

Sex, sexes, sex roles, and gender in land plants

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“When we view gender as an accomplishment, an achieved property of situated conduct, our attention shifts from matters internal to the individual and focuses on interactional and, ultimately, institutional arenas. In one sense, of course, it is individuals who “do” gender. But it is a situated doing, carried out in the virtual or real presence of others who are presumed to be oriented to its production. Rather than as a property of individuals, we conceive of gender as an emergent feature of social situations: both as an outcome of and a rationale for various social arrangements and as a means of legitimating one of the most fundamental divisions of society.”

West and Zimmerman (1987, p. 126)

“The discrete, typological nature of the morphological terms [i.e., *male*, *female*, *hermaphrodite*, etc.] does not lend itself readily to the recognition of intermediate conditions or to the description of differences in the relative pollen and ovule contributions of flowers and individuals of the same morphological type. Morphological descriptions of sex tend to rely on appearance rather than function. Moreover, they ignore the fact that the sexual performance of a flower or plant depends not only on its own nature, but also on the gametes produced by other flowers and plants in the same population.”

Lloyd (1980, p. 104)

The terminology of plant reproduction is daunting, and students are likely to approach it with a vocabulary and preconceptions primed by their knowledge of animal systems and the vernacular use of labels for sex and gender in the human context. The potential confusion that such preconceptions can cause is not unique to discussions of plant sexuality; all science borrows words from the vernacular and often uses them with altered meanings, yet their resonance with previous experience and use may distort understanding and perspective in ways that are not intended. For instance, we casually teach students that atoms share electrons, that quarks have a spin, or that tectonic plates and allele frequencies drift, but the words *share*, *spin*, and *drift* may evoke images or notions that have little to do with the properties being discussed. In biology, we refer to selfish genes, to the barcode of a species, or to species invasions. Such metaphors might lead us to picture genes that express human-like selfishness and that have a “point of view” (Hamilton, 1964); to value biodiversity as consumers and imagine assessing it as easily as scanning a supermarket price tag (Larson, 2007); or to regard warlike defense as the most appropriate response toward a species expanding its range into new environments (Larson, 2005). Clearly, we need to choose our metaphors with care. But even when we do, connotations of the words we use in scientific discourse may change over time. These risks apply to the concepts of “gender,” “male,” and “female,” which are frequently used to describe plant sexual reproduction and sexual systems.

Although the words *gender*, *male*, and *female* have acquired new resonances in society, to which we need to be sensitive, in this commentary I defend their use in

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the context of botanical discourse where *function* is of primary concern. I wish to make two principal points. First, although *male* and *female* are used with different meanings in different biological contexts that have the potential to hamper communication, and although they are often strongly colored by unhelpful cultural stereotypes (Martin, 1991), substituting these terms with alternatives would promote more confusion than clarity. And second, while continued use of *gender* in the context of plant sexuality may seem insensitive to the substantial changes in that word's vernacular meaning in some societies, its use to denote the context-dependent and quantitative (nonbinary) sex roles played by plants would, in fact, be coherent with some features of these societal trends; we might thus exploit this resonance in opening the botanical world to our students, rather than seeking to avoid it.

I begin by drawing attention to the important distinction between sexes and sex roles, and to how these two perspectives on reproduction may apply to plants, which display an alternation of generations between sporophytes and gametophytes that are sexual in very different ways. I go on to argue that, although *male* and *female* might seem to be misleading in the context of sporophytes, which do not produce gametes, alternative terms have other limitations. Moreover, the apparent problems with *male* and *female* dissolve if they are used to refer to sex roles rather than to sexes. I then briefly review Lloyd's (1980b) notion of "functional gender" as a quantitative measure of plant sex roles that is firmly grounded in evolutionary theory. Importantly, the functional gender of a plant depends not just on the sex-allocation strategy it adopts but also on that of other individuals in the population. In this sense, a plant's functional gender is a constructed variable in ways that resonate with the notion of constructed gender in human societies. I conclude with several arguments for retaining *gender* as a term for the quantitative measure of sex roles in plants, despite its changing vernacular use.

