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An Herbiary of Plant Individuality

Sophie Gerber*

Questioning the nature of individuality has a long and a rich history, both in philosophy and in biology. Because they differ in several features from the pervasive vertebrate-human model, plants have been considered as complicating the question. Here, the various plant species on which authors—whether biologists or philosophers—rely to build the picture of plant individuality are examined and tracked for their peculiarities, thus constituting an "herbiary" of plant individuality. The herbiary of plant individuality has as its members species exhibiting a diverse collection of traits and illustrating different questions related to plant individuality. This essay assesses the peculiarity of the features of these plants and the reality of their differences from animals. Because some plant features are supposed to pose a threat to individual genetic homogeneity, higher heterogeneity has been assumed for plants compared to animals. Moreover, individual plants are sometimes identified with communities. How does this supposed heterogeneity appear in particular species? Cultivated plants exhibit distinctive diversity, and their overrepresentation in the study of plant diversity might bias the way plant individuality is understood. Just as there is a vertebrate bias, there may also be a cultivated plant bias. Recent results bring plants much closer to animals in terms of cellular functioning, so plants might not be so different from animals with respect to their diversity, and consequently their individuality.

Keywords

plants • genetics • individuality • heterogeneity • cultivated plants

Herbiary [*Bestiary*]: *a medieval collection of poetic, allegoric, and moralizing descriptions, and often illustrations, of real and mythical plants* [*animals*]

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1 The plant problem with individuality

If the nature of individuality has been a subject of debates in philosophy since immemorial times, it has also been, for decades, a meeting point for biology and philosophy, and it is still a lively question (Pradeu 2016). Thinking about individuality in philosophy of biology was a road paved by Hull, who called for common and clear criteria for individuality (spatiotemporal continuity, unity, and location), unifying philosophical and evolutionary approaches (Hull 1980, 1992). For him, a clear notion of an individual organism is, in particular, an absolute prerequisite for defining a human person, in order to protect fragile categories from exclusion. It should, moreover, be applicable to any living species (Hull 1978). Plants have been the starting point of debates on this topic since the early nineteenth century (Godfrey-Smith 2013). And plants indeed occupy a particular place in the biological individuality landscape (Herrera 2009). They have been thought to challenge criteria for individuality.

In this paper, we wish to question whether plants constitute a challenge for the conception of biological individuality, in particular because their differences from animals in their features are said to be too important. We intend to examine the different plant species on which authors rely to build the picture of plant individuality, tracking their peculiarities among higher plants and constituting thus an herbiary of plant individuality. We have assumed that looking closer at plant species that authors—biologists or philosophers—rely on to draw individuality of plants, can help us to assess the claimed peculiarities of plants and the reality of differences between plants and animals, particularly concerning individual genetic heterogeneity.

Historically, plants have been endowed with a supposedly heterogeneous and plural nature, and they are still described with similar words. For many authors in biology and philosophy, a plant is best represented as a *community* rather than as an individual (White 1979; Marder 2014). If so, the plant model could be too different from the animal model to qualify for "true" individuality.

Very broadly, an "individual" is often described as an entity that can be isolated and counted, is cohesive, persists through time, and is possibly unique (Chauvier 2015). Hence, at least four criteria can be defined for individuality, and we see in Table 1 that plant features do not fit easily into them. Some of these features are also shared with other living entities, for instance fungi (Molter 2016) and some colonial animals (Santelices 2004; Reusch and Boström 2011).

The common and intuitive use of the notion of individual is based on approximations that are inappropriate for a large part of the biological world: intuitive individuation identifies implicitly, and in a narrow sense, the biological individual with a mammal. This results in "the damage that our vertebrate bias can do" (Hull 1978, 1992). Plants, deviating from our anthropocentric vision, are compound (or modular) organisms; for this reason they have traditionally been compared to colonial invertebrates, for instance by botanists (de Candolle 1832). And debate about the individuality of these entities was vivid in the nineteenth century (Nyhart and Lidgard 2011).

In marked contrast with two of the four criteria characterizing individuality, unity and homogeneity (Table 1), individual plants were described historically—and are still characterized—with several terms commonly expressing an opposite idea of diversity appearing at different levels (Table 2).

These perceptions can be explained partly by the specific biology of the plant kingdom. We would like to establish whether these apparent oppositions between animals and plants are appropriate. We will, more precisely, question the common idea that an individual should be a genetically homogeneous entity, and wonder in what way this idea should differ between animal and plant species. The assumption that plants are genetically heterogeneous at the individual level has generated debates in philosophy of biology (see, for instance, Clarke 2011). What do

Table 1: Four criteria for individuality, and plant features that do not fit in

Criterion	**The individual:**	**The plant:**
Indivisibility	Is an entity that cannot be divided without destruction (Latin etymology, from *individuus*, "indivisible")	Can be fragmented into elements with physiological autonomy: (a) layering, sprouting, division of tuber, bulb, rhizomes, stolon, etc. (naturally observed); (b) cutting, grafting, *in vitro* culture, etc. (artificial use)
Unity	Is a single recognizable whole with boundaries	Possesses both: (a) Visible aerial part and below-ground root system; (b) Roots of different plants can be linked
Uniqueness	Is unique	Is often issued from the same and unique genotype: frequent and diversified reproductive systems (sexual, asexual) are causing genetic duplications
Homogeneity (all parts of the same nature)	Is associated with a criterion of genetic homogeneity	Genetic heterogeneity is traditionally assumed to be higher (see Table 3)

Table 2: Expressions used to qualify plant constitution

Term	**Meaning**
Community	Group of interdependent elements occupying the same space and interacting with each other
Heterogeneity	Composed of parts that are of different kinds
Metapopulation	Shared elements that make up the morphological structure of a genetic individual or population of populations
Mosaicism	In genetics, the presence in an individual of two or more cell lines derived from a single zygote, that are genetically distinct
Multiplicity	Composed of several parts or elements
Plurality	Consisting of more than one kind, or of different kinds

the different plant species used as examples for these debates exemplify? Are the descriptions, analyses, and interpretations of the diversity of these individual plants, both historical and more recent, consistent with available scientific data on plant genetic diversity? Our assumption is that this comparison should help us to shed light on plant individuality.

