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Viewpoints

Greenbeards in plants?

Summary

Greenbeards are selfish genetic elements that make their bearers behave either altruistically towards individuals bearing similar greenbeard copies or harmfully towards individuals bearing different copies. They were first proposed by W. D. Hamilton over 50 yr ago, to illustrate that kin selection may operate at the level of single genes. Examples of greenbeards have now been reported in a wide range of taxa, but they remain undocumented in plants. In this paper, we discuss the theoretical likelihood of greenbeard existence in plants. We then question why the greenbeard concept has never been applied to plants and speculate on how hypothetical greenbeards could affect plant–plant interactions. Finally, we point to different research directions to improve our knowledge of greenbeards in plants.

Greenbeard theory and empirical examples

In his foundational work, Hamilton demonstrated that genetic relatedness between individuals is a key driver of social evolution (Hamilton, 1964b). In particular, he showed that individuals need to be related for altruism to evolve. However, Hamilton also highlighted that individuals do not need to be related across their entire genome. To illustrate this, he imagined a hypothetical gene (or a cluster of tightly linked genes) with three functions: (1) generating a signal that is perceivable to other organisms; (2) perceiving this signal when present in other organisms; and (3) adjusting social behaviour in such a way that altruism is directed preferentially towards individuals from which the signal is perceived (Hamilton, 1964a). He then showed that such genetic elements would be favoured by natural selection whenever social partners share similar copies, even if their relatedness is no greater than expected by chance in the rest of their genome. This simple thought experiment illustrates that altruism is a selfish behaviour from the perspective of the genes. Dawkins later coined the term ‘greenbeard’ to illustrate Hamilton’s idea in a scenario where altruistic individuals would bear a greenbeard and preferentially direct altruism to other greenbeard bearers (Dawkins, 1976).

It is not clear whether Hamilton’s thought experiment was intended to be a testable empirical prediction. In fact, greenbeards were initially thought to entail a biologically unrealistic degree of pleiotropy (Madgwick *et al.*, 2019). Theoretical works also suggested that, if greenbeards were to appear, there would be multiple constraints on their maintenance. For example, several

types of greenbeards only have an advantage when they reach a critical frequency in the population, which means that they will only spread under restricted conditions, for example population viscosity (Gardner & West, 2010). Greenbeards can also be easily invaded by ‘falsebeards’, mutated copies, which do not engage in the costly social behaviour, but benefit from it by expressing the greenbeard signal (Dawkins, 1976, 1982; Gardner & West, 2010; Biernaskie *et al.*, 2013). Finally, if greenbeards do fixate, they are likely to remain undetected because all individuals will behave in the same way (Dawkins, 1982; Crozier, 1986; Rousset & Roze, 2007; Gardner & West, 2010).

Despite all these constraints, empirical research has reported an increasing number of greenbeards over the last two decades (see review in Madgwick *et al.*, 2019; Fig. 1). The first greenbeard was discovered in the fire ant *Solenopsis invicta* (Keller & Ross, 1998). In this species, the greenbeard effect is associated with a supergene that comprises two haplotypes: the *Social b* (*Sb*) and *Social B* (*SB*) haplotypes. Workers bearing the *Sb* haplotype identify homozygous *SB/SB* queens based on their cuticular chemical profile and kill them before they can reproduce, favouring the *Sb* haplotype (Zeng *et al.*, 2022). Further greenbeard examples, mostly in microorganisms, showcased the various ways a single genetic element can selfishly increase its reproductive output using interactions between individuals, which led to the identification of four basic greenbeard types (Gardner & West, 2010; Madgwick *et al.*, 2019; Fig. 1).

The empirical literature on greenbeards has expanded the scope of the initial thought experiment of Hamilton by showing that greenbeard genes can evolve and operate in a wide range of taxa, including animals, fungi, and prokaryotes. However, no greenbeard has been reported in plants. In this paper, we: (1) discuss the theoretical likelihood of the existence of greenbeards in plants; (2) propose explanations as to why greenbeards have not been reported in plants; (3) speculate on the nature and mode of action of hypothetical greenbeards in plants; and (4) suggest directions for future studies on greenbeards in plants.