SEXES, SEX ROLES, AND THE ALTERNATION OF GENERATIONS IN LAND PLANTS

In biology, the terms *male* and *female* are used as discrete labels for the binomial variable "sex." They are defined in relation to the relative sizes (small and large, respectively) of the gametes produced by male and female individuals, or by intra-individual modules with male and female functions. We also use *male* and *female* as adjectives describing the small and large gametes themselves. Isogamous species (in which all gametes are of the same size) do not have sexed individuals (in the sense that they do not have males or females). While isogamous species may have different mating types that can number many more than two, anisogamous species have only two gamete sizes and thus two sexes, and the economic theory of reproduction offers a satisfying explanation for this simple duality (Parker et al., 1972). Hermaphrodites are sometimes

regarded as a third sex, but this usage is clumsy. Hermaphroditism or bisexuality might rather be regarded as falling on a continuum between two extremes in sex allocation (Lloyd, 1980a). This usage represents a conceptual shift from the fundamental notion of two discrete sexes to the notion of the non-discrete sex allocation strategy that individuals may adopt (Lloyd, 1979, 1980b)—a notion that we might label a "sex role."

The terminology of sex roles is often used in the contexts of sexual selection and sexual dimorphism (secondary sexual differences between males and females). In a large majority of animal species, males play the sex role of searching and competing for mates, whereas females show greater reluctance to mate and a higher degree of mate choice (Janicke et al., 2016). These patterns have been labeled "conventional," and exceptions to them as "sex role reversals" (Fritzsche and Arnqvist, 2013), but this terminology is unhelpful and unnecessary. The sex roles adopted by males and females in a given population depend on critical details of the mating system and other aspects of sex allocation and behavior, rather than on convention. It would arguably be better to label the more frequent pattern of sex roles as "Darwinian" (in recognition of Darwin's role in defining them; Darwin, 1871), rather than as "conventional"—and, perhaps, to refer to sex role reversals as "non-Darwinian." This neutral labeling would remove normative connotations from discussions about sex roles without loss of clarity or biologically meaningful content.

It is useful to characterize an individual's primary sex role as its "gender," and to denote "male" and "female" as the two extreme end points on a continuous distribution of primary sex roles or gender. "Male" and "female" are then either sex roles or instances of the binomial (categorical) variable "sex." There seems little risk of confusion in the context of dioecious populations, in which there is a one-to-one mapping of sexes to sex roles: usually, the sex role of purely male individuals is just male. However, this simple one-to-one mapping of sexes to sex roles breaks down for the male or female modules of hermaphrodites, and this is where the notion of quantitative gender is most helpful, even necessary.

Distinguishing between sexes and sex roles, using the notion of gender, also helps maintain clarity in the context of the complexities of the alternation of generations between gametophyte and sporophyte generations in land plants. Unlike some green algae (Togashi et al., 2012) and many other more distantly related eucaryotes (Billiard et al., 2011), all land plants are anisogamous, and thus all have two sexes. In all land plants, however, it is the gametophytes that produce the gametes and are thus sexed as male or female; sporophytes produce spores and do not have sexes. Our frequent reference to the sporophytes of dioecious species as male or female may therefore appear to be erroneous and misleading, but problems with this usage dissolve if we shift our perspective from the binary category of two sexes (where the error resides) to the nonbinary notion of sex roles.

The principles that relate sex roles to sexes apply to both seed and non-seed plants. For non-seed plants (i.e., the three major nonvascular “bryophyte” lineages and the ferns and fern allies, monilophytes and lycophytes), the mapping of sex roles to sexes is relatively straightforward. This is because the sexed individuals in these lineages, the gametophytes, are almost always physiologically and physically independent of the sporophyte. In dioecious species, gametophytes produce either antheridia (and sperm) or archegonia (and eggs), and there is thus a clear mapping of sexes to sex roles: it is straightforward to refer to the sex role of sperm-producing microgametophytes as “male” and to that of the egg-producing megagametophytes as “female.” In monoicous species, there are still two sexes (the sperm and eggs are produced in the antheridia and archegonia, respectively), but the sex role of the bisexual gametophytes may be hermaphroditic.

In the seed plants (i.e., gymnosperms and angiosperms), gametophytes are always dioecious and never monoicous (though their sporophytes may be either dioecious or monoecious; see below), and they thus always adopt either a male or a female sex role, never a bisexual one. But because the gametophytes are microscopic and fully subsumed within structures of the sporophytes, discussion relevant to the sexual systems of seed plants tends to address the sex roles vicariously played by the sporophytes and not their sexes—although the functional implications of the two different sex roles played in the gametophytic generation are attracting increasing interest (Tonnabel et al., 2021). Sporophytes adopt sex roles, in the sense that they express traits that promote the successful transmission of genes to future generations via the small or large gametes produced by their gametophytes. Their sex roles thus correspond to the outcome of their sex allocation and the traits that influence the translation of sex allocation into fitness (i.e., the traits that underlie the shape of the so-called male and female fitness gain curves, whether in a dioecious or a hermaphroditic context; Charnov et al., 1976).

