed in the animal kingdom as well as in the dikaryotic fungi on land. The line in the gametogenesis and fusion is marked by the sequence of iso-, aniso- and oogamy in water. On land the water for the gamete fusion is changed in cytoplasm as new medium. Finally the oogamy in gymnosperms is altered in a fusion via cytoplasm of sperm cells with an egg cell, in angiosperms of two sperm cells with an egg cell initial and central cell. Gametogenesis means also sex differentiation. There is a line expressed at first as

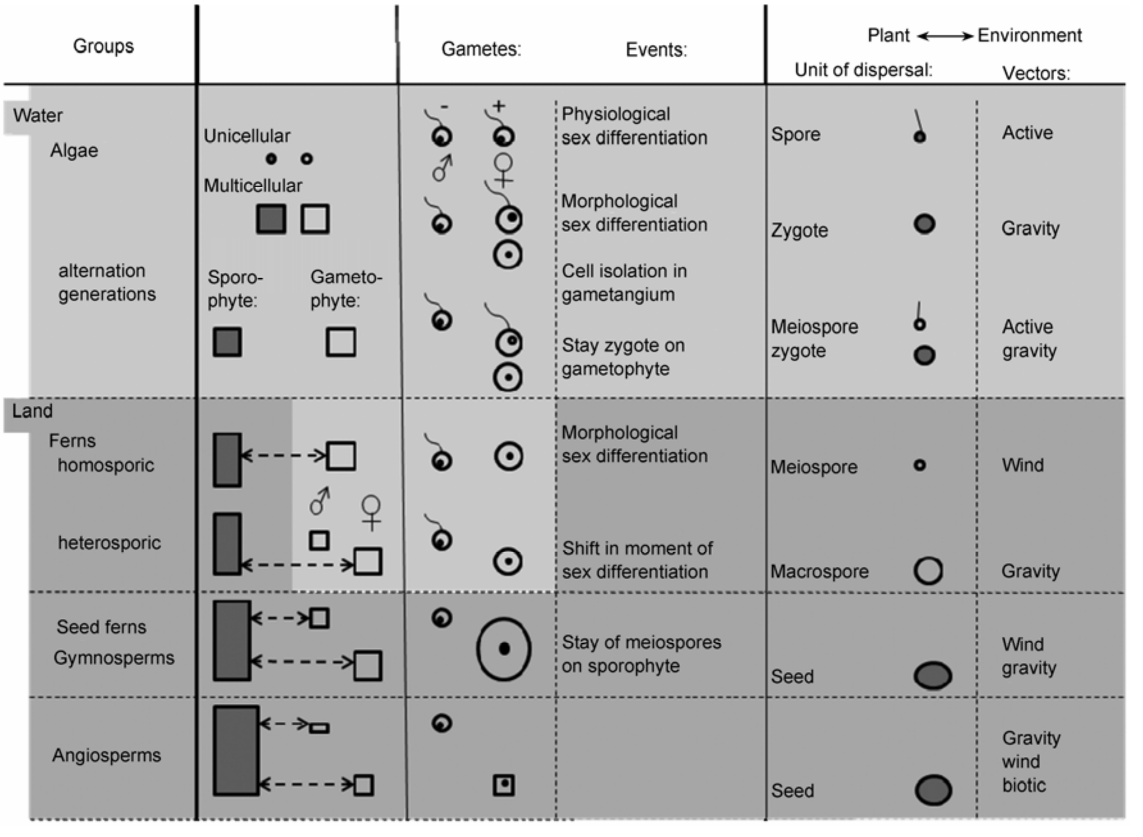

Figure 5 The main events in water and on land from algae to seed plants. The change in diploid organisms is presented by black boxes and the haploid by open boxes. The series of immobile gametes is followed by the immobile oocyte and finally also the immobile sperm cell. The main events are given expressing sex differentiation, cell isolation and stay of zygote and meiospores. The units of dispersal with their vectors are given. In a dotted arrowed line the plant-cell and plant-plant interaction are noted on land, the plant-environment interaction, marked by an arrowed cline, is related to the dispersal.