Are there theoretical limitations to the existence of greenbeards in plants?

Greenbeards rely on interactions between individuals (Hamilton, 1964a; Dawkins, 1976; Gardner & West, 2010). Plants interact in many ways, particularly through resource competition (e.g. competition for nutrients, water, or light; Tilman, 2020). Plants can also interact through chemical compounds released into the air or into the soil, which have classically been associated with toxic effects (i.e. allelopathic compounds; Hierro & Callaway, 2021). More indirectly, plants can affect their neighbours by modifying the local abiotic or biotic conditions (e.g. by changing the chemical or physical properties of

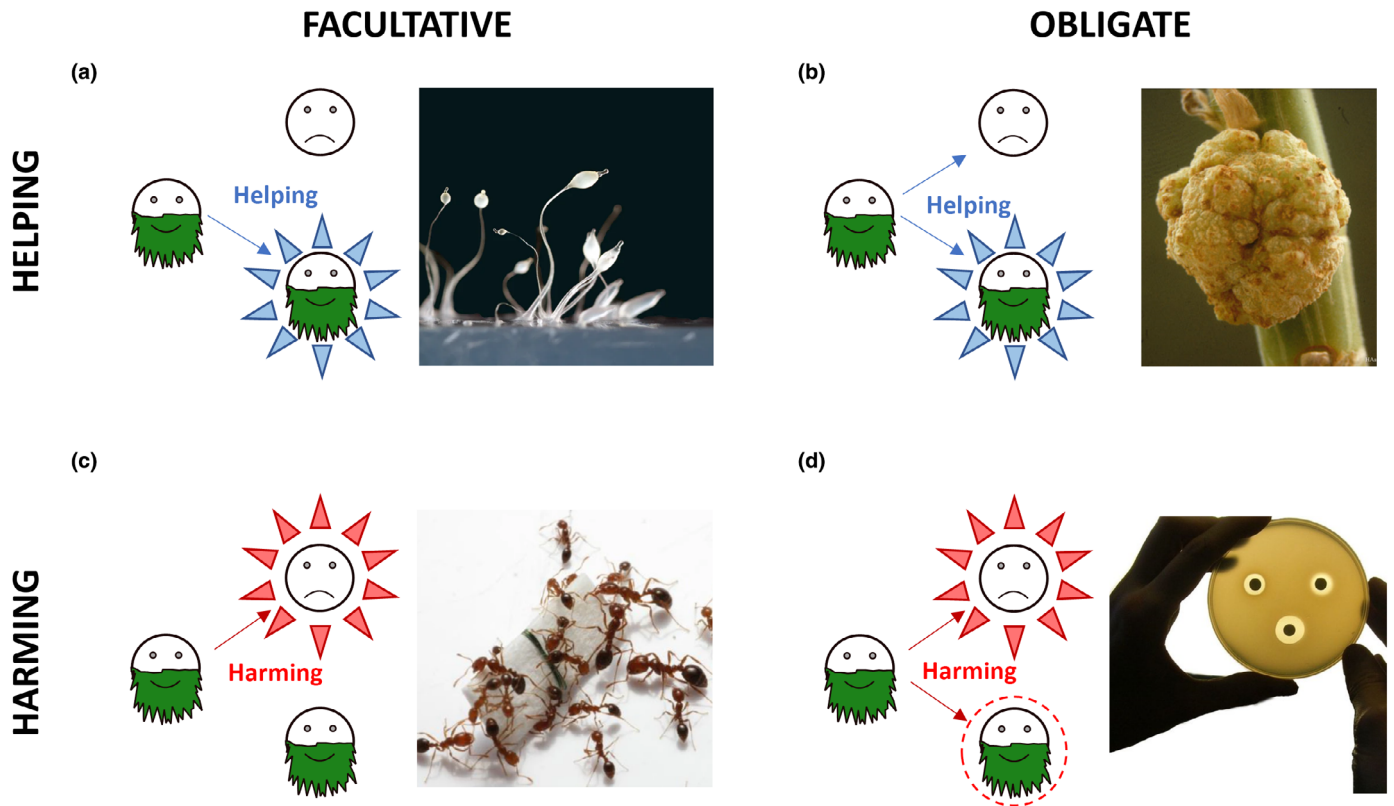


Fig. 1 Greenbeard typology (redrawn from Gardner & West, 2010; Gardner, 2019 with permission). Theoretical extensions have generalized the concept of greenbeards, accounting for the multiple ways through which a gene can increase the relative reproductive output of similar gene copies present in other individuals (Gardner & West, 2010; Madgwick *et al.*, 2019). Facultative helping, as initially proposed by Hamilton, is one type of greenbeard where carriers express altruistic behaviour only towards other greenbeards carriers. A famous example is the aggregation behaviour displayed by the unicellular amoeba *Dictyostelium discoideum*. When food runs out, individuals carrying the same allele at the *csA* gene can adhere to each other and form a single cooperative fruiting body, excluding individuals bearing a different allele (Queller *et al.*, 2003; a, typical fruiting bodies of *D. discoideum*; photo credit, A. Wild). The helping behaviour can also be obligate, meaning that it is always expressed by the greenbeard carrier, but only other greenbeard carriers can benefit from it. For example, the pathogenic bacteria *Agrobacterium tumefaciens* can infect plant tissues by inserting a plasmid into their root (tumour inducing (Ti) plasmid) where it induces cell division and the synthesis of opines, an energy source that can only be used by bacteria carrying the same plasmid (White & Winans, 2007; b, a typical tumour induced by *A. tumefaciens*; photo credit, H. Aarnes). Instead of helping similar gene copies, greenbeards can also be harmful towards alternative gene copies, which results in the same evolutionary outcome. In fact, the first greenbeard gene ever reported is based on such harmful behaviour in the fire ant *Solenopsis invicta* (Keller & Ross, 1998). In this species, a supergene allows