In dioecious seed plants, we label as males those sporophyte individuals that transmit genes to future generations exclusively by promoting the collective reproductive success of their pollen (and their male gametophytes), and we label as females those sporophytes that transmit their genes exclusively by promoting the collective reproductive success of their ovules (and the female gametophytes). Here, the mapping of sex roles onto sexes seems straightforward, but we should bear in mind that the mapping is a projection across generations and scales, from the sporophyte with its many spore-producing modules to the uniformly male or female modules of the gametophytic individuals subsumed by, and diffusely distributed over, the sporophyte's branches, inflorescences, flowers, and carpels or stamens. In hermaphroditic or monoecious species, or in bisexual species that arrange their stamens and pistils in other ways (see below), we can no longer think in terms of any equivalence between nonbinary sex roles and the binary sexes. Again, the notion of

gender may provide a basis for clarity and consistency when discussing sexual systems involving bisexuality.

MAINTAINING “MALE” AND “FEMALE” AS LABELS FOR THE SEX ROLES OF SPOROPHYTES

We might wish to avoid referring to the sporophytes of dioecious species as male and female, but what are the alternatives? We might, for example, replace *male* and *female* with the morphologically more consistent terms *staminate* and *pistillate* (or *carpellate*), or *polliniferous* and *ovuliferous*—terms that appropriately point to the production of either stamens and pistils (or carpels) or ovules and pollen grains. These alternatives are valuable in discussing the alternation of generations, or when making sense of developmental differences among land-plant lineages in terms of homology and morphological modification, but they do not provide a neat label for individuals with a bisexual sex role. For bisexual gymnosperms, we might refer to “monoecious individuals,” and, for angiosperms, we might distinguish between “hermaphrodites” (individuals with bisexual flowers), “monoecious individuals” (those with separate staminate and pistillate flowers), “andromonoecious individuals” (those with staminate and bisexual flowers), and “gynomonoecious individuals” (those with pistillate and bisexual flowers) (Tomaszewski et al., 2018). These categorical terms may be useful in certain contexts, but they fail to characterize the fundamentally quantitative nature of sex roles in bisexual plants. Lloyd's (1980b) concept of phenotypic or functional gender provides such a perspective.

LLOYD'S CONCEPT OF PHENOTYPIC OR FUNCTIONAL GENDER

Lloyd (1980b) revolutionized discussion of plant sexual systems by providing a quantitative perspective on sex roles and by insisting on a coherence with Fisherian sex-ratio theory (Fisher, 1930). In Lloyd's (1980b) formulation of prospective functional gender, “male” and “female” are simply labels for the extreme ends of a sex-role continuum that spans sex-allocation strategies on a scale of 0 (fully male) to 1 (fully female) and that recognizes the context-dependent nature of male and female prospective reproductive success. It is computed as

$$G_i = \frac{g_i}{g_i + a_i E} \quad (1)$$

where g_i and a_i are the number of allocation units to female and male function, respectively (e.g., the number of male inflorescences—male flowers, stamens, or pollen grains; and the number of female inflorescences—female flowers, carpels, or seeds), and $E = \sum g_j / \sum a_j$ is an “equivalence factor” that

divides the total sum of female units in the population by the total sum of male units (Lloyd, 1980b). The variable E accounts for the fact that, at the population level, the genetic transmission of genes to progeny is exactly the same through the male and female functions. In a hermaphroditic population in which all individuals only produce bisexual flowers, they would also all have a prospective gender of 0.5 if we simply count flowers. Because fruit:flower ratios are frequently <1 , fruits, not flowers, may often provide a more accurate estimate of a plant's female function, with flower number being a better estimate of its male function (Willson and Radcke, 1974; Bell, 1985); the distribution of fruit and flower number among individuals may thus more closely reflect variation in prospective gender in populations with bisexual flowers. Many plants produce bisexual flowers with different numbers of carpels and stamens, and counting these units rather than the flowers or fruits would provide an alternative view of variation in prospective gender. In these various scenarios, the realized gender of an individual (in terms of numbers of genes transmitted to progeny via the male and female functions) may, of course, differ substantially from its prospective gender.

