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An updated definition of genet applicable to clonal seaweeds, bryophytes, and vascular plants

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Abstract

The genet of clonal plants is currently defined as the genetic individual that develops from the zygote and that produces ramets vegetatively. Genetic individuality refers to the fact that it is considered to be a genetically uniform plant. However, somatic mutations may give rise to genetic mosaics within the genet, invalidating the assumption of its genetic uniformity. On the other hand, zygotes are not the only initial cells of genets, since parthenogenetic female gametes may also develop into new individuals directly. Sexual and asexual types of reproduction are similar in terms of dispersal, dormancy, recruitment, and seedling development, especially compared with vegetative fragmentation, process that does not create new genets. For other clonal autotrophic macroorganisms, such as clonal bryophytes and red seaweeds, new individuals that result from reproduction develop from a variety of spores, not from zygotes. These considerations suggest that the existing definition of genet should be updated. For clonal autotrophic macroorganisms, in general, the genet may be defined as the free-living individual that develops from one original zygote, parthenogenetic gamete, or spore and that produces ramets vegetatively during growth. The degree of genetic differentiation between consecutive generations of genets will primarily depend on the type of reproduction involved.

Der Genet klonaler Pflanzen ist definiert als das genetische Individuum das sich aus einer Zygote entwickelt und das auf vegetative Weise Rameten produziert. Der Begriff der genetischen Individualität besagt, dass das Individuum genetisch homogen ist. Jedoch können somatische Mutationen innerhalb des Genets dazu führen, dass sich ein genetisches Mosaik entwickelt, das die genetische Individualität des Organismus verletzt. Andererseits können Geneten sich nicht nur aus Zygoten entwickeln, aber auch parthenogenetisch von weiblichen Gameten abstammen. Sexuelle and asexuelle Fortpflanzung gleichen einander in Verbreitung, Ruhezustand, Rekrutierung, und Keimlingsentwicklung, speziell verglichen mit vegetativer Fragmentation, einem Prozess bei dem sich keine neuen Geneten entwickeln. Neue Individuen von anderen klonalen, autotrophen Makroorganismen wie klonale Bryophyten und Rotalgen entwickeln sich aus einer Vielfalt von Sporen, nicht aus Zygoten. In dieser Hinsicht sollte die Definition von Genet für klonale autotrophe Makroorganismen aktualisiert werden. Generell kann der Genet als das freilebende Individuum definiert werden, das sich aus einer Zygote, einem parthenogenetischen Gameten oder einer Spore entwickelt, und das Gameten auf vegetative Weise produziert. Der Grad der genetischen Differenzierung zwischen konsekutiven Generationen hängt primär von der Reproduktionsart ab.

Key words: clonal fragment – genet – genetic individual – parthenogenetic gamete – ramet – spore – vegetative fragmentation – zygote

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Clonal plants are those that spread vegetatively by producing a number of similar functional units (such as shoots) that are potentially able to live on their own if they become physically separated from the parent plant. Such vegetative units are termed ramets, whereas the entire plant is termed genet. Clonal species can be found among vascular plants (Klimeš et al. 1997), bryophytes (van der Hoeven & During 1997), and seaweeds (Scrosati & Servière-Zaragoza 2000; Fig. 1). Seaweeds are also known as marine macroalgae and are included in a variety of different kingdoms, depending on the author (Campbell et al. 1999). The term 'genet' was originally defined for clonal vascular plants as the genetic individual that develops from a seed and that produces a number of ramets (Harper & White 1974, Kays & Harper 1974). More recently, the zygote was specifically defined as the initial cell of the genet (de Kroon & van Groenendael 1997, Andrews 1998). In light of recent developments in plant genetics, there is a problem with the existing definition of genet. Additionally, the current definition cannot be applied adequately to clonal bryophytes and seaweeds. The objectives of this contribution are to discuss these issues and to propose an updated definition of genet that can be applicable to clonal autotrophic macroorganisms, in general.

One of the limitations of the current definition of genet relates to the term 'genetic individuality', which may be interpreted as all of the parts of the genet (ramets, stolons, rhizomes, bulbs, etc.) being genetically identical. However, somatic mutations normally occur during plant development (Gill et al. 1995, Klekowski 1997), which results in genetic mosaics being accumulated in the genet. Spontaneous mutation rates are generally between 10^{-4} and 10^{-6} mutations per gene per generation (Hartl & Clark 1997), but, in regions of the genome termed VNTR (variable number of tandem repeats), they may be up to 10^{-2} per generation (Slatkin et al. 1995). Considering the entire genome of a plant, the number of mutations during its lifespan can be considerable (Futuyma 1998). Also, the longer the lifespan of the plant is, the higher the number of mutations will likely be (Klekowski 1997). Thus, the assumption that the genet is a genetically uniform plant should be abandoned. Under such assumption, for example, we might find in the field separate individuals differing genetically for certain markers that could be interpreted as different genets, when they may have actually resulted from the vegetative fragmentation of one original chimeric genet.

The key attribute to consider when defining the genet may actually be the fact that the genet is an individual that develops from the zygote, as opposed to the individual that results from vegetative fragmentation from one original genet (this second type of individual is known as clonal fragment, *sensu* Eriksson & Jerling 1990). However, if only the zygote were considered as the initial cell of the genet, as presently done, the definition of genet would be too limiting. For ex-

Fig. 1. Example of a clonal seaweed: *Mazzaella cornucopiae* (Rhodophyta, Gigartinales) from Pacific Canada. An individual of this alga is composed of a crustose holdfast and several upright fronds, each of which represents a ramet. The largest fronds depicted here are 3–5 cm long.

ample, several plant species reproduce through asexual seeds, which involves the parthenogenetic development of the embryo directly from the female gamete (Mogie 1992). Sexual and asexual types of reproduction are similar in terms of dispersal, dormancy, recruitment, and seedling development, especially compared with vegetative fragmentation, process that does not create new genets. Thus, it may be also appropriate to include parthenogenetic female gametes as initial cells in the definition of genet.

Even with the above modifications in the definition of genet, we would still be prevented from applying it to clonal bryophytes and red seaweeds. For these autotrophic macroorganisms, the free-living individuals that result from reproduction (as opposed to vegetative fragmentation) develop from a variety of spores, not from zygotes. Examples are the carpospores and tetraspores of red seaweeds and the spores of bryophytes. Carpospores develop into tetrasporophytes and tetraspores into gametophytes (Graham & Wilcox 2000), while bryophyte spores develop into gametophytes (Raven et al. 1999).

Therefore, given the above considerations, it may be appropriate to update the existing definition of genet. For clonal autotrophic macroorganisms, in general (including clonal seaweeds, bryophytes, and vascular plants), the genet may be defined as the free-living individual that develops from one original zygote, parthenogenetic gamete, or spore and that produces ramets vegetatively during growth. It may be pertinent to clarify that meristematic cells cannot be considered as initial cells of genets, because meristematic cells just promote the growth of existing individuals, without developing into new ones directly. It is important to note that, under this updated definition, the degree of genetic differentiation between consecutive generations of genets will primarily depend on the type of reproduction involved. For example, sexual reproduction will likely result in a higher degree of genetic differentiation than parthenogenesis.

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