workers to identify queen genotypes based on their cuticular chemical profiles and to eliminate the queens that do not share the same haplotype (c, *S. invicta* workers attacking a surrogate queen made of a paper dummy soaked with cuticular extracts; photo credit, K. Ross). The harmful behaviour is facultative because it is only expressed towards alternative gene copies. As with helping greenbeards, harmful greenbeards can be indiscriminate, in which case only non-greenbeard individuals are impacted by the harmful behaviour. Bacteriocin genes typically operate as obligate harming greenbeards. These genes are expressed in most bacterial lineages where they produce a toxin (bacteriocin), which only harms bacterial clones that lack the bacteriocin-producing gene (Riley & Wertz, 2002; d, filter paper discs soaked with regular antibiotic (left), bacteriocin (right) and the two in combination (bottom) create inhibition zones within which bacteria cannot grow; photo credit, S. Bakkal & M. Riley). This selective toxicity arises from tight linkage between the bacteriocin-producing gene and the gene encoding the toxin deactivator.

the soil, or by acting as a physical barrier against pathogens; Callaway, 1995). It is reasonable to think that at least some of these effects can be controlled by one or few loci (e.g. genes involved in the production of allelopathic compounds, or genes involved in pathogen resistance). There are thus multiple ways through which a gene in a focal plant can affect the fitness of its neighbours. Moreover, because plants cannot move away from their neighbours, the effect of any potential greenbeard (for either of the helping or harming type, see Fig. 1) on the fitness of similar or alternative gene copies is expected to be strong as it would accumulate over the whole life of the organisms.

Greenbeards are based on a mechanism that detects allelic similarity/dissimilarity at the greenbeard locus in other individuals, such as the use of cuticular chemical profiles to distinguish the *Sb* from the *SB* haplotype in the fire ant (Keller & Ross, 1998; Zeng *et al.*, 2022). Recently, multiple studies have reported differential phenotypic responses of plants when exposed to kin vs non-kin neighbours, which could be compatible with a genetic recognition mechanism (but see the limitations of these studies in the next section; Dudley & File, 2007; Karban *et al.*, 2013; Crepy & Casal, 2015; Torices *et al.*, 2018). Even if such a mechanism has not been described so far, we know that plants have already evolved