Lloyd's (1980b) formulation of functional gender assumes a linear correspondence between allocation to each sex function and fitness gained through that function (i.e., linear fitness gain curves). More generally, if $f(a)$ and $h(g)$ denote the functional relationship between fitness through male and female function, respectively, and allocation to the male and female functions, a and g , then the terms a_i and g_i in expression 1 (including those implicit in E) can be replaced by $f(a_i)$ and $h(g_i)$. To my knowledge, all empirical use of Lloyd's (1980b) functional gender has so far assumed linear gain curves, reflecting our almost complete ignorance of the actual shape of the gain curves for plant populations, but its more general application in terms of $f(a_i)$ and $h(g_i)$ could be envisaged as an ultimate goal for the study of sex roles in plant populations.

Lloyd's (1980b) concept of functional gender has at least three advantages. First, computing the functional gender for a sample of individuals in a population allows us to view sex roles in terms of a distribution—distinguishing between, for instance, hermaphroditic populations in which gender is highly canalized, with all individuals adopting a similar sex allocation or sex role, and hermaphroditic populations in which gender among individuals might range from 0 to 1 (Lloyd, 1980a). Distinguishing among populations with different distributions of functional gender helps us discern the evolutionary forces likely acting on a population and the potential paths of transitions between different sexual systems (Lloyd, 1980a).

Second, a functional perspective of plant gender draws attention to the fact that an individual's sex role depends not only on its own morphology, sex allocation, or sexual strategy, but critically on the sex roles adopted by *other* individuals in the population: gender is context- and frequency-dependent (see the extracts cited at the head of this article). For example, consider a self-incompatible hermaphroditic individual with a particular sex allocation (a particular strategy in terms of values a_i and g_i). This individual placed into a population of

females (for which $a_i = 0$ and $g_i > 0$) will have a functional gender of 0.0 and will thus play a purely male sex role. Such an individual will fail to produce progeny as a seed parent, but, because it will sire all the seed progeny of the population via its pollen, it may have very high relative total fitness. Significantly, the very same individual with unaltered phenotype but placed into a population of males (for which $g_i = 0$ and $a_i > 0$) will have a functional gender of 1.0 and thus play a purely female sex role. The context dependence of gender illustrates why hermaphrodites in a gynodioecious population must, on average, play a male-biased sex role, irrespective of their sex allocation. Lloyd went so far as to suggest that we refer to hermaphrodites in gynodioecious populations as “male” to reflect this logical necessity (e.g., Lloyd, 1982), a usage that was initially taken up (e.g., Delph, 1990) but that has not been widely maintained (because referring to such individuals as “hermaphrodite” recognizes that they usually play a female role too, albeit to a lesser extent).

Third, a functional perspective on plant reproduction may accommodate the modular nature of plant development. Plants are highly modular organisms, with the sexed individuals, the gametophytes, nested within carpels or stamens, flowers, inflorescences, branches, and ramets. Lloyd's (1980b) formulation of prospective functional gender to quantify sex roles can, in principle, be applied to any level of this modular hierarchy. Such module-based estimates can reveal the position-dependent and dynamic nature of variation in sex roles even within genetic individuals (Harder and Barrett, 1995). For example, in species with protandrous hermaphroditic flowers presented in vertical spike-like inflorescences, and in which bumblebees forage from older lower flowers to newly opened upper flowers, the sex role adopted by flowers passes from male to female as they age (Harder and Barrett, 1995; Harder et al., 2000). Species displaying gender diphasy (Policansky, 1981; Schlessman, 1988) provide another example: here, plants begin their reproductive lives playing an exclusively male role and, as they age or grow in size, shift their role to female or bisexual. Of course, the hierarchical modularity of plants applies at numerous levels (male and female organs within flowers, flowers within inflorescences, inflorescences on branches or ramets, etc.). Lloyd's formulation of prospective gender cannot accommodate all these levels simultaneously, and any singular formulation will miss important components of variation on which selection may act and that thus may constitute an adaptive strategy (e.g., Haig and Westoby, 1988; Burd, 2008). However, it nevertheless usefully focuses our attention on the quantitative and context-dependent nature of plant gender.

SEX ROLES AND GENDER IN BOTANY AND SOCIETY: DO WE NEED A NEW TERMINOLOGY?

The changing vernacular and biological uses of the word *gender* were reviewed by Haig (2000, 2004) and have been discussed in the social sciences (Muehlenhard and

Peterson, 2011). Vernacular use distinguishes socially constructed gender from biologically determined sex. Ironically, in apparent “sympathy with the ideas and goals of feminism” (Haig, 2000), biologists have increasingly used the word *gender* as a simple synonym for *sex*. This trend has been criticized, with the suggestion that we desist from using *gender* in the specific context of plant sexuality, both in deference to the feminist cause and because the word has come to have meanings that might compromise our communication and teaching (Oberle and Fairchild, 2023).