physiological, thereafter as morphological and finally in a life cycle with alternation of generations the shift of the moment of sex differentiation towards the sporophyte takes place. The line in dispersal is from active to streaming and gravity in water. The morphological sex differentiation is connected with gravity dispersal. The formation of an oocyte or macrospore leads to gravity dispersal which permits the settlement on the substrate. The alternation of generations in a life cycle has two types of dispersal of meiospores by wind and of the zygote by gravity. By a stay of the zygote on the gametophyte this way of dispersal is hampered. The most striking is the shift to wind and biotic dispersal on land. The stay and further development of the macrospore on the sporophyte form the basis for pollen and seed dispersal. The flower realizes the transport by abiotic and biotic vectors. Also the stay of the microspore evokes the pollen dispersal by abiotic or biotic vectors. On land the sporangium gets a function in meiospore dispersal. The line in the interactions begins with the plant environment interaction, which is connected with the dynamic environment and always present. The next interaction is the preparation of the gamete fusion, a cell-cell interaction. In multicellular plants gametangia develop and the oocyte stays and develops on the plant. This leads to the plant-cell interaction. The alternation of generations of land plants permits the stay of the meiospores on the sporophyte and this is a new element on land and evokes the plant-plant interaction. This phylogenetic line is a basal process but together with this a diversity of plants appears. This diversity is not only expressed in the habitus of a plant but also in the way of sexual reproduction. Each group of plants develops their own ways during the sexual reproduction process and dispersal such as the quality and quantity of storage may differ, the molecular pathway leading to recognition differs and the products involved in the gamete attraction are different. The phylogenies along the line from algae to seed plants are equipped by a variety of specific characteristics with as consequence the diversity. This diversity is related to the dynamic environment with its changing conditions and composition and innovation of biotopes.

5.2.2 Plant reproduction: from phylogeny to evolution.

(i) The processes behind the phylogeny. The phylogenetic reproductive lines reveal the processes of sex differentiation and of the interactions with environments and after cell isolation as main events. These processes are sustained by the diploid plant or the sporophyte. The change from unicellular cells to multicellular organisms as well as the invention of alternation of generations in life cycles is crucial for the development of algae and land plants. The physiological sex differentiation leads to isogametes and the enlargement of the female cell by morphological sex differentiation is a next step. The origin of alternation of generations results in water as well as on land to + and – meiospores by the shift in the moment of sex differentiation. The morphological sex differentiation happens in water and land and has a consequence for the way of dispersal. Sex differentiation is coupled on dispersal. Sex differentiation prepares a controlled interaction between gametes to promote cross fertilization. This cell-cell interaction between gametes and the determination of the way of dispersal marks sexual reproduction. The continuous interactions with the environment are expressed in the different units and ways of dispersal and a key part of the reproduction process is to realize the settlement in the biotope. In the plant-environment interaction the biotic vectors become involved in the reproduction process by the sporophytic offer of nutrients and signals to the animals. In this way the reproduction is connected with the existing nutrient chain. The plant-environment interaction as part of reproduction is a need to realize successful dispersal on land by the invasion of new biotopes or adaptation to the changes in the biotopes. This runs by a unit of dispersal with a renewed genome. The interaction of the multicellular plant with the isolated cell after meiosis is also the first step of the mutual nutrition and signaling between the mother plant and the cell. Since the isolated cell needs a further differentiation the interaction is necessary. The formation of a gametangium or sporangium permits the apoplastic transport and the differentiation. Gradually the plant-cell development turns to a plant-plant development. Plant-plant interaction happens in algae but the prolonged stay is a very important step in the transition from macrospores to seeds, from heterosporic fern to seed plants. The sporophyte plays a key role in all types of interaction by nutrient supply and signaling. Sex differentiation and interactions run together in the sexual reproduction and dispersal. The development in sex differentiation and interaction both become expressed in multicellular organisms in water and are repeated on land in multicellular organisms with alternation of generations. On land the shift in sex differentiation leading to the stay of the micro- and macrospores on the sporophyte is a new event. The plant-plant interaction and especially the plant-environment interaction are far more elaborated by the dominating sporophyte on land. During the phylogeny the mutuality of sex differentiation and interaction runs via the sexual reproduction along the line of unicellular to multicellular organisms and the alternation of generations. Compared with the development to a high diversity of organisms, the development in sexual reproduction shows less striking changes. Diversity is more expressed in the way of attraction and dispersal. Attraction and dispersal are effects of the organism related to the dynamic environment and evoke more changes. The variety and development from flower bud to fruit express the dynamic unity between organisms and environments. The phylogeny points to a process of reproduction which enrolls via sexual differentiation and interaction to a renewal and diversity of life. Such processes fit in the process of evolution.

