Tree Selection Series

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Tree Sex:

Gender & Reproductive Strategies

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Your grandmother suggested sex would get you into trouble if you were not careful. For tree professionals, not appreciating tree sexual expression can lead to unexpected tree growth performance, failed client expectations, and liability and maintenance problems. Tree sex expression is more complex than simply thinking of a "boy" or "girl" tree.

Not Animals

For animals, gender is visible as sexual parts, secondary features, and behavior. Having bright feathers, unique coloration, manes of hair, and acting either male or female is a fact of life. Sexual identity is usually accepted as a function of physical features. For humans, maleness and femaleness are polar ends of genetic programing and social life. Not so for trees. While human gender issues spawn jokes and angst, tree gender identification can cause great confusion. Preliminary tree gender is determined by the types of flowers produced. Tree flowers can have male parts, female parts, both male and female parts, or none at all. Some of these parts are functional and some are not. You can not tell flower function (or gender) just by looking.

Nebulous

Tree gender can change -- from season to season, over the life of a tree, as the environment changes, or can remain constant for life. Historically, at a particular life stage tree flowers were examined for the presence, distribution, and number of male and female sexual parts. Gender was recorded based upon appearance at one point in time. Unfortunately, sexual appearance and function are not tightly bound in trees. It is not what flowers look like, but how they function over time that determine a tree's true gender.

Tree sexual classes are not always as they appear nor are they discrete opposites. Male and female functions exist along a wide morphological gradient. Two examples are given in Figure 1 for *Fraxinus* (ash) and Figure 2 for *Populus* (aspen / cottonwood). Ash and aspen are viewed as significantly different in their sexual reproduction strategies, but the figures appear much more similar than simple botanical descriptions would suggest.

Maturity

Trees become sexually mature, depending upon species and the individual, anywhere between 1 and 50 years of age. Figure 3. Sexual maturity is commencing the generation of functional flowers. Tree flowers can range from: large, colorful and showy; tiny, green and inconspicuous; or small cones. A single flower can have: male parts which may or may not work; female parts which may or may not work; both male and female parts all of which may or may not work; or flowers without sexual parts (asexual flowers).

A single tree flower with both fully functional male and female parts is called "cosexual." Many terms have been used for this flower type including bisexual, perfect, or hermaphroditic. A single tree flower could also generate only male ("andro") or female ("gyno") functional parts, but not both. In addition, any tree might produce only cosexual, male, or female flowers, in any combination. Figure 4 shows a simple tree sexual strategy triangle.

Tree Flowers

Functional sexual reproductive parts in trees allow male genetic components (pollen) to reach female components of the same species, and then grow to fertilize an egg, producing a viable embryo held within a seed. This fertilization process is facilitated by flowers. A cosexual angiosperm tree flower is shown in cross-section in Figure 5. The distances between flower parts, the absolute and relative size of different parts, and the aerodynamic shape, aesthetic appeal, color, and odors of different parts all can be varied genetically in order to maximize chances of successful pollination, fertilization, embryo growth, and seed or fruit distribution.

For example, if the stamens (male parts with pollen) are very short and the pistil (female part with an ovary) is long, pollen will be less likely to fall onto the pistil within the same flower. Tree flowers (young gymnosperms cones are considered flowers) have standard parts. Some parts are modified or emphasized in different flower forms. Male or female flowers can have some stunted vestige parts, or full sized nonfunctional parts, of the opposite sex visible inside each flower. Figure 6.

In The Genes

An angiosperm tree flower for example consists of four stacked components. (Figure 7). The components include the sepal area, petal area, male area and female area. The sepal and petal areas are not part of the functional reproductive parts but influence wind flow and animal pollinator effectiveness. Genetically, the four flower components are controlled by separate gene sets in three zones within a tree flower:

Zone 1 = female and male part development controlled by specific gene sets.
Zone 2 = male part and petal area development controlled by gene sets which assure pollen distribution and pollinator attraction.
Zone 3 = vegetative zone development controlled by specific gene sets which display, support and protect reproductive parts.

In this case, instead of one set of genes conveying gender, trees have developed three unique gene sets which control flower formation and gender expression. Each of these gene sets have been separately driven by many agents to affect efficient reproduction.

Modified

Sex of a flower is governed by genetic components within flower bud meristems modified by growth regulators. Growth regulators involved in modifying gene expression, regulators like auxin, cytokinins, and gibberellins, are in-turn modified by tree health and environmental impacts. For example, applications of single growth regulators or mixes of regulators have caused reversals of flower bud gender expression.

In addition to biology, flowering season weather can play a critical part in reproductive success. Frosts can kill sensitive reproductive tissues. For example, freezing Spring temperatures can damage white oak (*Quercus alba*) female flowers leading to acorn crop failures 3 out of every 5 years in some locations. Severe flowering season heat loads and drought conditions can prevent proper flower expansion or cause premature tissue aging. For example in sugar maple (*Acer saccharum*), stigma (female) receptivity is governed by temperature. The greater temperatures above average, the fewer days female parts are functional.

Sex Classes

In a group of trees of the same species, some trees might generate only male flowers while other trees might generate only female flowers. In some species, a group of trees could have cosexual, male and female individuals. A predominantly male tree might generate a scattered few female or cosexual flowers. A predominately cosexual tree might generate a few male flowers. A predominately female tree could generate occasional cosexual flowers. The variation in tree flowering is great!

There are a number of terms used for all these different combinations of tree sexual strategies. Some terms have been misused and many are complex combinations of morphological terms. One of the best way to visualize the many different tree sexual strategies is given in Table 1. Note if the prefix "andro" is used, it denotes male dominance, while the prefix "gyno" denotes female dominance.

Gender Walk

Tree sexual classification depends upon both the flower parts present and their function. The proportion of male and female parts in flowers, and the proportion of cosexual, male and female flowers on a tree, begin to determine potential gender. The functional sexual class of a tree is based upon performance as a viable pollen provider or successful ovule parent in passing genes onto another generation. Functional estimates of gender are made by counting the number of flowers producing pollen grains and the number of flowers generating fruit and viable seeds. Individual trees which produce proportionally much more pollen within a species can be considered functionally male. Individual trees which produce proportionally much more seed within a species can be considered functionally female. Figure 8.

Deception

Male and female flower parts are functional if they preform reproductive services. Appearances can be misleading. Functional flower parts in the same species can look quite different from individual to individual. Nonfunctional male and female parts can be fully developed, modified, or stunted in appearance, or missing altogether. Functional male and female tree parts on the same tree, may be present but may not successfully generate viable seed.

There is a strong trend in trees to be self-incapable. Many trees, through flower timing, pollen identification markers, and female part physiology, minimize self-pollination and maximize genetic advantages of cross-fertilization (called allogamy). Self incapability systems in trees tend to be concentrated at the point where pollen attaches to a pistil. To prevent selfing, female parts kill pollen from the same tree upon arrival, or slows pollen grain growth and the fertilization process. Trees can also undergo early seed abortion if selfed.

No Selfing!

The large size of trees with huge surface areas for flowers opening all at once, coupled with long lives over many flowering seasons, can lead to many self-fertilizing events. Each selfing event can generate a seed and seedling which at the start or even into middle age, can suffer from inbreeding depression and less efficient growth. For example in longleaf pine (*Pinus palustris*), selfing was found to cause a

60% decline in seed yields, a 53% increase in young tree mortality up to 8 years of age, and 33% less height growth through age 8. A number of trees are polyploid (having multiple sets of chromosomes) which can strengthen inbreeding depression in offspring.