Notwithstanding the importance of remaining vigilant to changes in the meaning of words or to their inappropriate or inaccurate deployment in scientific discourse (for all sorts of reasons—see, e.g., my comment on “conventional” sex roles above), I argue that there are several reasons for maintaining the gender terminology in discussions of plant sexual systems and allocation strategies. First, redefining established terms in current usage is difficult, and the problems they pose must surely be substantial before it is worth the risks that changes pose to communication. For better or worse, the term *gender* has become well established as a label for an essential feature of plant sexuality. Lloyd might have chosen a different term, but he did not. Words borrowed by science from the vernacular are necessarily burdened by their associated connotations—which, moreover, may change over time, such that the burden is relieved or enhanced. However, as noted at the beginning of this article, the use of the same words often differs between science and society, and indeed between subfields of science. These differences, which might be labeled “dialects” (Wear, 1999), can emerge even when science coins its own terminology, because borrowings can go in both directions. One could cite countless examples. One is the acronym *DNA*, which is now often used in the vernacular to refer to culturally acquired traits (e.g., Hedges, 2017). The evolution of meanings in different disciplines, and in science and society in general, makes communication among the users more difficult, but it is not obvious that we should, or even could, change scientific terminology such as *DNA* in response. Of course, notions and vocabulary that betray unacceptable and, indeed, “unscientific” preconceptions, implications, or conclusions (e.g., in the domain of eugenics), should very much be rejected—but I do not think that “gender” in plants is one of them. In continuing to use *gender* as a useful notion in studying plant reproductive strategies, it would still pay to be sensitive to the potential obstacles for understanding that resonance with societal use might pose (Oberle and Fairchild, 2023).

Second, the use of the term *gender* to quantify the nonbinary sex roles of plants in some ways resonates with the notion of the nonbinary constructed gender that emerges on the basis of social interactions (West and Zimmerman, 1987); see the extracts cited at the head of this article. In this sense, Lloyd's conception of prospective gender and its dependence on the sexual expression of the rest of the population is strikingly similar to the suggestion that, in the human societal context, while *gender* is “a property of individuals, we

conceive of gender as an emergent feature of social situations” (West and Zimmerman, 1987, p. 126). Thus, I wonder whether classroom discussions of plant gender might, in fact, help to promote awareness of the importance of variation and diversity and to cast doubt on the validity of conventional notions of sex and gender. Such discussion, if led sensitively, seems to me unlikely to reinforce such notions.

Third, it is also worth recalling that plant sex expression is often extraordinarily plastic. In some homosporous ferns, sex is determined by responses to the social environment via hormonal signaling among neighboring gametophytes. The sensitivity of plant sex expression to quantitative differences in plant hormone concentrations in general, whether exogenous (as in homosporous ferns) or endogenous (Dauphin-Guerin et al., 1980), illustrates the nonbinary manifestation of gender in the natural world beyond humans and other animals. In many angiosperms, sex allocation is size-dependent, including extreme examples in which individuals switch between male and female or hermaphrodite sex expression. Transitions in sex expression also include cases of trees that, after many years of acting as male, may switch to being female (e.g., Isadi, 2015). All such examples raise interesting questions concerning function, but they also illustrate that within-sex variation in sex role is by no means “unnatural,” contrary to widespread belief in some social circles (Mathers et al., 2018).

Finally, the concept of functional gender provides a language for us to appreciate the interesting fact that natural selection has often acted on traits or organs that are anatomically related to one primary sex function to promote the sex role of the other. For instance, the dispersal of pollen in some species (a male function), is promoted by its secondary presentation to pollinators on the pistil (a female function) (Howell et al., 1993), such that the pistil has partly adopted a male sex role. Similarly, pollen (primarily a male function) is produced by many species as the sole reward to pollinators whose visits also deliver pollen and thus promote the fertilization of ovules; here, the pollen has partly adopted a female sex role. Similarly, the production of male flowers by andromonoecious individuals, usually seen as a male strategy, may actually serve to promote the female component of fitness and thus play a female sex role (Vallejo-Marin and Rausher, 2007). The mapping of sex roles and gender to sexes in plants may thus often differ from what our preconceptions lead us to anticipate. Challenging such preconceptions would open new vistas of understanding in our students—as indeed would an appreciation of the multiplicity of the meaning of words in different contexts and its implications for the communication of ideas.

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