genetic recognition mechanisms in the context of sexual reproduction. Self-incompatibility (SI) systems prevent self-fertilization and inbreeding in *c.* 40% of flowering plant species. Self-incompatibility is often mediated by a single genetic element (the *S* locus, which encompasses several genes, notably a male and a female determinant). In most SI systems, interactions between pollen and stigma proteins that originate from the same Shaplo type in the male and the female lead to the arrest of the growth of the pollen tube and thus to the failure of fecundation (Fujii *et al.*, 2016). However, SI is not greenbeard-like since the effect is within a single individual and because high relatedness at the SI locus results in the absence of fertilization and, consequently, lower fitness – the opposite of the greenbeard mechanism. However, SI systems illustrate that plants already have evolutionary mechanisms that enable genetic recognition at a single locus – a key feature of greenbeard genes.

A necessary condition for the maintenance of the greenbeard effect is that the locus controlling the fitness effect ('behaviour locus') and the locus controlling the recognition mechanism ('matching locus') are maintained in tight linkage disequilibrium and transmitted as a single mendelian unit (Rousset & Roze, 2007). The multiplication of supergene discoveries in recent years suggests that such strong association between co-segregating loci might not be as uncommon as previously thought, including in plants (e.g. Joron *et al.*, 2011; Li *et al.*, 2016; Helleu *et al.*, 2022). In many cases, co-segregation results from chromosomal rearrangements that suppress recombination between the different genes (Gutiérrez-Valencia *et al.*, 2021). For example, the *Sb* haplotype of *S. invicta* results from three large inversions (Yan *et al.*, 2020), and the *S* locus in *Primula vulgaris* from one insertion (Li *et al.*, 2016). Such chromosomal rearrangements could as well create a genetic association between a recognition locus and a locus involved in plant–plant interactions, and, as such, be at the origin of a greenbeard.

Why have greenbeards never been reported in plants?

Social evolution concepts were first applied to plants in the late 90s when multiple empirical studies showed that kin selection could affect plant–plant interactions in the wild (Goodnight, 1985; Stevens *et al.*, 1995; Kelly, 1996; Donohue, 2003). However, it is not until recently that social evolution theories have really started to percolate into plant sciences (Biedrzycki & Bais, 2010; Dudley *et al.*, 2013; Anten & Chen, 2021). Despite the recent multiplication of studies on kin selection and kin recognition in plants, greenbeards have never been reported. The greenbeard concept has not even been applied to plants. How can we explain this?

A primary and simple reason is that few people working with plants are familiar with the field of social evolution. Despite recent efforts to popularise social evolution concepts among plant scientists (e.g. Dudley, 2015), a historical gap remains compared with animals and microorganisms where researchers have largely appropriated social evolution principles (West *et al.*, 2021). This historical gap has certainly contributed to limiting the diffusion of the greenbeard concept among plant scientists.

Perhaps due to this recent appropriation of social evolution concepts by plant scientists, the claim that plants can recognize the

genetic identity of their neighbours and change their phenotype accordingly is still debated (e.g. Klemens, 2008; Till-Bottraud & de Villedemereuil, 2016; Pennisi, 2019). While many studies have reported differential phenotypic responses according to neighbour relatedness, the fitness consequences of these responses, when reported, do not always align with theoretical expectations (i.e. higher fitness in groups of kin vs groups of non-kin; Andalo *et al.*, 2001; Donohue, 2003; Milla *et al.*, 2009; Stachowicz *et al.*, 2013). Moreover, even if some mechanisms involving, for example chemical (Karban *et al.*, 2013) or spectral cues (Crepy & Casal, 2015), have been proposed to explain how plants could detect neighbour relatedness, no recognition mechanism has been described so far. Part of the confusion surrounding plant studies also stems from the experimental designs used to test neighbour recognition. In most experiments, individuals are typically grown with 'kin' vs 'non-kin' neighbours (Dudley & File, 2007; Murphy & Dudley, 2009; Biedrzycki *et al.*, 2010; Bhatt *et al.*, 2011; Fang *et al.*, 2013). First, these designs often explore a limited range of extreme relatedness values. For example, many studies use either clones or offspring obtained from highly selfing lineages as neighbours in their 'kin' treatment, corresponding to a scenario where $r \approx 1$. Consequently, the 'kin' treatment is actually closer to a 'self' treatment, and self-recognition rather than kin recognition can explain the results (Mazal *et al.*, 2023). Second, these designs have been shown to be poorly adapted to test for genetic recognition because confounding factors such as differences in competitive ability between genotypes (Masclaux *et al.*, 2010) or nonlinear relationships between vegetative and reproductive biomass (Ehlers & Bilde, 2019) can also result in a higher performance of kin groups compared with non-kin groups. Given current debates and challenges associated with social evolution in plants, it is not so surprising that the idea of a greenbeard, that is a single genetic element influencing plant–plant interactions for its own benefit, has not yet become a realistic and testable biological hypothesis in the eyes of most plant researchers.