Selfing is a problem for many trees. For example, each Douglas-fir (*Pseudotsuga menziesii*) in one study was found to trap ~50% of its own pollen, but only 7% of derived seedlings were from self fertilization. In addition, one-third of all mature Douglas-firs produced less than 2% of seeds which were selfed, and it is rare for a mature tree to produce more than 20% filled seed from selfing. Alternatively, some trees do self-pollinate as a standard practice, or on sites away from other trees of the same species. In large, wind-pollinated trees there is a tendency to either self-pollinate or cross-pollinate. In animal-pollinated trees there is usually a mix of selfing and cross-pollinating accepted.

Choices

Trees have developed many ways to prevent the problems of selfing. There exist in trees three primary means of minimizing self-pollination and maximizing out-crossing. The first is by separating male and female parts in different flowers on the same tree (monoecious), or on different trees (dioecious). The second minimizes selfing through having male and female parts or flowers become functional at different times. The third means to minimize selfing is by physically separating male and female parts by a distance within a single cosexual flower.

Many trees are cosexual. A number are monoecious. Relatively few are dioecious where one tree is female and one tree in male (termed dioecy). Table 2 shows the percentages of worldwide trees in each sexual strategy classification. In-depth, long-term studies have only been completed in limited locations with trees, and so this information is not complete.

Got Mono?

Monoecious trees separate genders into different flowers within the same tree. Male and female flowers will usually have some residual nonfunctional parts of the opposite sex present. In monoecious trees, male and female flowers are separated from each other in a number of ways to minimizing selfing. Separation can be from top to bottom of the crown, branch tips to branch bases, or simply on individual branches. There is a tendency to isolate female flowers and the embryos they will generate farther from the ground to be away from some types of flower and seed predators, and grazers. In these situations male flowers are clustered in the lower crown to make use of unstable air temperature patterns to aid in the buoyancy of wind distributed pollen.

Wind dispersed seeds and temperate zone climates are associated with monoecious trees. Monoecious trees which are animal pollinated tend to be pollinated by poorly flying or non-flying insects which congregate only on a few local trees. The flower gender mix on monoecious trees varies from year to year based upon available resources and climatic conditions.

Living Di

There are distinct advantages and disadvantages to living a dioecious life for a tree species. Dioecy is found in both primitive and advanced seed plant families, and in both angiosperm and gymnosperm trees. Dioecy is rare in herbaceous plants. Dioecious trees make good use of site and tree resources through a division of sexual reproductive efforts. Male trees make genetically directed resource investments to maximize mating events. This is done by generating and effectively releasing many pollen grains. It requires relatively few male trees producing pollen to maximize cross-fertilization. Figure 9. Males are only limited in reproductive success by the number of females.

Female tree success is constrained by site resource quality and quantity, and by internal allocation processes. Female trees trend to decrease the number of flowers and increase the resources spent on seeds because no pollen has to be produced and no self-fertilization problem exists. Dioecy in trees tends to generate more male flowers and pollen, fewer female flowers, and a higher percentage of viable seed.

Di Characters

There are a number of characteristics which tend to be found in dioecious trees. Tropical and island ecological zones with minimal seasonal climatic changes tend to favor dioecy. Pollination of dioecious tree flowers in the tropics is almost exclusively by small, unspecialized insects especially bees. They utilize the small, pale colored, simple, inconspicuous flowers common in dioecious trees. (This points out the danger to dioecious trees of bee pollinator problems.) In temperate zones, proportionally more dioecious trees tend to be wind pollinated. Trees with large showy flowers for animal pollinators in temperate zones are almost never dioecious.

Guidelines Not Rules

In dioecious trees, there is a trend toward large, fleshy, single-seeded fruits distributed by animals, especially in under- and mid-story forest trees. In the tropics, a great deal of this fruit and seed distribution is by birds. In gymnosperms, wind pollination and animal seed dispersal is usually associated with dioecious trees. In temperate zone dioecious trees, there is a tendency toward wind pollinated and wind dispersed seeds.

Unfortunately, hard and fast rules do not apply in trees. For example, *Populus tremuloides* (quaking aspen) is traditionally listed as a dioecious species, but one study found as many as 38% of individual trees generating some cosexual flowers. Table 3 shows a composite view of the sexual system for this *Populus* species as observed in three research studies.

Changeling

Some trees can appear to be one gender producing only male or female flowers. The same individual in another year (maybe the next year) can be seen to generate only the opposite sex flowers or cosexual flowers. Trees changing gender from year to year can be mistaken for dioecious. Sex appearance changes in trees can occur once some minimal size or age is reached. This change in flowering is termed a “sequential cosexual” process since a tree is not either male or female but can generate both flower genders over time including cosexual flowers.

For example, in the maple *Acer pennsylvanicum*, 10% of young sexually mature trees in the understory of a forest changed sex from year to year. See Figure 10 to track the number of sexually mature trees changing from male to cosexual to female from one year to the next. Note there is a large death rate among females probably caused by limited light and site resources. The authors of this study believed the genetic strategy of this maple was to reproduce before death.

There is a tendency for some angiosperm trees just exiting their juvenile period to generate male flowers first and then eventually generate female flowers. The opposite pattern occurs in some gymnosperms, female flower (seed cones) are generated for many years before male flowers (pollen cones) are produced on the same tree. For example in Western white pine (*Pinus monticola*) females flowers can be generated as early as eight years of age with male flowers not produced until 20 years of age or older. In Virginia pine (*Pinus virginiana*) male flowering cab be delayed in individuals for as much as 40 years.

Polygamous

Some trees can not be clearly and easily classified into neat gender units. Generally a polygamous tree has cosexual, male and female flowers on the same tree. A tree is polygamodioecious (subdioecious) if different trees have cosexual and male flowers, and cosexual and female flowers. It is very rare in trees but a species could be called trioecious if cosexual, male and female flowers are generated all on separate trees.

Fraxinus spp. (ash) are notorious for confusion and blurring of tree gender lines. For example, in one *Fraxinus* species a study found trees averaged 63% male flowers, 36% cosexual flowers, and 1% female flowers. A closer examination of the data revealed that of all the male flowers, 99% were functional. Of all the cosexual flowers, 25% were truly cosexual, 61% were functional females, and 4% were nonfunctional. Of all the females flowers, 99% were functional. It is clear there is a mix of gender appearances and functions not always clear by a single look at a few of a tree's flowers.

The maple genus (*Acer*) contains cosexual, monoecious, and dioecious species and individuals. Most maple species are called andropolygamous with many male trees and some andromonoecious (male and cosexual flowers) trees. In addition to functional flowers, some maple species (i.e. *Acer platanoides* and *Acer pseudoplatanus*) generate flowers without any sex organs (asexual flowers).

Self Timing

One method seen in trees to minimize self-pollination is "dichogamy." Dichogamy is male and female reproductive organs maturing at separate times on the same tree. This timing difference helps pollen of a single tree to be shed before its own female flowers are receptive, which is called "protoandry" or male-first flower timing. If a tree generates female flowers first before its male flowers release pollen it is called "protogyny" or female-first flower timing.

There are two great examples of dichogamy (actually heterodichogamy) in trees. The first type is found in some *Juglans* (walnut) and *Acer* (maple) species. For example, Figure 11 (*Juglans*) and Figure 12 (*Acer*) show differences in flower timing among a group of trees of the same species. One tree will generate male flowers first and females later (protandry). Another tree will generate females first and males later (protogyny). Both types of flower timing overlap with the opposite flowering periods in surrounding trees. There remains, depending upon flowering season weather patterns each year, a variable period of flower overlap on the same tree between male and female. Maples are highly variable as a genus and can generate six general types or patterns of flowering as shown in Figure 13.

A second type of flower timing difference in trees occurs in *Persea* (red-bays) where flowers open twice across several days. In individual trees, flowers open as females either in the morning or afternoon of one day, and then the same flowers reopen as males the following afternoon or morning. This flowering system effectively minimizes self-fertilization.