1.1 Some plant species from the herbiary of individuality

Our herbiary finds some of its members inside "the Menagerie" of Godfrey-Smith (2009), which is composed of "puzzles or illuminating oddities" like aspen, strawberries, apple trees, and violets. The herbiary is probably constituted with a certain bias due to the species on which authors work and write; some of them are more popular than others, including model plants, for reasons that should be analyzed. These include our first species below, which has been prevalent in texts for several centuries. Additionally, plants included in our herbiary—exemplifying the plant kingdom's peculiarities—exhibit very variable features, in their taxonomy, ways of reproduction, life cycle, morphology, etc.

Let's start with a species highly symbolic of the plant kingdom, even in the seventeenth century: the oak tree. Locke (1690) explains that its plant life, thanks to the "organization of parts," constitutes "one coherent body, partaking of one common life." Plant identity, its sameness, exists as long as the same life is shared, in space and time, by the parts of a unique plant which are different from any other one. The same oak tree is analyzed around fifty years later by Hume: "An oak, that grows from a small plant to a large tree, is still the same oak; tho' there be not one particle of matter, or figure of its parts the same. An infant becomes a man, and is sometimes fat, sometimes lean, without any change in his identity" (Hume 1739). In these two excerpts, the oak has the individuality features of a human being.

On the opposite end of the herbiary, and more recently, another tree species is highly cited. Pando (which means "I spread" in Latin) is a quaking aspen (*Populus tremuloides*) growing in Utah, USA. It has regularly been assumed that an initial tree, born from a single sexual reproduction event, had been able to generate, by simple clonal, asexual reproduction, about 47,000 stems covering 43 ha (Kemperman and Barnes 1976; Mitton and Grant 1996).

At a more restricted, herbaceous scale, another species raises a similar question. The dandelion (*Taraxacum officinale*) has apomictic reproduction[1] and establishes vast clonal populations, which are nonetheless composed of independent physiological units. A confusion existing between the individual as seen by a layperson (that is, in the common view) and the evolutionary biology conception of individuality (qualified by its fitness) was stressed by Janzen (1977). He sees dandelion as a very large tree with a highly diffuse crown but no investment in trunk, major branches, or perennial roots. Using the same tree image differently, Ariew and Lewontin (2004) state that all the ramets of a violet, connected above ground, are like a tree, seen as a single individual, with elements connected below ground. Strawberry and thyme (*Thymus praecox*) have been treated similarly (Godfrey-Smith 2009; Wiggins 2008).

We also find one of the oldest domesticated species in our herbiary, *Vitis vinifera* L., the grapevine. Clones of this species have been vegetatively propagated for centuries. Very ancient genotypes are still recognizable, in varieties cultivated until now (like Muscat and Pinot) exhibiting features close to those of the wild vine, *Vitis* spp., that crosses with its domesticated relative (Di Vecchi-Staraz et al. 2009). If a few vine types, often related, dominate world vineyards, high variability is still present in the populations (Myles et al. 2011).

A particular puzzle, a fern—a non-flowering plant—has to be added to the herbiary. Analyzing both spatial and temporal parts of a system into a living individual, Godfrey-Smith (2015) wonders how diploid sporophyte and haploid gametophyte, two very different forms that alternate in the fern life cycle, are involved in its individuality. Over space (or time), division of labor is a form of heterogeneity that does not compromise collective individuality; it is heterogeneity with "common purpose" (Godfrey-Smith 2015).

Lastly, we include a representative of algae in our herbiary, part of the volvocine green algae clade. The *Volvox carteri* species is a model for the evolution of multicellularity and cellular differentiation, and it possesses a complicated life cycle. Algae invent unseen oddities that open new individuality questions (Herron et al. 2013; Hanschen et al. 2017).

2 Plant genetic homogeneity

Two similar studies have attempted to locate individuals from different living species in a three-dimensional representation, according to some biological criteria (Santelices 1999; Godfrey-Smith 2009). Vertebrates are placed identically in both authors' schemes, as exhibiting maxi-

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[1] Seeds produced asexually, without fertilization, genetically identical to the mother plant

mum trait values for all criteria, confirming that they constitute references for defining individuality. Santelices distinguishes the kingdom of plants (*Plantae*) from the kingdom of animals (*Animalia*). Godfrey-Smith includes two plants from our herbiary, aspen ramet[2] and oak from acorn, among a total of eight organisms. They both conclude that genetic uniqueness or its related trait, clonal (vs. sexual) reproduction, sets apart plants from other organisms. The distinctive way plants produce genetic homogeneity, but at the population level, is exemplified here.

In his nineteenth-century theory of heredity, Weismann distinguished germ, the only carrier of hereditary material, from soma.[3] Weismann's doctrine is bound to the assumption that the individual should be considered a genetically homogeneous unit; selection will necessarily work on the entire individual and not on the cells or their constituents, because not all cells contain heritable substance. Homogeneity provides similar cells which cooperate to ensure organism stability and are protected from lower-level conflicts. Therefore selection will work at the individual level and not among cells; the individual has to be homogeneous to survive (Buss 1987; Clarke 2011). When the material support of hereditary transmission was proved in the early twentieth century, biological unity and homogeneity were assumed to have mostly a genetic nature.

Many plant species of our herbiary—the aspen clone Pando, dandelion, strawberries, thyme, etc.—exemplify in an emblematic way, and at the population level, a first threat of plants: the peril of uniqueness (Bouchard 2008). Likewise, defining an individual by its genetical homogeneity is a commonly shared assumption in biology. But in plant species, a second threat occurs: the individual seen as a unique genetic entity is expected to be problematic because some of their features are supposed to be a menace to individual genetic homogeneity. Higher heterogeneity is assumed for plants, in comparison with animals. Examining our herbiary, is this assumption generally supported and validated?