How could greenbeards operate in plants?

A key difference between animals and plants, which is important in relation to interactions between conspecifics, is that plants do not move, so they cannot 'choose' with whom they interact, contrary to animals. There is currently no clear hypothesis regarding the role of motility and partner choice in the evolution of greenbeards. Recent theoretical results have shown that the ability to encounter multiple individuals before engaging in a social interaction is an important trait to stabilize kin recognition (Scott *et al.*, 2022). This may suggest that greenbeards of the facultative type (i.e. where the helping or harming phenotype is plastic) should be less likely to evolve in plants. However, empirical results in microorganisms show no clear relationship between motility and greenbeard types (Madgwick *et al.*, 2019).

The absence of motility does not seem to have been an obstacle to the evolution of selfish genetic elements in plants. For example, Pollen Killing (PK) genes cause hybrid incompatibilities and segregation distortion in several species, including *Arabidopsis thaliana* and rice (*Oryza sativa*; Ouyang & Zhang, 2013; Vaid &

Laitinen, 2019). These genes operate following a typical poison-antidote model (Yu *et al.*, 2018; Simon *et al.*, 2022; Fig. 2a): Before the meiosis that precede pollen production, two genes in tight linkage produce a long-lived poison and a short-lived antidote in the cytoplasm of the mother cell (the microsporocyte). After meiosis, the poison remains in all daughter cells (the microspores), but not the antidote, leading to the death of the daughter cells that do not bear the matching antidote allele. Because they ultimately

favour some gametes over others, PK genes are traditionally classified as segregation distorters and gamete killers. However, in most plant species, meiotic products are not gametes but gametophytes that later produce the ‘real’ gametes through additional mitoses and cellular rearrangements. In fact, pollen grains can be seen as haploid individuals (male gametophytes) that are released from the plants’ anthers, carry the male gametes, and have an independent life cycle in which they express their own