Tree Sex

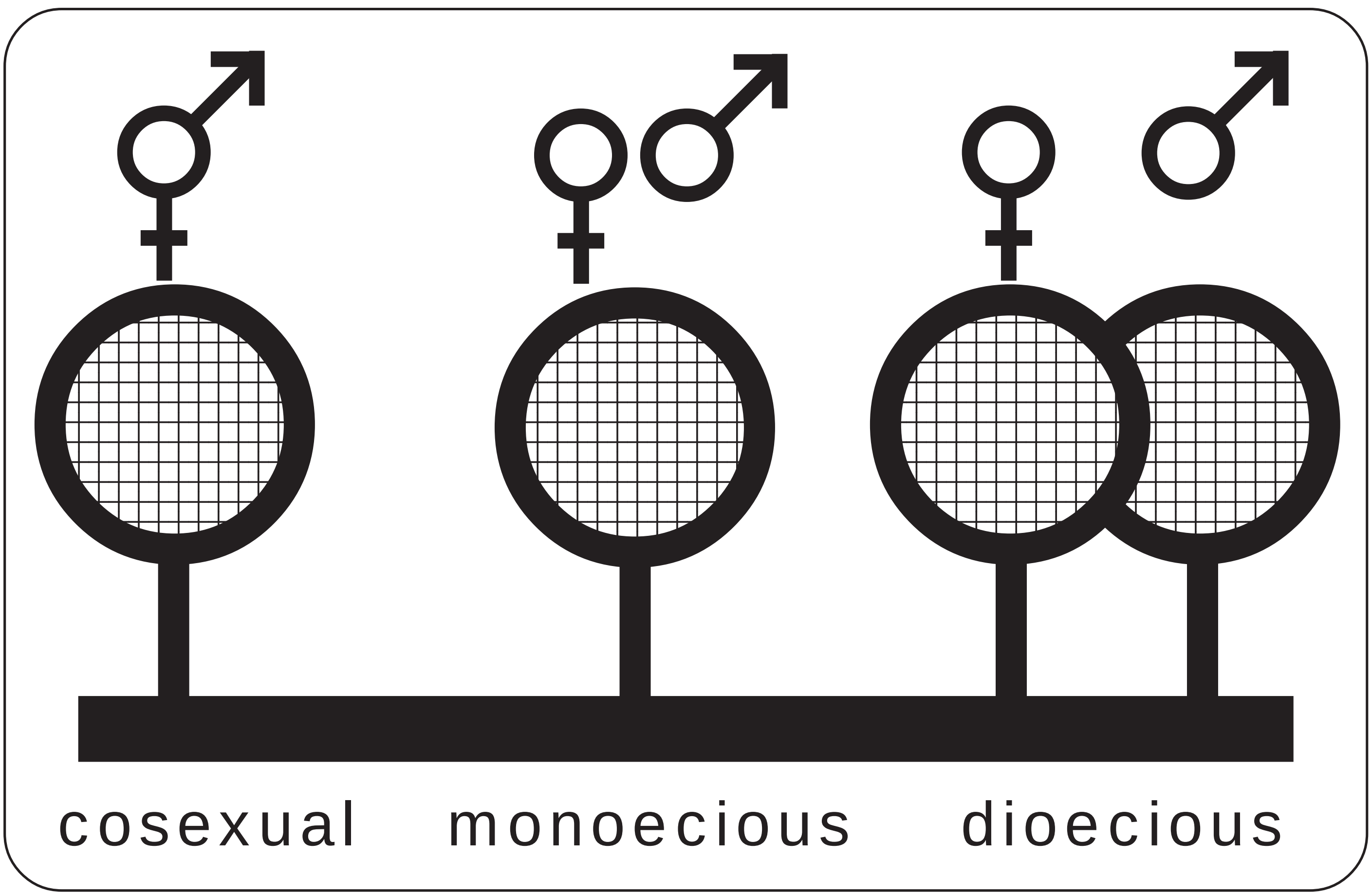
As seen in the previous text, figures, and tables, tree gender identification is difficult to categorize with any certainty. It takes careful observations of many individual trees made over many flowering seasons to be confident. Table 4 provides a list of tree sexual strategies and sexual maturity ages, as can best be determined. Some trees are listed with multiple strategies arising from various observations of different researchers or from actual biological realities of the species. Note if a genera has low variation and strong consistency of sexual strategy through each species, only the genera name may be listed.

Table 5 is a summary of Table 4. Remember this summary is for Table 4 only, and not for all tree species in a specific area. Table 5 provides a breakdown of trees having been identified in the literature with one sexual strategy, and trees classified with multiple strategies. Table 5 also shows the numbers of trees with multiple strategies and the average sexual maturity ages by strategy.

It is interesting to note in Table 5, 16 trees are listed as having both dioecious and monoecious sexual strategies by various authors. Table 5 also shows 10 trees listed with both cosexual and dioecious strategies, 6 trees with cosexual and monoecious strategies, and 3 tree species listed having cosexual, dioecious, and monoecious strategies. Table 5 shows a tendency for dioecious trees to become sexually mature earlier and monoecious trees to become sexually mature later than other trees.

Conclusions

For most trees, sexual behavior is not strictly male or female at the species and individual level. Trees effectively reproduce using different combinations of functional sexual parts distributed in different types of flowers. The type of flowers produced can change from one flowering season to the next, and across many years within a single tree or among a population of trees. The strict gender concepts we understand with animals must be dimmed and flexible when applied to trees.



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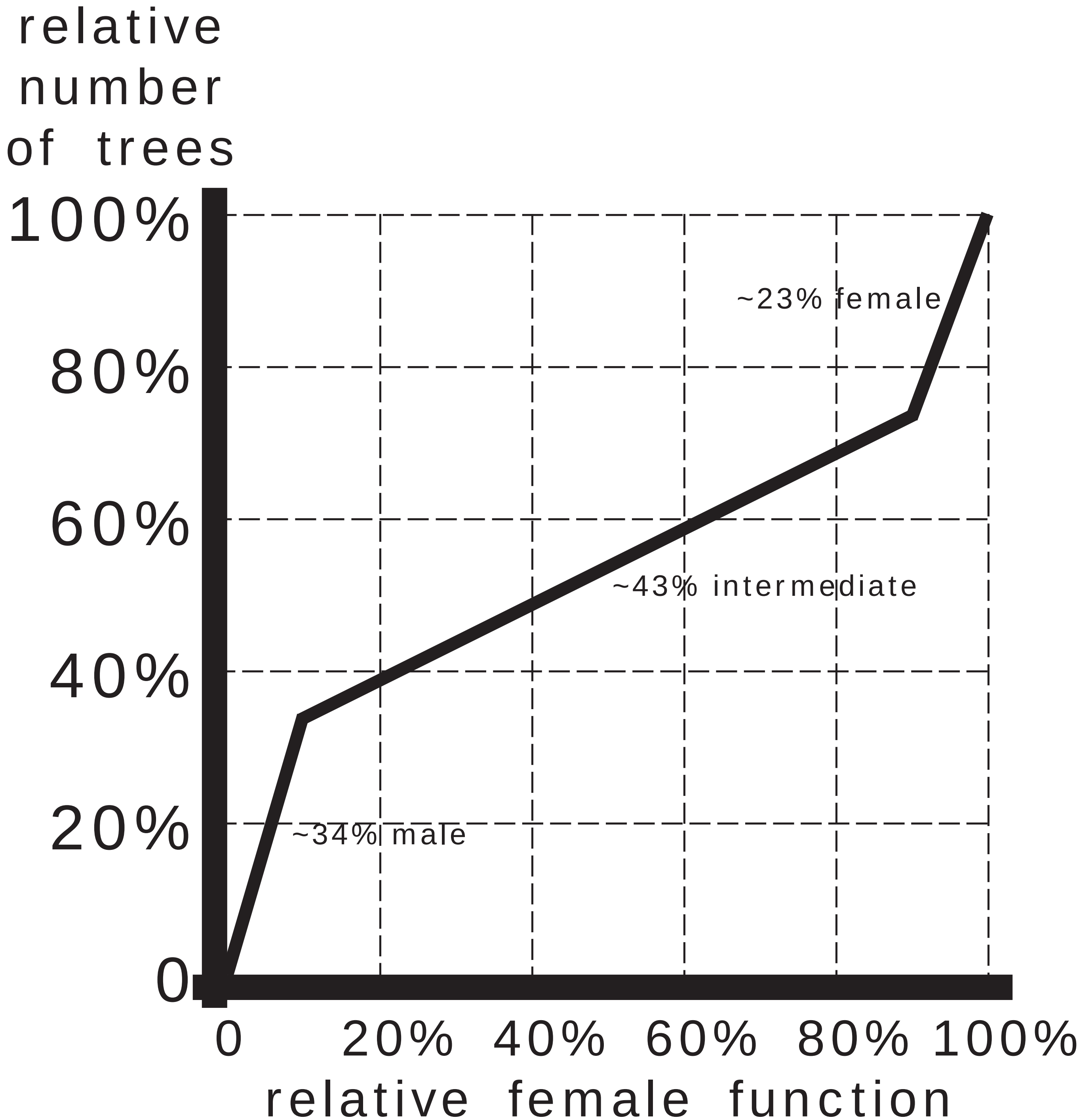