3 A plant seen as a community

The title of White's (1979) review identifies the plant as a metapopulation (Table 1). The review describes the perceptions and descriptions of plants by authors through history. Hence, in the eighteenth century, Bradley (1721), an English botanist, stated that "The buds … did in every respect perform the office of a seed." The same idea is present in Linnaeus's (1751) *Philosophia Botanica* (Nyhart and Lidgard 2011). The German writer Goethe (1790), Darwin (1845), and his grandfather Erasmus Darwin (1800) accordingly shared the idea of a "bud-individual," a term coined by the Swiss botanist de Candolle (1832). Botanists from all over the western world agreed with this idea, for instance Gaudichaud (1841) from France, Braun (1851) from Germany (Guédès 1972, 1973), and Gray (1876) from North America.

Power has thus been given to buds, seen as autonomous entities, for centuries. This has resulted in considering a plant to be a heterogeneous whole composed of subunits. Quoting Darwin, de Candolle states that a plant "presents the highest analogy with a polyp, that grows sort of buds, here and there; but in the polyp, buds or new individuals are drawing apart by themselves, and in the plant, they ordinarily stay, bound in a single body with their mother" (de Candolle 1832). "A plant is a family, a republic, a kind of living hive which inhabitants,

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[2] The genet is the product of a zygote (Harper 1980); it is the entire clone, a genetic individual. The ramet is the clonal growth unit (Harper 1977); it is a physiological unit, able to live an independent life separate from the genet (Jackson et al. 1985). Genets are from reproduction, ramets are from growth.

[3] "Soma": all cells of a living organism except the reproducing cells. "Germ": all reproductive cells and all the elements that give rise to them.

citizens, share food and eat in the refectory" writes Dupont de Nemours (cited by Fabre 1892). Trees—one of which "is more a society than an individual" (Bergson 1908)—or more broadly plants, are considered to be "communities of individuals" (Clarke 2012), comparable to colonial animals (like the polyp mentioned above).

If a plant is equated with a metapopulation, we have to come back to the original meaning of the term, coined in a population dynamics framework to mean "population of populations" (Levins 1968). This meaning can already be seen in Leibniz's words illustrating a plant in a poetic way: "Each portion of matter may be conceived as like a garden full of plants …. But each branch of every plant … is also some such garden …" (Leibniz 1714, 67).

The study of plant architecture was inspired by the plant seen as a colony. Goethe (1790) was the first to introduce and define plant morphology, and since then, tropical-tree botanists have created architectural models describing the great variety of structures encountered on limited surfaces, due to high species diversity (Hallé and Oldeman 1970). Higher plants possess modular growth and develop by the repetition of elementary botanical entities, or modules[4] (Barthelemy and Caraglio 2007), as do colonial animals (Hydrozoa, Cnidaria, Bryozoa, Ascidiacea, etc.).

All these views escape the unitary conception of higher animals and move away from the common definition of individuality. It has been suggested, and particularly for defining the individual, that the most appropriate division in ecology was not between animals and plants, but between unitary and modular organisms (Jerling 1985; Vuorisalo and Tuomi 1986).

4 Modularity, mutation, homogeneity and plants

4.1 Why would plants be more diverse than animals?

The description of a plant as a community has persisted much later than the historical texts cited above. Some authors state that somatic mutations may be an important source of heritable variation in plants; they describe the branches of an individual tree or parts of a clone as similar but distinct genetic islands, constituting genetic mosaics produced by mutations (Whitham and Slobodchikoff 1981).[5]

The higher level of intra-individual genetic diversity attributed by several authors to plants as compared to animal species is explained by particular plant features. Weismann observes the separation between germ and soma, theoretically preventing the transmission of acquired traits. However, plants do not possess any distinct germline. Hence for the plant kingdom, but also for colonial invertebrates and fungi, rejecting the inheritance of acquired characteristics seems more problematic (Buss 1987). Moreover, in unitary organisms like animals, the body plan is settled during the early stages of development, thanks to the moving animal cells. In contrast, the plant's rigid cell wall limits cell movements. Apical cell lines remain therefore flexible, totipotent, and mitotically active. If animals are vulnerable to variations and have developed complex programs to protect early determinism of embryo, plants are less sensitive (Buss 1987; Klekowski and Godfrey 1989). Hence modular-growth organisms, including plants, are supposed to constitute genetic mosaics more often than unitary organisms do, because of their long lifespans, because their germlines are not protected, and because multicellular propagation is possible (Clarke 2011); see Table 3.

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[4] A "module" refers in plants to the set formed by a node, an internode, a leaf and an axillary bud (Edelin et al. 1995) and in animals to a zooid or a polyp (Jackson et al. 1985).

[5] Clarke's reasoning relies utterly on elements of this paper: it is cited nine times in Clarke 2011, with four excerpts.

Table 3: Comparison of unitary and modular organisms for features supposed to be connected to heterogeneity

Trait	**Unitary organism**	**Modular organism**
Soma-Germ	Separated	Confounded
Distinct germline, protected	Yes	No
Body plan	Early settled	Unsettled
Differentiation in space and time	Decoupled	Associated
Inheritance of acquired characteristics	Protected	Less protected
Cells	Moving	Fixed
Multicellular propagation	Absent	Possible
Heterogeneity, mosaicism	Supposed to be lower	Supposed to be higher

In strong contrast, Gill et al. (1995) explain that theoretical models predict that genetic mosaics are rare and that intra-clonal genetic variations are difficult to detect. They conclude that only high somatic mutation rates associated with important selective benefits could generate mutants sufficiently frequently to be detected.