(ii) Plant and animal sexual reproduction. Reproduction is a main key in the evolution and it is striking that the gradual change in water to cytoplasm as medium for gamete fusion also happens on land in the animal kingdom by the production of seminal fluid. Besides the care for the embryo development as happens in mammals is a same tendency elaborated in the seed plants. The origin of the flower as advertising organ towards animals and as nutrient source expresses in numerous different ways the connection with the animal world, sometimes even invading the animal world by imitating a female bee. The attraction of the partner, already obvious in fishes, is an aspect that the sexual reproduction on land becomes expressed in the courtship of animals, and a comparable tendency in plants on land is built up by the advertisement. Plants and animals show the ability to use advertisement connected with reproduction. Next to these evolutionary similarities are other resemblances in reproduction between plants and animals[16]. It is peculiar that the terms expressed as placenta, ovary and ovule are used for many years in seed plants and mammals.

5.2.3 Evolution and communication

From the beginning the dynamic environment and organism are unified and this is expressed in continuous interactions. Evolution runs via sexual reproduction and dispersal and both processes show a mutual interaction with the dynamic environment. The process of reproduction plays a key role in the renewal of life. Reproduction includes renewal and persistence in the dynamic environment and this result in an increasing complexity of the biotopes together with the extension of interactions. Unicellular organisms develop the process of genome renewal by meiosis and complementation by fusion. The sex differentiation is leading to the preparation of attraction, recognition and fusion by gametes, a cell-cell interaction. In multicellular plants after cell isolation the plant-cell interaction and later the plant-plant interaction develop. The origin of alternation of generations in a life cycle permits the dominance of the sporophyte and an intensification of the interactions. The cell-cell, plant-cell, plant-plant and the permanent plant-environment interactions keep going the process of reproduction, the motor of evolution. During the development of life on the earth the interplay between organisms and biotopes is present also in the nutrient chain, and permanent associations between organisms during symbiosis with, commensalism, parasitism and mutualism[17]. Organisms and environments are from the beginning unified and this is expressed in the adaptation. In case the environment is changing the organism should change too and this is *vice-versa*, in case the organization of the biosphere changes, the environment changes too. Interactions result in an increase of complexity expressed in the diversity and extinction of species which can be followed during the evolution by phylogenies and earth history.

The story of sexual reproduction and dispersal in plants reveals interactions from gamete-gamete to plant-plant and plant environments. These interactions and the interactions as symbiosis and in the nutrient chain are permanently active. This presence and activity can be expressed as a persisting cooperation between environments and life, a process that runs in the evolution. The persisting cooperation is expressed in a growing diversity and complexity and points to a permanent push. This push can be expressed as communication. Such communication is a prerequisite for development and can be considered as a driving force leading to evolution. The continuous communication results in the increase of diversity and complexity in biotic as well as in the prebiotic world. Such communication is expressed in sexual reproduction, dispersal, the nutrient chain, symbiosis and the invasion in a new biotope. The characterization of life presented in terms of movement, reproduction, assimilation and dissimilation, or respiration, the strong relationship with the environment is expressed. Life is marked by communication.

The process of evolution runs via reproduction and is characterized by interactions, therefore the potency of communication drives the evolution. Communication can be considered as a driving force to evolution of the diversity of both: environment and life.

6 Final remarks and conclusions

Reproduction is the way along which organisms multiply and in case of sexual reproduction renew the genome to persist in the dynamic environment. The reproduction process prepares the unit of dispersal and the way of dispersal. Sexual reproduction is a key process in evolution.