Figure 1: Example -- relative number of trees in a group functioning along a gender gradient between male (0% female) and female (100% female) in a *Fraxinus* species. Intermediates would have a combination of male, female, and cosexual flowers.
(after Binggeli & Power, 1991)

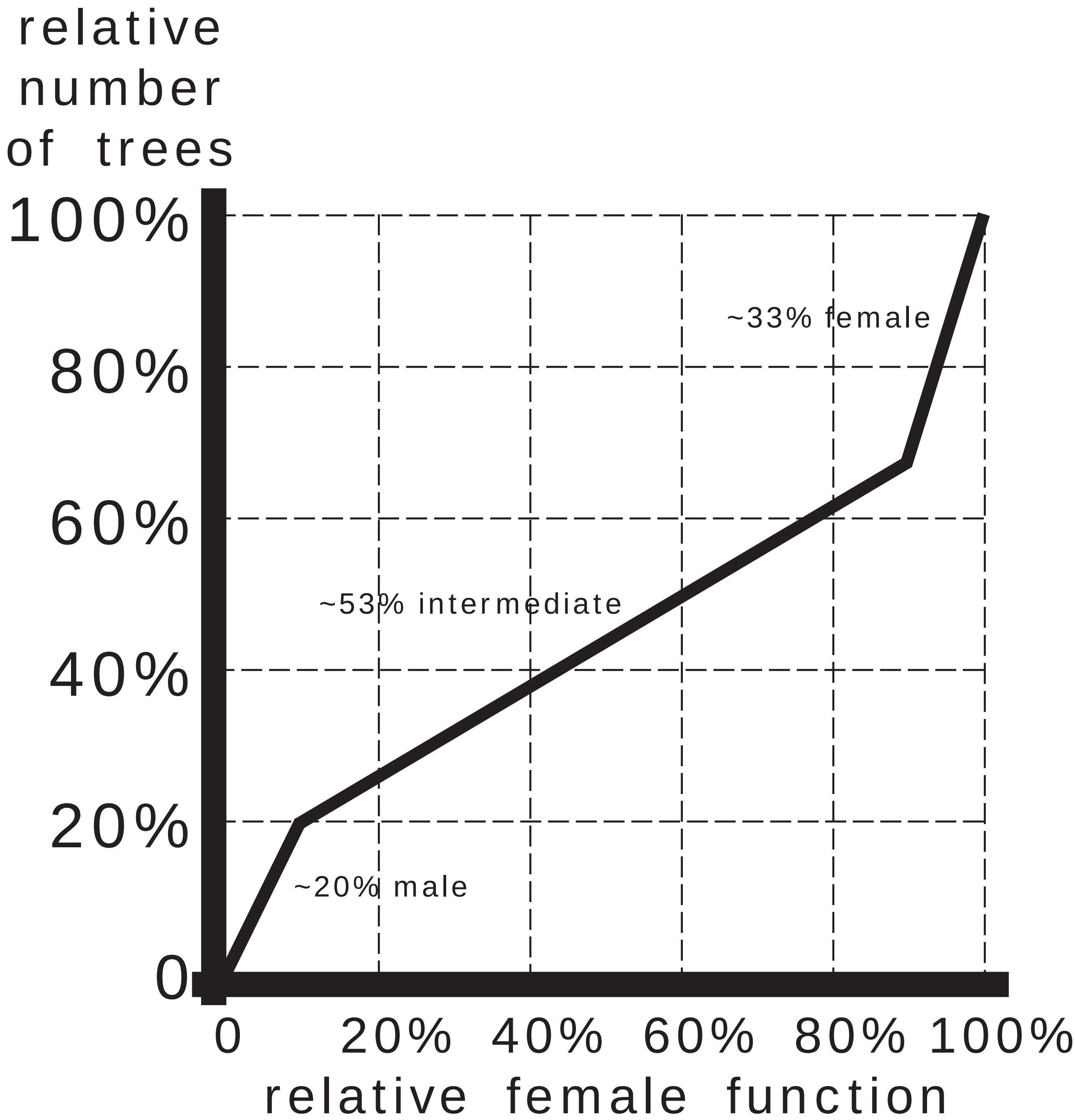

Figure 2: Example -- relative number of trees functioning along a gender gradient between male (0% female) and female (100% female) in a *Populus* species. Intermediates would have a combination of male, female, and cosexual flowers. (after Lester, 1963)