Several mechanisms can generate intra-individual genetic variations, and these variations can become heritable, threatening the idea of a genetically homogeneous individual and allowing a type of selection that would act not only on the individual as a whole but also on sub-individual parts (Buss 1985). The individual is submitted, at different levels, to clonal replication. At the same time, copying errors can occur and can remain present (Table 4).

But what is the frequency of these kinds of events? Clarke (2011) states: "Somatic selection might be particularly important in the evolution of plants and other modular organisms, because of their high rates of mutation." Comparing the importance of mutations in plants and animals, and assuming that the number of cell divisions is correlated to somatic mutations, Buss estimates that the unitary organism (the frequency of variants arising in a human being 10^{-8}) and the modular one (the frequency of variants arising in an oak being 10^{3}) correspond to highly different numbers (Buss 1985). Papers dealing with the frequency of somatic mutations are faced with the difficult question of how to evaluate it. Clarke (2011) cites, for instance, a sentence from Otto and Hastings (1998): "the sheer number of cells that must be produced during the development of all but the smallest of organisms ensures that almost every individual is a genetic mosaic," and adds: "Plants and other modular organisms are known to show much, much higher genetic heterogeneity, because they lack mechanisms for minimizing it" (Clarke 2011).

Table 4: Clonal duplication units and genetic errors (Buss 1985)

Units capable of clonal replication	**Errors in copying**
Mobile genetic elements (transposons)	Genomic changes at transposon insertion sites
Organelles (mitochondria, chloroplasts)	Inversion at transposition sites
Cells (mitosis)	Deletions
Organism as a whole (ramet production)	Duplications
	Gene duplication in multigene families
	Intragenomic recombinations
	Ploidy modification

It is therefore important to ask what scientific information is available about plants' mutation rates and whether such assertions are supported by experimental evidence.

4.2 Mutation rates measured in plants

Several authors have aimed to measure mutation rates in plants, but it is an arduous task. Klekowski and Godfrey (1989) evaluated mutation rate (by looking at albinism) in mangrove trees, and conclude that their mutation rate is 100 times higher than the one measured for the same trait in annual plants. This difference was expected because species like trees, being long-lived, were supposed to accumulate more mutations than annual plants. However, Cloutier et al. (2003), following variations at nuclear and chloroplastic microsatellite loci between and inside clonal copies of Weymouth pine (*Pinus strobus*), observed a much lower somatic mutation rate than the one published for microsatellite loci in other plant species, and they deduced that somatic mutations do not significantly contribute to overall genomic mutation rate. Several approaches for indirect estimations of plants' deleterious somatic mutations have been suggested: a theoretical method for trees using within-crown tests (Schultz and Scofield 2009), the use of molecular markers in aspen clones (Ally et al. 2010), and comparison of phenotypes from controlled crosses in blueberry (Bobiwash et al. 2013). Indirectly estimating mutation rates in two plant species, Schoen (2005) observed values in between the extremes reported in other eukaryotes, with no evidence to support a qualitatively higher or lower mutation rate in plants.

DNA sequencing technologies give access to direct mutation rates; more precisely, they provide measures of the average spontaneous DNA base substitution rate per site per generation (Table 5).

Comparing mutation rates estimated with high-throughput genome sequencing in different species, Lynch (2010) observed that their values are often substantially different from those derived by indirect inferences from natural populations. Data are still scarce for plant species, with four references: a grass (*Cynodon dactylon*), *Arabidopsis*, rice (*Oryza sativa*), and peach (*Prunus persica*). These exhibit close values despite their perennial (grass), annual (*Arabidopsis*, rice), and woody (peach) features (Table 5). Estimations given in Table 5 are prone to uncertainty: differences are likely to appear, depending on the lab, methods, tissues, sequencing techniques, and associated sequencing errors. Yet the values are in the same order of magnitude in different kingdoms and species (from 0.3 in yeast to 194 in rat, $\times 10^{-9}$). And the four plants for which data are available are not showing higher mutation values, but rather intermediate rates, between the smaller ones of yeast, worm, and insect on one side, and the higher ones in mammals on the other side. The study of mutation-rate differences between species reveals relationships between genome size, effective population size, and mutation rate, with no direct causality assumed (Lynch 2010; Lynch et al. 2016). Interpretations are not trivial, as natural selection is supposed to work at the generation level to improve replication fidelity, and thus supposed to minimize the mutation rate at the cell level (Lynch et al. 2016).

5 The genetically heterogeneous individual plant

5.1 Are cultivated plants biasing views?

Whitham and Slobodchikoff (1981) acknowledge that evidence for somatic mutations in plants is mostly found in horticultural literature. To defend this bias in their supporting references, they offer that Darwin also "relied heavily on such literature," drawing on domesticated species for evidence in *The Origin of Species*. However, this analogical reasoning and argument from authority does not justify the bias. In a similar way, Gill et al. (1995) state that "the propagation

Table 5: Mutation rates per nucleotide site per generation in different species ($\times 10^{-9}$)

Species	Mutation rate	Reference
Yeast, *Saccharomyces cerevisiae*	0.3	(Lynch et al. 2008)
Worm, *Caenorhabditis elegans*	2.7	(Denver et al. 2009)
Insect, *Drosophila melanogaster*	3.5	(Keightley et al. 2009)
Plant, *Cynodon dactylon*	10.5	(Caetano-Anollès 1999)
Plant, *Arabidopsis thaliana*	7.0	(Ossowski et al. 2010)
Plant, *Oryza sativa**	1.7	(Yang et al. 2015)
Plant, *Prunus persica*	7.8	(Xie et al. 2016)
Rat, *Rattus norvegicus*$^+$	194	(Lynch 2010)
Mouse, *Mus musculus*$^+$	118	(Lynch 2010)
Human, *Homo sapiens*	25	(Nachman, Crowell 2000)

*mean value: 3.2 for an heterozygous plant and 0.11 for an homozygous plant
$^+$mean value over 8 (rat) and 7 (mouse) different tissue estimations

of bud sports in horticulture proves the existence and importance of genetic variation within clonal plants." Studies dealing with variations among ramets of a same clonal parent seem to be restricted to laboratory culture, greenhouses, and agriculture (Buss 1985).