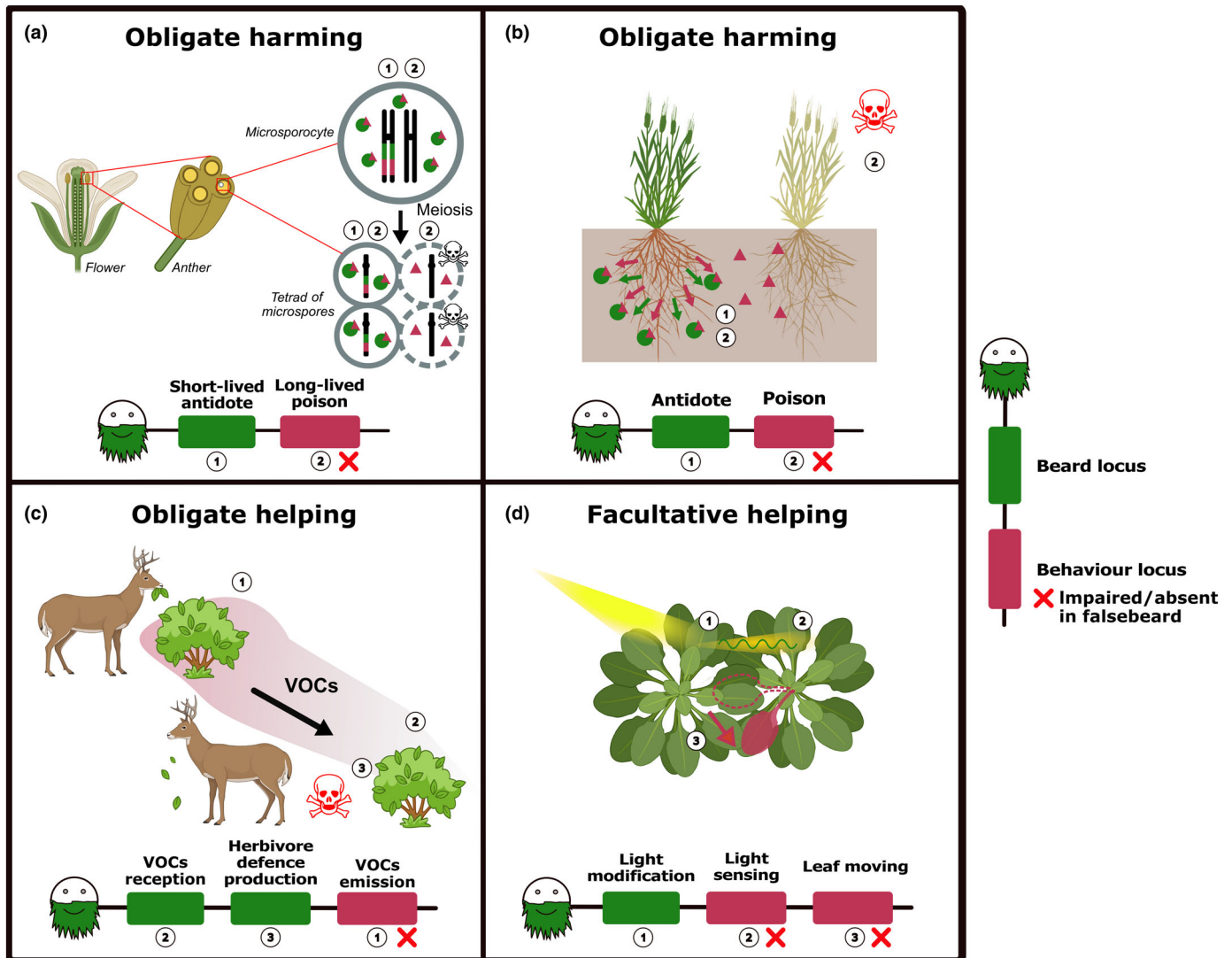


Fig. 2 Illustration of four hypothetical greenbeards in plants. (a) A Pollen Killing (PK) system revisited as a greenbeard. Pollen Killing occurs in hybrid plants during the meiosis that precedes pollen production. A PK factor composed of two genes in tight linkage produces both a poison and an antidote that counteracts the poison in the microsporocyte. After meiosis, the poison remains in all daughters cells (the microspores), but not the antidote. Then, only the cells that possess the antidote allele are rescued, while the others are killed. Such PK genes have been reported in rice (Yu *et al.*, 2018) and in *Arabidopsis thaliana* (Simon *et al.*, 2022). (b) A model of obligate harming greenbeard inspired by results from Montazeaud *et al.* (2022). A single genetic element controls the production of a toxic allelopathic compound (2) and a detoxification compound (1), as in a typical poison–antidote system. Neighbours who do not carry the matching poison–antidote allele are negatively affected. (c) A model of obligate helping greenbeard inspired by Karban *et al.* (2013). A single genetic element controls (1) the emission of volatile organic compounds (VOCs) following herbivory damage, (2) the detection of VOCs by neighbouring plants, (3) the production of plant defence compounds that decrease leaf palatability for herbivores. (d) A model of facultative helping greenbeard inspired by Crepy & Casal (2015). A single genetic element controls (1) a modification of the light spectrum that is transmitted and/or reflected on neighbouring plants, (2) the detection of this light modification in neighbouring plants, and (3) the horizontal leaf movement leading to reduced shading on the neighbour. In the four examples, the different greenbeard functions are represented with different boxes corresponding to different genes in linkage. Theoretically, the different functions could equally be achieved by a single pleiotropic gene.

genes. From this perspective, PK genes could be qualified as greenbeards because they harm non-matching alleles in other individuals.