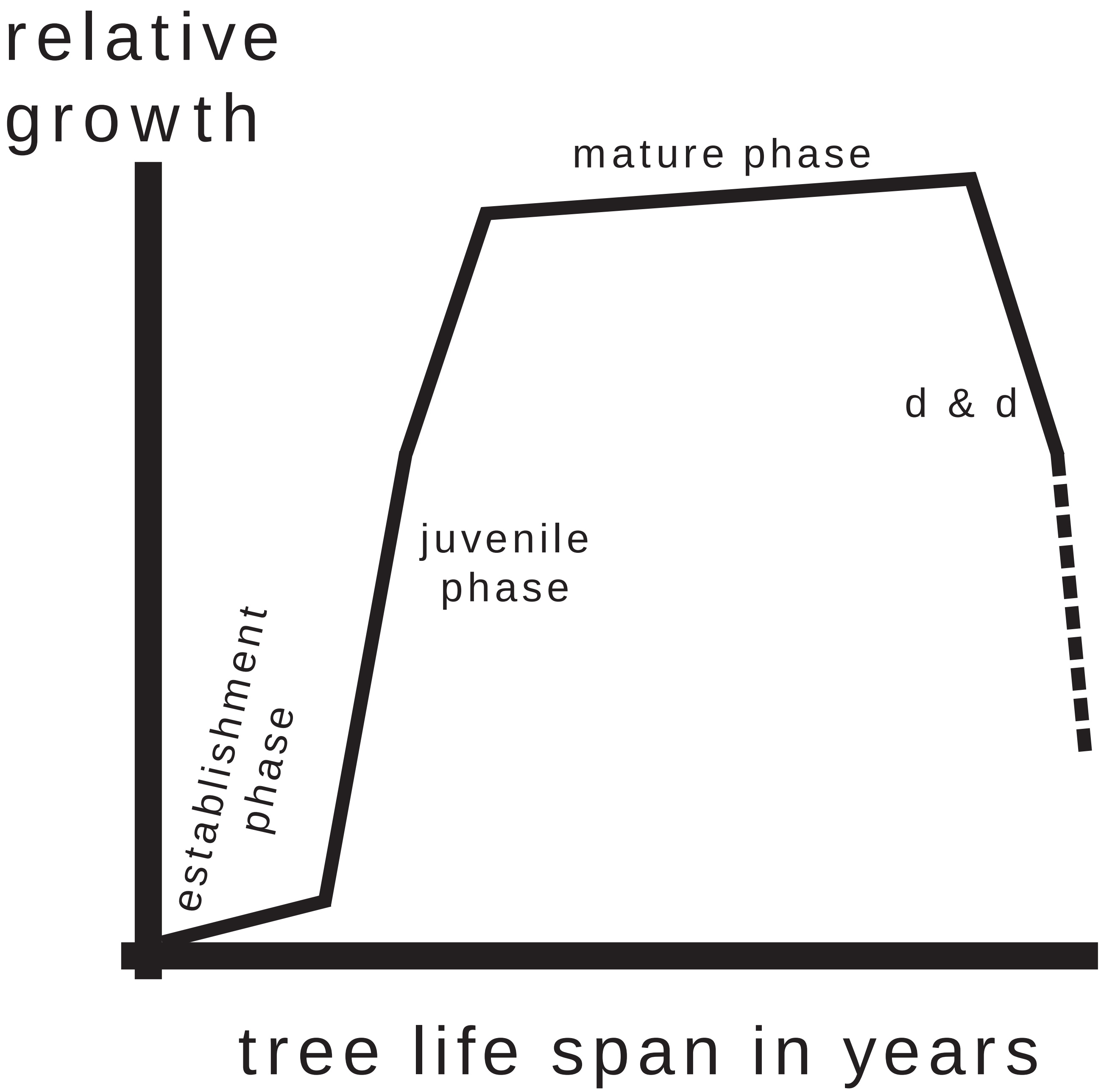

Figure 3: The four life phases of tree life:
I. an early establishment phase;
II. a rapid growing juvenile phase;
III. a sexually mature phase; and,
IV. decline and death.

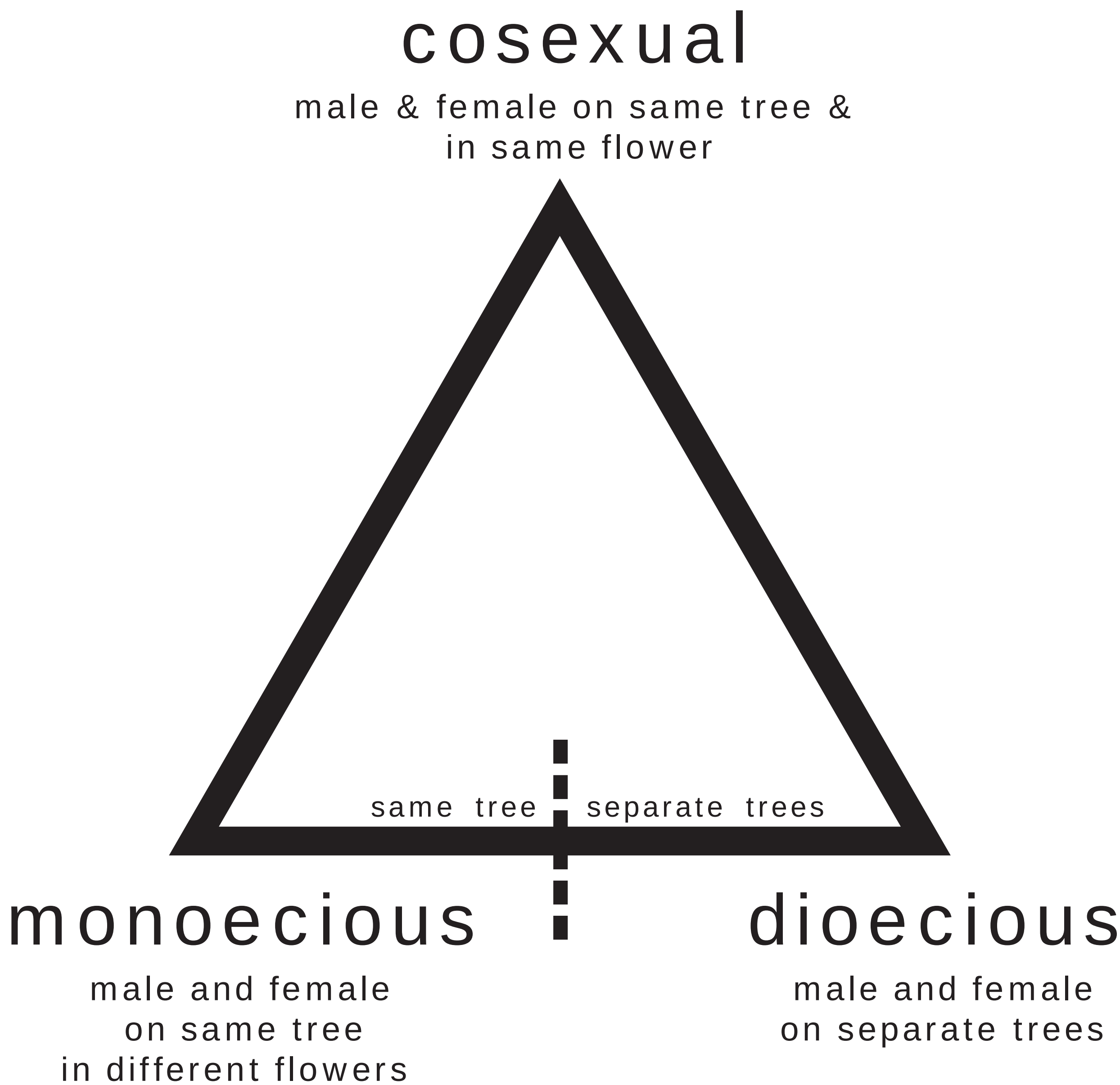

Figure 4: Simplified flowering / sexual reproductive strategy triangle for trees. Intermediate forms exist.