Indeed, variants have been artificially reproduced when aesthetic and commercial novelties have spontaneously appeared in cultivated species. These are related to somatic mutations caused by physical and chemical agents (D'Amato 1997). Such variants are bud sports, a typical phenomenon observed during plant and (particularly) horticultural selection, which has been employed by humans for thousands of years. In 1845, Darwin wrote, as if it were obvious: "it is familiar to every one, what singular and numerous peculiarities are transmitted with certainty, by buds, layers, and grafts, which by seminal propagation never or only casually reappear" (Darwin 1845). In 1936, Shamel and Pomeroy (1936) observed that in the USA, between 1931 (the date of the first plant patent) and 1936, 33% of fruit patents were of bud origin, with a long list of such origins in flowers and ornamental plants as well. Herrera (2009) stresses the overrepresentation of cultivated plants in the study of plant diversity, stating that, if cultivated and wild plants are not expected to differ in biological features, they might differ in the frequency with which certain biological phenomena occur.

Intraorganismal genetic heterogeneity might not threaten the integrity of the individual, but may rather be adaptive (Folse and Roughgarden 2012), as mutations in some parts of plants could provide them with a resistance against pests (Antolin and Strobeck 1985; Lev-Yadun 2014). Adaptation to changing environmental conditions is a challenge for sessile organisms like plants that do not have animal-type mobility for escaping. Hence intraorganismal selection could be a way for them to circumvent this limitation (Clarke 2011). This idea has not been much explored (Pineda-Krch and Lehtilä 2004), and, moreover, the study of within-plant variation has been largely neglected (Herrera 2009). The genetic mosaic[6] theory of plant defense (Whitham and Slobodchikoff 1981; Gill et al. 1995) suggests that within-plant genetic mosaics caused by somatic mutations might have direct ecological and adaptive significance, contributing to the defense of long-lived plants against short-lived herbivores (Herrera 2009). Published studies aiming to evaluate the importance of intra-individual genetic variability in plants are

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[6] "Chimerism" refers to an individual composed by two or more fused genotypes that come from different zygotes. A mosaic individual is composed of two or more genotypes that originated from a single zygote but diverged during mitotic (somatic) growth (Clarke 2011).

scarce, and this is not just a recent trend (Sutherland and Watkinson 1986; Herrera 2009). In addition, it has been difficult to prove that such variations have been sources of clear gains in fitness for plants, and that intra-individual variations provide protection against predators (Buss 1985). In a review of intra-individual genetic variations observed in species from bacteria to vertebrates, Pineda-Krch and Lehtilä (2004) acknowledge that horticultural and cultivated plants are over-represented examples. They cite papers showing variations in a fig tree used for bonsai, in juniper, tobacco, pelargonium, and maize. Except in two studies dedicated to mangrove trees and fig trees from Panama, all these species are intensively manipulated for and by humans. Published examples of mosaicism observed in plants include a single eucalyptus tree showing variation for volatile oil composition (Edwards et al. 1990). It is one of the very few genetic mosaics that have been described among non-clonal plants and non-crop species (Padovan et al. 2013). In the morning glory *Ipomoea*, somatic mutations caused by the excision of a transposon create heritable flower color variations (Inagaki et al. 1996). The flower color phenotypes are thought to have been selected by pre-Columbian peoples who favored plants answering in more flexible ways to their domestication wishes (Glover et al. 1996; Clegg and Durbin 2000).

In a thorough review, Herrera (2009) observes that descriptions of genetic mosaicism among cultivated plants are abundant, while there is very little evidence gathered from wild plants, and that evidence is mostly gathered in an indirect way. Noticing the extreme scarcity of unambiguous cases of genetic mosaics in wild plants, despite biased research efforts toward species expected to be more prone to mosaics (long-lived, clonal, highly branched), Herrera hypothesizes that they are far less frequent among wild plants than among cultivated plants (Herrera 2009). Domesticated peach, compared to wild peach, did not show any increase in recombination rate and mutation rate near recombination events in a sequencing study (Wang et al. 2016). However, no general conclusion can be derived from this unique study with its sample size of one.

On the one hand, the plant species selected by human for domestication have, according to Darwin, “an extraordinary tendency to vary and likewise to withstand diverse climates” (Darwin 1876, cited by Brown 2010), as phenotypic diversity is generated by human selection on plant species. On the other hand, according to more recent studies, domestication reduces cultivated species’ global genetic diversity compared to wild species. This opposition constitutes what is called “the Darwin paradox” (see Glémin and Bataillon 2009, on grasses). In common bean, for instance, domestication has a pervasive effect throughout the genome for both gene expression patterns and diversity, and it is responsible for an overall reduction in diversity associated with an increase in the functional diversity at target loci (Belluci et al. 2014). The genetic diversity of cultivated species, engineered by human agency, is indeed particular (Gerber 2018).

The place of domesticated plants in the debate about plant individuality must therefore be questioned. If, as Hull (1992) said, vertebrates bias the way biological individuality is understood, cultivated plants might similarly bias the way plant individual heterogeneity is understood, and thus our understanding of plant individuality as a whole.

5.2 *Molecular stories from the herbiary*

When data are available, comparison of assertions made about particular plant species with information provided by genetic diversity analyses of the same species can be enlightening. Let’s have a look at some species from our herbiary that have been studied in this way.