6.1 Reproduction

Considering reproduction as a process at first directed to dispersal by mitosis, the meiosis adds genome renewal. The process of reproduction has similarities between asexual and sexual reproduction. Sexual reproduction prepares a cell-cell interaction and dispersal. The sex differentiation causes the gravity dispersal by cell enlargement and the moment of cell differentiation can shift and cause a sex-separated dispersal to promote cross fertilization, but evokes a risk in dispersal. Cell isolation and its stay play an important role in reproduction and evoke nutrition and signaling interaction. Next to this, sporangia get a function in dispersal. One should keep in mind that the reproduction process unifies in a sequence the meiosis with recombination, sex differentiation, interaction and the preparation to dispersal.

6.2 Regulation of reproduction

There are consequences on the way of regulation during the reproduction process. In unicellular plants it can be considered as a process sequence governed by the cell genome leading to the gamete formation and preparation of the dispersal in one process. In multicellular organisms there is a plant genome action and the apoplastic interplay during the interactions is added. In the plant kingdom is an increasing dominance of the sporophyte in water on land and a shift in functions from the gametophyte to the sporophyte happens. The regulation of reproduction realized in the cell or organism concerns the sequence of gene actions. During plant-cell and plant-plant interactions is interplay of the genes expressed on both sides. From both plants there should run a process of signaling with reception and acceptation of signals. The sequence of interactions forms a complex situation in higher plants. In angiosperms there are involved a haploid gametophyte, diploid sporophyte and triploid endosperm together with the interaction between the gametophytes and sporophyte, the sporophyte with the embryo and endosperm and in the free seed between the new plant and the endosperm in case of germination. Such row of interactions plays a certain role in the unraveling of the reproduction process. Topics to day such as the ABC model, sex differentiation, incompatibility, *in vivo* or *in-vitro* fertilization, embryogenesis and apomixis, all included moments of interaction governed by the sporophyte. During induction of the reproduction and the pollen or seed dispersal the interaction with the environment is active. External factors can be hastened as well as hamper the process sequence. Since an increasing plant-animal relationship develops, the way along this interplay run needs far more attention with respect to the regulation. The progressing interaction between plants and animals shows the increasing sensibility for the changing events in the environment.

Regulation of reproduction is a complex topic but in the progress of data a survey of the development of this process can help to place the findings in this process or it can result in the selection of a more simple and crucial step of this process. The ferns as *Psilotum, Selaginella* and the gymnosperms Ephedra*, Welwitschia* and *Gnetum* show basal and intermediate processes. In Algae the focus on isogamy, the different types of apomixis and origin of multicellular organisms and alternation of generations can offer more insight in reproduction and the relation to the evolution process.

6.3 Evolution

Communication evokes a dynamic process and this is expressed in an abiotic and later in a biotic environment. The connection between environment and life and the running communication as a driving force include adaptation as well as selection. Adaptation expresses the interactions between organism and environment and is always realized, in some cases very clearly expressed. Selection is the result of the dynamic interplay between organisms and environments and is expressed by the genome renewal prepared during sexual reproduction and shows the fit in the environment. Within the interaction between organisms and environments, adaptation represents the environmental aspect and selection the genome aspect. Reproduction and nutrition are processes along which the evolution runs. The bisexual potency of the diploid organism and the ability to use several vectors of dispersal show the plasticity of the reproduction process. The origin of land plants and the offer of nutrients mainly by the angiosperms during biotic pollination and seed dispersal are an expansion of the nutrient chain and let originate new biotopes. These events cause numerous types of new interactions between organisms and environments. The two moments of the plant dispersal by a life cycle with alternation of generations prepare the way to conquest land and permit the stay of the zygote to the gametophyte and dispersal by meiospores. In water all conditions to run the sexual reproduction are already present and the shift to an earlier moment of sex differentiation to the meiospores as well as the following enlargement of the macrospore can be considered as repetitions of what happens in water. With respect to reproduction the main changes on land are related to the way of dispersal and the use of the biotic vectors. The same tendency is visible in apomictic asexual reproduction. In water the sex differentiation to oogamy and the alternation of generations by insertion of an extra moment of dispersal are the main events to go on land. Land plant evolution runs via the dispersal by the shift in sex differentiation and cell enlargement. The dispersal becomes connected with the nutrient chain by the sporophytic dominance especially in angiosperms, as dressed gymnosperms.

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