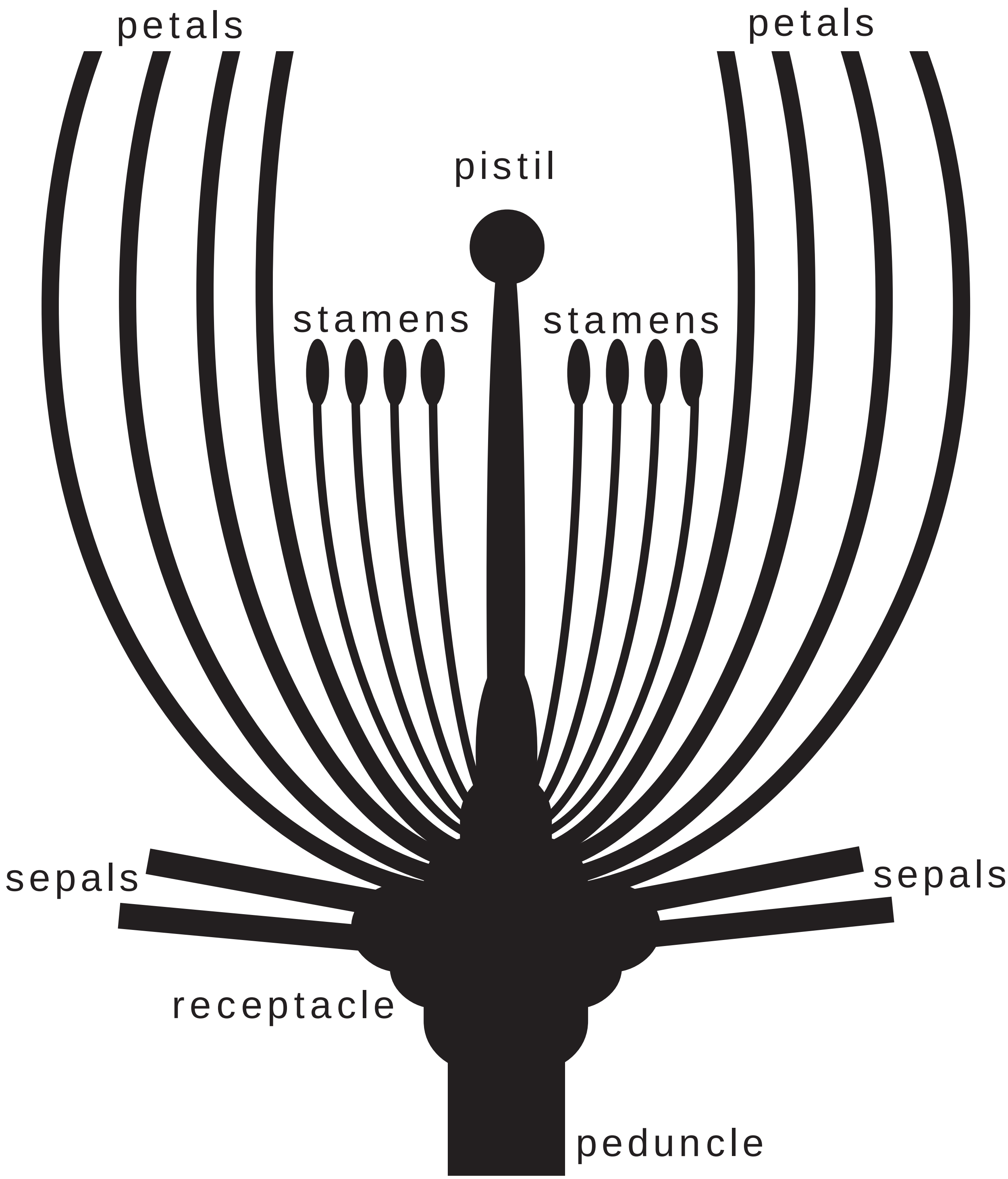

Figure 5: A general cross-sectional diagram of primary cosexual flower parts in angiosperms. The male parts are individually called stamen composed of an anther and a filament. The female part is a pistil composed, from top to bottom, of a stigma, style, and ovary.

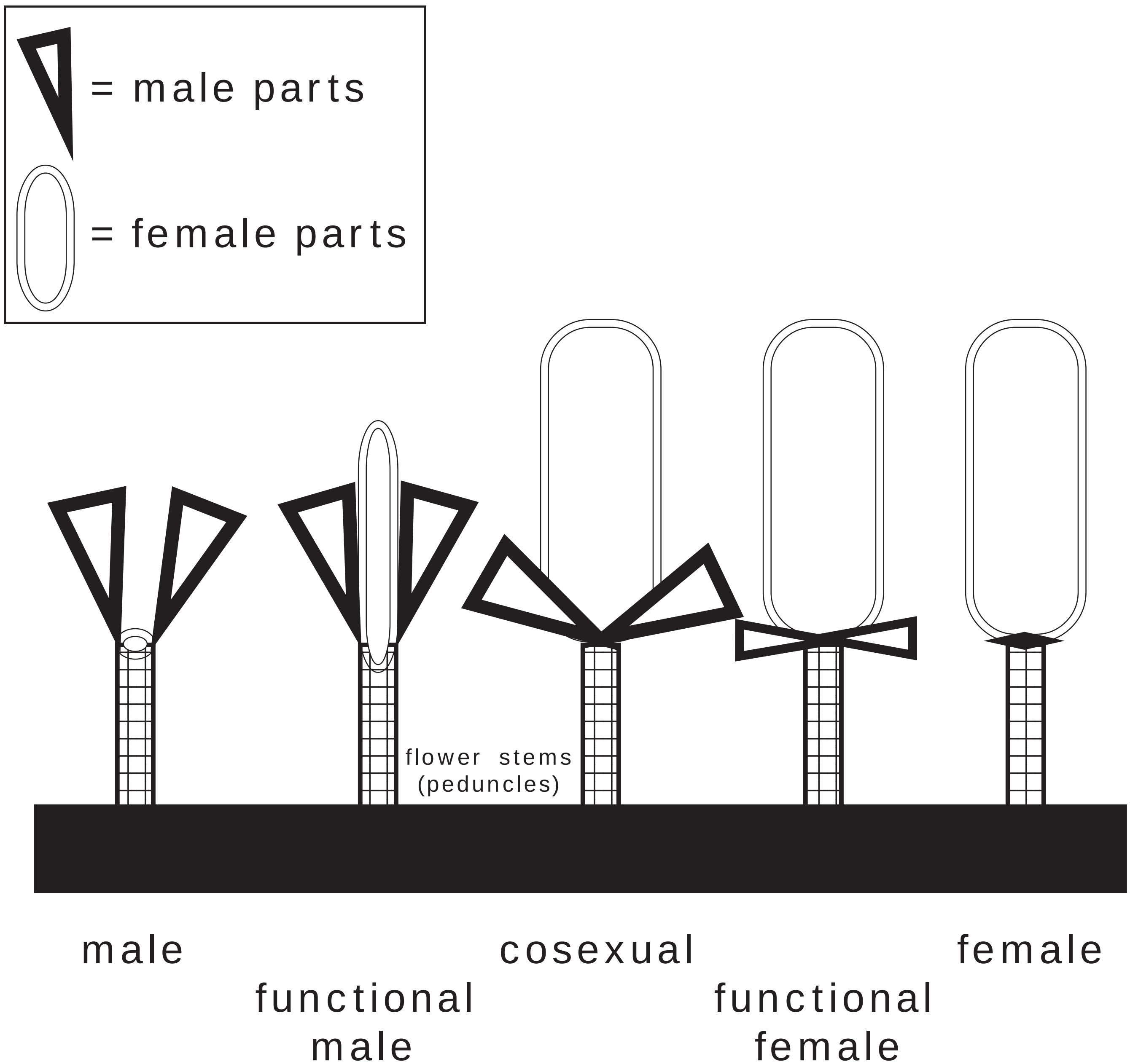

Figure 6: General diagram representing five different appearing tree flower types along a gender gradient. Triangles represent male flower parts (stamen) and elongated ovals represent female flower parts (pistil).