The genetic diversity of Pando, our large aspen clone, was studied with microsatellite markers, and Mock et al. (2008) showed that over 256 ramets analyzed, only 6 different variants were exhibited, suggesting that the clone, albeit covering a large surface, had an origin too recent to harbor many somatic mutations. In a broader zone, a large number of different genotypes was revealed. The hypothesis of a predominantly clonal evolution of the population did not fit with the observations. Hence, sexual reproduction through gene flow had more influence on the population's evolution than somatic mutations related to clonality did (Mock et al. 2008; DeWoody et al. 2008). Genetic diversity is probably also maintained thanks to root graft between different trees: roots surviving below trees which had been dead for several years were observed (Jelínková et al. 2009). The few papers dealing with plants in philosophy of biology often refer to the Pando case. Clarke (2011), for instance, writes: "There are known aspen genets that are 50,000 ramets strong and estimated to be over 10,000 years old." Godfrey-Smith (2009) suggests "we have hundreds of distinct ramets, but a single genet, or genetic individual." The Pando genetic-analysis results probably contradict these assertions. If clonality is indeed important in Pando, sexual reproduction is present, providing genetic novelty. Moreover, the clone is much more recent than previously assumed, and somatic mutations, supposed to play a major role in the clone functioning, are not that important. Trends similar to Pando were observed in other *Populus* species in Spain, in a hybrid *Populus alba-Populus tremula* clonal zone (Macaya-Sanz et al. 2016).

Our apomictic *Taraxacum* species, dandelion, highlighted by Janzen (1977), has also been studied with molecular tools. Genetic mutations were detected between generations, at a low rate, in the absence of sexual reproduction—that is, without meiosis (King and Schaal 1990). In the same species, different stresses were similarly shown to trigger considerable DNA methylation variation throughout the genome, and that was inherited through successive generations, highlighting the potential of epigenetic inheritance in evolutionary processes (Verhoeven et al. 2010). Additionally, sexual reproduction appeared to be more important in this species than previously assumed (Majeský et al. 2012). Hence, the "large tree" suggested to describe a population of dandelions might not be as homogeneous as is supposed by Janzen.

One of the oldest domesticated species, grapevine, is particularly well studied with the tools of molecular biology. Vegetative propagation (through grafting) is a way to keep clone's interesting traits unchanged, yet the older the varieties, the higher the chance of finding differing individuals, as a result of somatic mutations (Crespan 2004). Sexual reproduction remained important in the history of vine domestication, as can be observed in pedigree reconstruction; for instance, Chardonnay resulted from a cross between Pinot and Gouais blanc (Bowers et al. 1999). Mobile elements represent 40% of the grapevine genome, and exhibit a high activity compared to *Arabidopsis* and *Populus* genomes (Pelsy 2010; Jiang and Goertzen 2011). They might play an important role in plant evolution, in cultivated as well as wild plants, and could partly explain the peculiarities of this kingdom (Biemont and Vieira 2006). Among other traits, berry skin color, probably dark at the origin, was turned light by transposition and maintained by domestication. The cluster size and shape of the cultivar Carignan were modified by transposon activity (This et al. 2006; Pelsy 2010; Fernandez et al. 2010). Sexual reproduction, with recombinations, provides one of the mechanisms suppressing mobile elements. On the opposite side, long term vegetative propagation—associated with aggressive management toward plants to increase productivity (grafting, pruning, etc.) and derived consequences (pathogen attacks, UV effects, etc.), and notably characteristic of viticulture—stimulates the spread of mobile elements (Jiang and Goertzen 2011). Rice domestication displays the same trend (Naito et al. 2006).

The phenotype of an organism can be modified by some epigenetic[7] information, that can be conserved and inherited in a stable way. Examples are described in wild and cultivated plants (Jablonka and Raz 2009): the symmetry of the *Linaria vulgaris* flower is modified by a methylation that is heritable (Cubas et al. 1999), epigenetic implications of ripening were shown in tomato (Ecker 2013), heritable epigenetic variation of complex traits was described in *Arabidopsis thaliana* (Cortijo et al. 2014), and local adaptation was explained by epigenetic changes in the same species (Bewick and Schmitz 2015). DNA modification through cytosine methylation, related to transposable elements (Law and Jacobsen 2010), is one of the mechanisms that can produce epialleles stably transmitted during meioses, having transcription effects and therefore consequences for morphology.

Overall, the detailed genetic analyses of some plant species from our herbiary provide contrasting visions of plant diversity. On the one hand, clonality is indeed important in aspen, but sexual reproduction, which supplies genetic novelty, is still there, and the clone, which is much more recent than assumed, exhibits few somatic mutations. Similarly, dandelion possesses sexual reproduction that has been underestimated and exhibits epigenetic variations. Grapevine genetic diversity has been determined by viticultural practices that favored the emergence of phenotypic novelties (and their maintenance), mostly through somatic mutations and the spread of transposons. We see here that human management of plants and their domestication have consequences for the generation of diversity and for its conservation. Epigenetic mutations' effects on phenotype were recently described in plants and constitute another original genetic mechanism creating diversity. Molecular stories of the herbiary are rich and sometimes reveal phenomena that were not previously foreseen.

6 Is a plant a true genetic community?

Following insights into the complexity of plant genome, we must come back to the whole plant. If the architectural models from botanists described above, used to analyze plant growth, were extended to a genetic dimension, a single tree could be made of a population of genotypes. This is indeed exactly what French botanist Hallé asserts in popular books with large audiences. Hallé states that the belief that trees are genetically homogeneous comes from an animal interpretation of these organisms. He assumes that their sizes and lifespans, much greater than those of animals, should influence their genetic constitution (Hallé 2005). He launched experiments to study the possible genetic heterogeneity of at least six single tropical trees with genetic markers—two species in Guyana (1996), one species in Gabon (1998), and three species in Madagascar (2002). However, no variation "consistent with the tree structure" was detected, and no scientific publication was produced (M. H. Chevallier, C. Lanaud, personal communications, 2013).