Similar poison–antidote systems could also mediate chemical interactions between plants through soil exudates. In a recent study, Montazeaud *et al.* (2022) found that mixtures of wheat varieties had lower yield and were more diseased when the varieties had different alleles at a single locus close to a gene involved in the synthesis of an allelopathic compound. If allelopathic compound production and detoxification were encoded by a single genetic element, as in a typical poison–antidote model, the system could evolve as an obligate harming greenbeard (Fig. 2b), analogous to the bacteriocin genes in microorganisms (Riley & Wertz, 2002; Fig. 1d). In this scenario, individuals carrying a given allele at the greenbeard locus may produce allelopathic compounds that harm individuals with different alleles but not individuals with a matching allele.

The greenbeard model can also be applied to other types of plant–plant interactions, such as volatile organic compound (VOC)-mediated interactions. For example, *Artemisia tridentata* exhibit reduced herbivore damage if they have previously been exposed to VOCs emitted from other plants that were themselves chewed by herbivores (Karban *et al.*, 2006). Intriguingly, plants exposed to VOCs from kin neighbours tend to show less herbivory damage than plants exposed to VOCs from non-kin, which has classically been interpreted as plants stimulating the defence of their kin to help them anticipate herbivore attacks (Karban *et al.*, 2013). However, this result could also be interpreted as an obligate helping greenbeard gene (or a cluster of genes in tight linkage) that would: (1) produce the volatile signal; (2) receive the volatile signal; and (3) stimulate plant defence against herbivores upon signal reception (Fig. 2c). Interestingly, current models of VOC-mediated plant–plant interactions suggest that the cellular and molecular pathways of VOC reception mirror those involved in VOC emission (Kessler *et al.*, 2023), supporting the notion that the same cluster of genes could control both sides of the interaction.

Other results previously interpreted as kin recognition could also be the manifestation of a single genetic elements acting like greenbeards. In *A. thaliana*, some genotypes have been shown to move their leaf away from their kin neighbours to reduce shading, a phenotype that was not observed with non-kin (Crepy & Casal, 2015). Evidence suggested that the recognition signal was transmitted through light and detected by photoreceptors. Instead of kin recognition, however, such pattern could be produced by a greenbeard with three functions (Fig. 2d): (1) leaving a spectral signature in the transmitted and reflected light; (2) perceiving such signature in the incident light; and (3) inducing leaf movement away from the neighbours upon signal perception.

These four examples illustrate that the greenbeard concept can be used to revisit existing results in the plant literature. The concept is applicable to mechanisms that are already well-described at the molecular level, such as PK genes, as well as to more intricate mechanisms of kin interactions that have yet to be resolved. Importantly, we are not claiming that these interactions are driven by greenbeard genes; rather, we want to draw researchers' attention to the possibility that greenbeards may play a role in intraspecific interactions between neighbouring plants. As with any novel

hypothesis, further research and experimentation will be essential to test whether greenbeards also occur in plants.

Perspectives for greenbeard research in plants

Demonstrating the existence of greenbeards in plants would broaden our vision of cooperation, highlighting the diverse ways in which organisms, even without mobility, can influence the reproductive success of their conspecifics. This discovery would also challenge our traditional view of plant ecology by revealing the intricate ways in which genetic elements shape plant–plant interactions, affecting not only the individuals that carry them but also the broader ecological dynamics of the population. Finally, understanding how genetic elements shape plant–plant interactions will be crucial for developing sustainable agricultural practices. Similar to how gamete killers can impact plant breeding by impeding hybridization between lineages, greenbeards could potentially reduce crop performance in genetically diverse crop stands, such as varietal mixtures. Controlling relatedness at greenbeard loci could thus be another way to use kin selection principles to achieve greater crop cooperation and higher yields (Montazeaud *et al.*, 2020; Biernaskie, 2022).