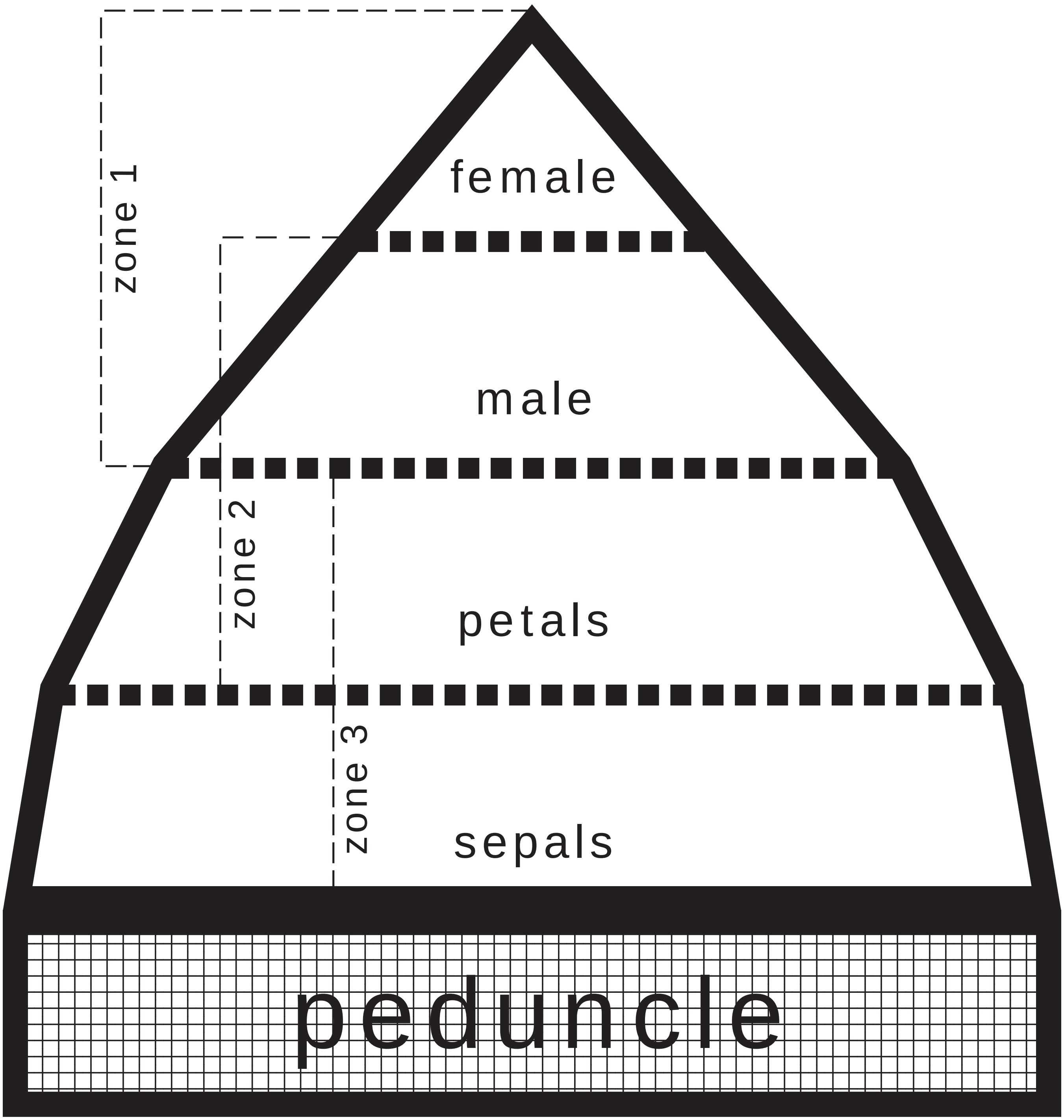

Figure 7: Diagram of a tree flower growing point. Multiple gene sets control expression of gender for zone 1, gender and vegetative expression in zone 2, and vegetative expression in zone 3.

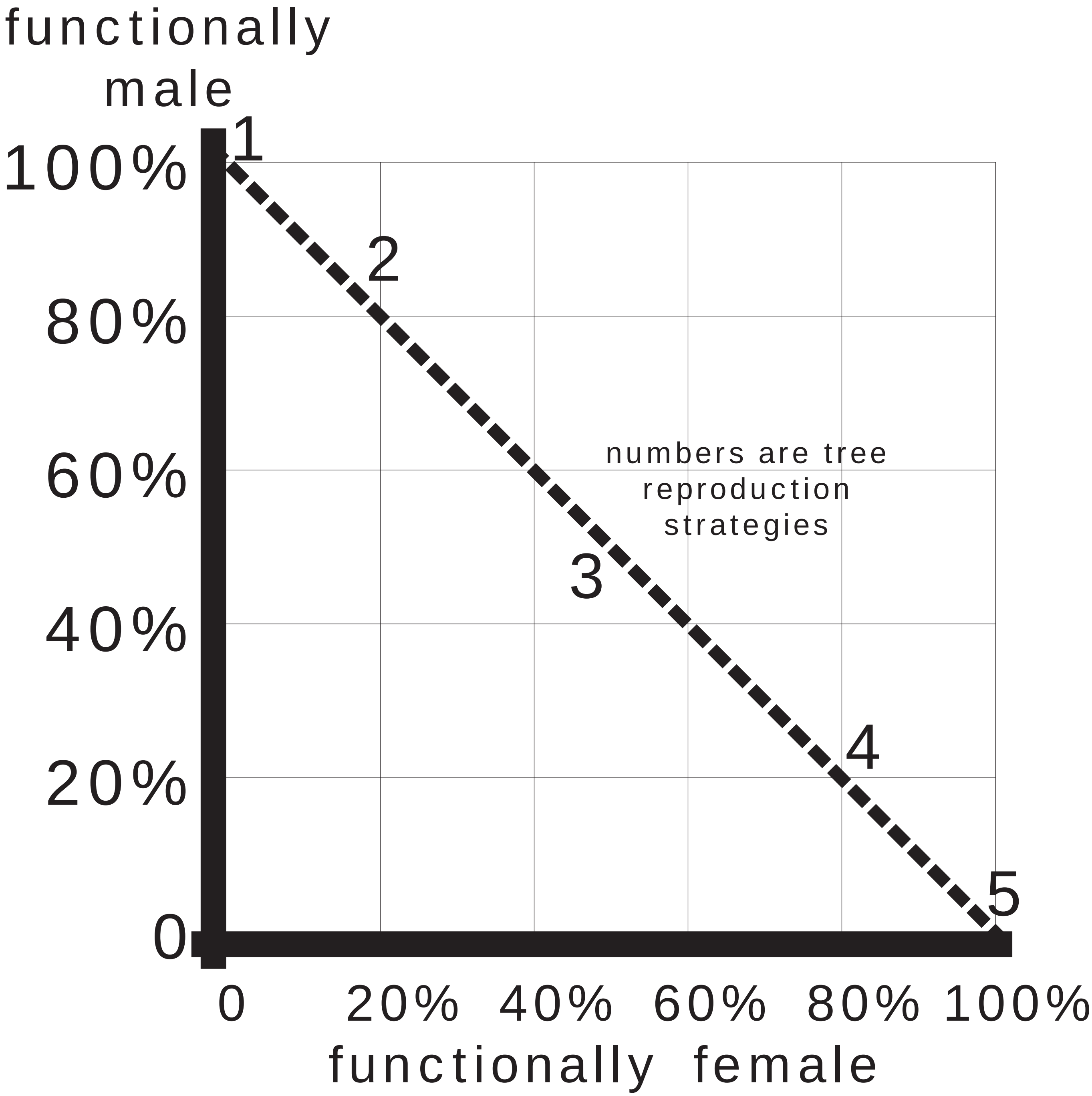

Figure 8: Tree sexual reproduction strategies:

A. For a group of trees of the same species:
Male = 1; Cosexual = 3; Female = 5; Androdioecious = separate 1 & 4; Dioecious = separate 1 & 5; Gynodioecious = separate 2 & 5; Trioecious = separate 1, 3, & 5.

B. For one individual tree:
Male = 1; Cosexual = 3; Female = 5; Andromonoecious = 1 & 4; Gynomonoecious = 2 & 5; Polygamous = 1, 3, & 5.