Population geneticists working on forest trees (usually wild but also planted species) will probably not be surprised by these unpublished results. Indeed, in their studies, population geneticists sample various kinds of material (leaf, phloem, cambium, and bud) from any part of a tree to obtain its genotype. The observed intra-tree heterogeneity remains low, with a rate of the same order of magnitude as genotyping error. The consistency of a single tree genotypic information makes it possible, for instance, to reconstruct relatedness and perform successful parentage analyses (Gerber et al. 2014).

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[7] "Epigenetic": when the environment and the individual history generate lasting changes of the genome thanks to epigenetic mechanisms (without modifying the DNA amino-acid sequence). Changes are reversible but also transmitted to subsequent generations. It is close to the Lamarckian notion of inheritance, "heritability of acquired characteristics."

The assumption made by Whitham and Slobodchikoff (1981) can therefore be questioned. They write that "since a plant is a population of competing buds which grow at different rates and regenerate each year (Harper 1977), the gene frequency of the plant or clone can change over a period of years and the parent genotype may be completely lost." This sentence is illustrated by the example of an ornamental maple, *Acer platanoides Drummondii*, with variegated leaf color, in which genetic mosaicism is artificially maintained. This hypothesis of a loss of parental genotypes, illustrated with a cultivated plant example and cited by Clarke (2011), does not correspond to the everyday experiments of tree population geneticists, who observe consistent genetic data over the space of tree organisms and their generation time. The Pando genetic analysis is in accordance with these experiments, suggesting a minor importance for somatic mutations, far from the one previously assumed.

The rate of molecular evolution is driven by generation time; it is low in trees and shrubs, which have long generation times, as compared with herbaceous plants, which have shorter generation times (Smith and Donoghue 2008). Families of taller plants are characterized by lower mutation rates per unit of time in nuclear, chloroplast, and mitochondrial genomes (Lanfear et al. 2013; Bromham et al. 2015). Moreover, somatic mutations accumulate during plant aging (Dubrovina and Kiselev 2016). Accordingly, in testing on compiled data (122 species) the possible difference between within-plant phenotypic variability of small, short-lived plants, in comparison with large, long-lived plants, no greater subindividual variability among comparatively larger and longer-lived plants was observed (Herrera 2009).

Using cell-lineage analysis and modeling, Burian et al. (2016) show that the reduction of cell division in apical meristem formation is similar to the one existing in the animal's germline, with a clear separation inside the organism. Surprisingly, the plant is also setting aside a quiescent population of cells for gamete production (Groot and Laux 2016). Burian et al. (2016) suggest that stem cell sequestration, meristem geometry, and intra-organismal competition thwart mutational meltdown, the accumulation of deleterious mutations. Contradicting the commonplace idea of highly heterogeneous plants, and especially trees, these mechanisms extend plant lifespan, a result also shown by Watson et al. (2016). The demonstration of the presence of a slowly dividing functional germline in most plant species is about to bring them much closer to animal functioning (Lanfear 2018). The idea that Weismann's theory is contradicted in plants is therefore put into question.

Nevertheless, estimation of the existence and the importance of intra-individual diversity in trees and plants remains to be done, by assessing and comparing variability at the different genome layers (with -ome suffixed names: genome, transcriptome, proteome, methylome, epigenome, mobilome, etc.). This will help us understand the levels of diversity, their origins, their phenotypic effects, and their evolutionary importance. The analysis of genome-wide changes due to crop domestication and breeding is now reachable (Shi and Lai 2015).

Genotyping errors are of course always present, due to mistakes that can take place at any step of experiments, from sampling errors to molecular biology reaction problems, to miscoding of samples or data, to error in analyses, and others. Genotyping errors can also be confused with true mutations, somatic mutation frequency probably being lower than mistyping rate. But there is no reason why those errors should be more numerous in plant studies than in animal studies.

Several studies have aimed to analyze within-plant genetic heterogeneity. Results are often unclear, or unpublished, or support limited possible generalizations.

In a short news publication, Yong (2012) described the genome-wide sequence analysis of several samples of black cottonwood trees (*Populus trichocarpa*), with reference to its genome, which was fully sequenced in 2006. The reported results say that connected clones have many genetic differences, even between tissues from the top and bottom of a single tree: "the variation within a tree is as great as the variation across unrelated trees." However, the study is still unpublished (B. Olds, personal communication, 2014).

A study looking for systematic genome sequence differences among leaf cells within individual trees was performed on Japanese beech (*Fagus crenata*) and Yoshino cherry (*Prunus × yedoensis*), using an indirect technique called genome profiling (Diwan et al. 2014). Several steps are involved in this technique that probably generate uncertainty and inaccuracy, many replicates should have been done, and sample variation should have been given. The results thus appear unreliable.

We have identified at least three studies aimed at evaluating the DNA variability inside a single pedunculate oak tree (*Quercus robur*) based on recent sequencing technologies. The first project was presented in 2011[8] and considered a 600-year-old tree. Four leaves from three branches were compared by high throughput sequencing, and almost 8000 point mutations were identified between branches (M. Blaxter, personal communication, 2013). No published results are available. The second project (Napoleome) aimed at sequencing the genome of two leaf samples collected at the top and bottom branches of a single 200-year-old oak tree on the Lausanne University campus. A low number of somatic mutations was detected (Schmid-Siegert et al. 2017). The third project was launched in 2011. The studied tree is about 100 years old. Its genome was sequenced and assembled. The DNA from three branches of this tree were resequenced. There were 2.7 times more somatic mutations ascertained than in the previous study, thanks to more resolving methods. The sequencing of acorns from two of the branches allowed researchers to trace the transmission of some of the somatic mutations. However, no global rates could be estimated from the study, somatic mutation remaining at frequencies too low to be unambiguously detected (T. Leroy, personal communication, 2016; Plomion et al. 2018).

Sequencing technologies now offer full genomes and somatic mutation detection is feasible. The possible confusion between a true mutation and an error can be solved by experimental designs. The two oak sequencing studies published reveal a limited number of somatic mutations and some transmission to offspring. Estimation of intra-individual somatic mutation will probably be achievable when technical limitations are overcome.