Several areas of plant sciences appear particularly promising for greenbeard discoveries, as indicated by published studies wherein relatedness between interacting plants was shown to affect the outcome of plant–plant interactions (Table 1). Exploring the genes and the molecular pathways involved in the different steps of these interactions (emission, reception, and reaction to the signal) could be a promising way to test whether these patterns could be manifestations of greenbeard genes. New greenbeards could also be identified using competition experiments in which plants are exposed to different conspecific neighbours. However, one important limitation of current experimental approaches is that they do not allow the effect of genome-wide relatedness to be distinguished from the effect of relatedness at the level of a single locus. Instead of focussing on kin vs non-kin neighbour comparisons, studies should be designed to test the effect of relatedness locus-by-locus, for example using statistical approaches already developed in agronomy (Montazeaud *et al.*, 2022), plant ecology (Wuest & Niklaus, 2018; Turner *et al.*, 2020; Sato *et al.*, 2021), or animal behaviour (Avalos *et al.*, 2020). Ideally, experiments should mix genotypes from different populations, which would allow the detection of greenbeards even when they have reached fixation within populations (selfish genetic elements are often revealed in hybrids obtained from crosses between different populations (Ågren & Clark, 2018)). Because known cases of greenbeards generally involve several linked genes, and such gene clusters are often maintained in linkage by chromosomal rearrangements (Joron *et al.*, 2011; Wang *et al.*, 2013; Li *et al.*, 2016; Gutiérrez-Valencia *et al.*, 2022), it would also be possible to identify greenbeards by searching for associations between structural genomic variants and specific phenotypic traits involved in plant–plant interactions.

The idea that a single genetic element can have a strong influence on intraspecific interactions may seem overly simplistic and too reductionist to many researchers in the plant community. However, this idea is increasingly supported by empirical data

Table 1 Most promising areas of plant sciences for greenbeard discovery.

Research field	Studies reporting greenbeard-compatible results	Follow up research questions for greenbeard investigation (apply to all research fields)
Pollen Killing	Yu <i>et al.</i> (2018) Simon <i>et al.</i> (2022)	<i>Identification of candidate greenbeard genes</i> Which genes or gene clusters are responsible for the observed interactions?
Allelopathy-mediated plant–plant interactions	Montazeaud <i>et al.</i> (2022)	<i>Functional characterization of the candidate genes</i> What roles do the identified genes play in the emission, reception or response to signals involved in plant–plant interactions?
Volatile-mediated plant–plant interactions	Karban <i>et al.</i> (2013)	<i>Evolutionary dynamics of the greenbeard genes</i> Is there genetic variation within the species for the candidate signal (e.g. allelopathic compounds, volatile compounds, and light signals)/at the candidate locus?
Light and photoreceptor-mediated plant–plant interactions	Crepy & Casal (2015)	What is the origin and selection pressures that have shaped genetic diversity at the greenbeard locus? What are the costs and benefits associated with the greenbeard? <i>Ecological consequences of greenbeard interactions</i> What are the ecological consequences of greenbeard interactions in plant populations (community dynamics, population structure, ecosystem functioning)? <i>Applied implications for agriculture</i> What are the consequences of greenbeard interactions for agricultural practices? Can we control/manipulate the greenbeard mechanism to enhance crop performance, pest resistance, and overall agricultural sustainability?

(Wuest & Niklaus, 2018; McGale *et al.*, 2020; Turner *et al.*, 2020; Barbour *et al.*, 2022; Wuest *et al.*, 2023). Moreover, there are already multiple examples of single genetic elements influencing social organization and collective behaviours in animals (Nelson *et al.*, 2007; Wang *et al.*, 2013). The greenbeard concept provides a theoretical foundation to explain how such genetic elements could work and how they could evolve, and as such, represents a promising (and unexplored) avenue to better understand the genetic basis of plant–plant interactions (Subrahmaniam *et al.*, 2018; Becker *et al.*, 2022).

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Competing interests

None declared.

Author contributions

GM and LK designed the research and wrote the manuscript.

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