7 Conclusion

The herbiary of plant individuality is composed of several members (Table 6), species differing in their traits—variously trees, woody, or herbaceous species, wild or cultivated, and even a lab species—and studied to answer different questions related to plant diversity and individuality. Looking more precisely at one of the members—a well-known one, present in many published texts—hypotheses about the history of the aspen clone Pando have stated that it was the result of a very ancient clonal reproduction, producing genetically identical trees, on a large surface, with no (or very little) sexual reproduction. Recent scientific publications have assessed the genetic diversity of these trees, and overall they cast doubt on these "classical" hypotheses. Clonality is not as ancient as announced. Diversity is present, but it is not explained by what was assumed—that somatic mutations accumulated during the long life-history of the clone—but rather by gene flow and sexual reproduction. In species with a largely clonal reproduction, sexual reproduction, even at a low rate, is often maintained.

The examples analyzed in the present study suggest that wild plants are not genetic mosaics. Rather, humans have favored and maintained a particular kind of diversity in some cultivated

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[8] "Evaluating somatic mutations in long living organisms: The Birnam Oak Project." Pablo Fuentes-Utrilla, John Davey, Cathlene Eland, Mark Blaxter, Karim Gharbi (The University of Edinburgh), 7 September 2011, 3rd UK RAD Sequencing Meeting, John McIntyre Conference Centre, Edinburgh.

Table 6: The herbiary of plant individuality

Plant type	Domestication*	Species	Studied features related to plant individuality questions
Tree	w	Oak, *Quercus* sp.	Unique plant, sameness through times, sequencing intra-individual variability
Tree	w	Aspen, *Populus tremuloides*; Poplar, *Populus alba-Populus tremula*, *Populus trichocarpa*	Clonality, longevity, asexual reproduction, aging, mutations
Tree	w, c	Mangrove tree, Fig tree, Juniper, Beech, *Fagus crenata*, Yoshino cherry, *Prunus* × *yedoensis*	Intra-individual genetic variability
Tree	w	Weymouth pine, *Pinus strobus*	Indirect somatic mutation rate
Tree	w	Eucalyptus (one tree), *Eucalyptus melliodora*	Mosaicism
Tree	c	Maple, *Acer platanoides Drummondii*	Mosaicism
Tree	w&c	Peach, *Prunus persica*	Sequencing, mutation rate, wild/domesticated
Woody	w	Lowbush blueberry, *Vaccinium angustifolium*	Indirect somatic mutation rate
Woody	c	Grapevine, *Vitis vinifera L.*	Somatic mutations, transposons, epigenetics
Herbaceous	c	Tobacco, *Pelargonium*, Maize	Intra-individual genetic variability
Herbaceous	w	Dandelion, *Taraxacum officinale*	Asexual reproduction, physiologically independent clonal units
Herbaceous	w&c	Violet, *Viola*; Strawberry, *Fragaria*; Thyme, *Thymus praecox*	Clonal reproduction
Herbaceous	c	Bermuda grass, *Cynodon dactylon*	Sequencing, mutation rate
Herbaceous	l	Arabidopsis, *Arabidopsis thaliana*	Sequencing, mutation rate, epigenetics
Herbaceous	c	Rice, *Oryza sativa*	Sequencing, mutation rate
Herbaceous	c	Morning glory, *Ipomoea nil*	Somatic mutation, transposon, domestication
Herbaceous	w	Toadflax, *Linaria vulgaris*	Heritable epigenetic mutation
Herbaceous	c	Tomato, *Solanum lycopersicum*	Heritable epigenetic mutation
Herbaceous	w	Fern, Algae, *Volvox carteri*	Complicated life cycle

*wild (w), cultivated (c), lab species (l)

plants. The existence of somatic mutations and their inheritance has been demonstrated, but with a rate much smaller than is commonly claimed. DNA sequencing suggests, in contrast to what has often been assumed, that an old oak tree is not a population of genetically variable branches (Kuhlemeier 2017; Plomion et al. 2018).

Hutchings and Booth (2004), writing about intra-organismal variability, and citing a much earlier similar statement by Harper (1988), point out that there is much more willingness to accept the importance of this variability, and its adaptive significance, than there is supporting data. Curiously, we can still make the same observation. As Herrera (2009) puts it, cultivated plants probably represent a heavily biased subsample of the plant world, one characterized by a particularly high incidence of genetic mosaicism. This mosaicism is maintained by vegetative propagation and thus uninterrupted by meioses.

Individuality has been questioned at all living levels, from gene to community (Michod 1999), and genetic analyses are, similarly and rather recently, examining different levels of genome diversity—genome, transcriptome, proteome, methylome, epigenome, mobilome, etc. These levels contribute to different types of information and generate complexity through their interactions. Plant phenotypes might be largely affected by these mechanisms, and especially so in cultivated species.

We suggest that plants might not be so different from animals in terms of their genetic heterogeneity, and recent results derived from studying plant cellular functioning bring plants much closer to animals than Weismann thought they were (Burian et al. 2016; Watson et al. 2016). We suggest that cultivated plants have been subject to specific human selection that has made them probably quite different from wild ones, especially in terms of their genetic diversity and heterogeneity. In parallel with the "vertebrate bias" identified by Hull, we argue that a "cultivar bias" exists in our knowledge of plant-diversity.

These points being settled, we think that plants do not threaten the general idea of biological individuality. If we want to see a plant as a community, let's follow the call for a pluralism in defining individuals' edges and consider biological entities like metaorganisms. Metaorganisms are made of disparate elements working together: genomic mosaicism, external and internal symbionts, microbiota, epigenetic elements, and others (O'Malley and Dupré 2007; Dupré 2010). In the plant kingdom, but also in the other kingdoms, multi-organism individuals do emerge and especially challenge homogeneity (Bouchard 2014).

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