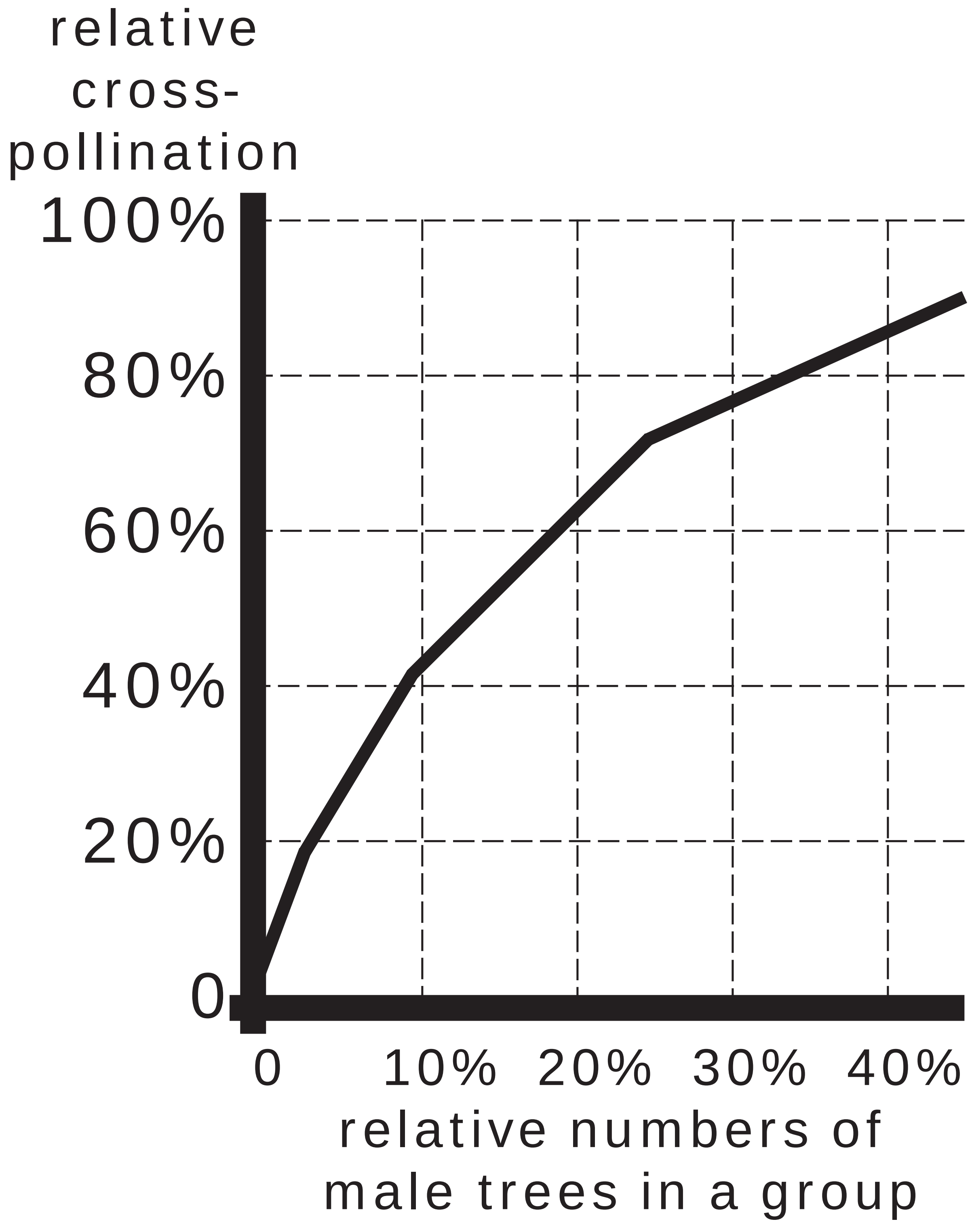

Figure 9: Relative number of functional males in a group of trees leading to successful cross-pollination (or minimizing inbreeding / self-pollination).

Note: Provided as an educational example only -- composite, highly variable estimate from multiple studies. (50% cross-pollination =14% males)

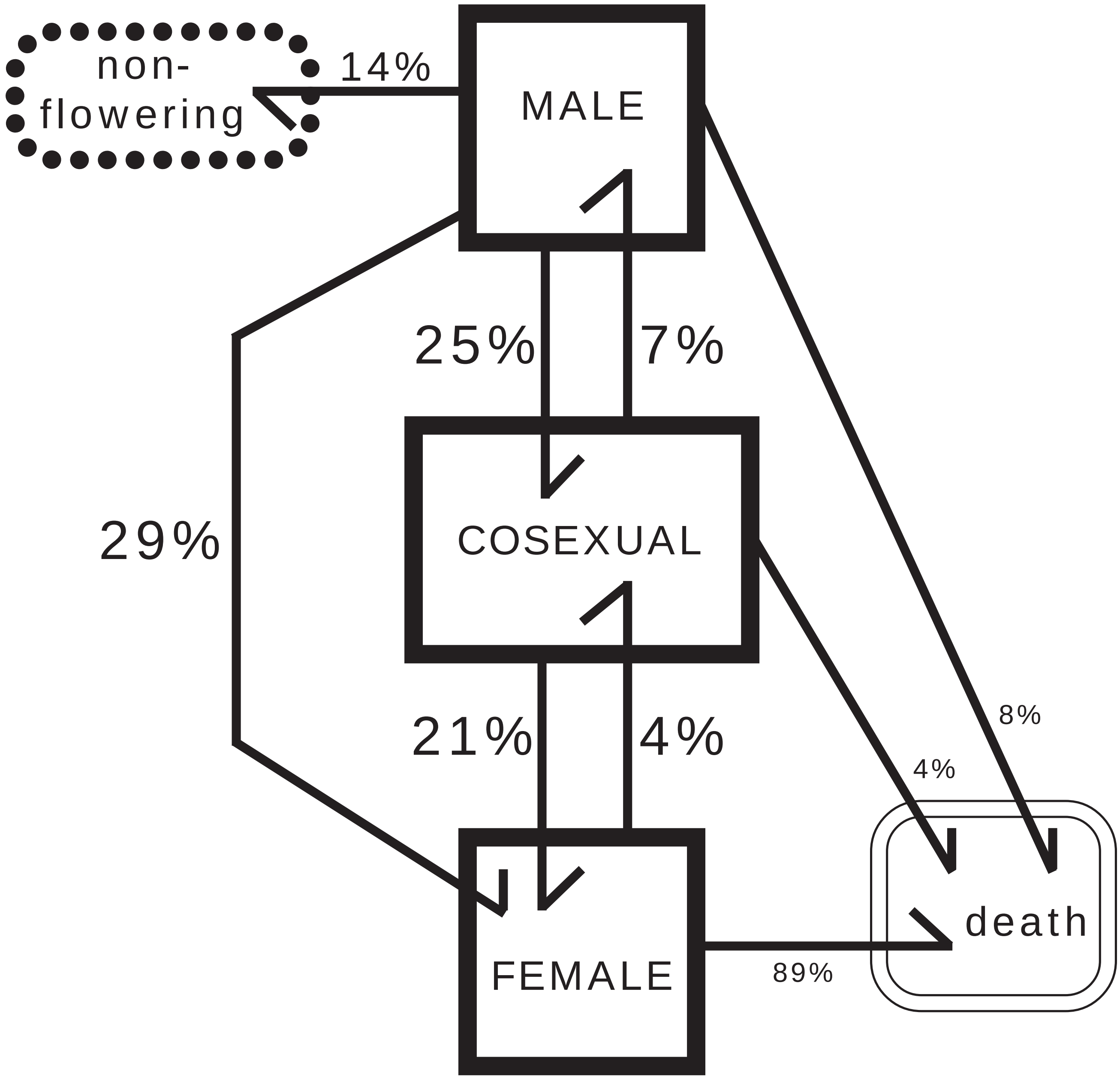

Figure 10: Example -- relative number of tree sex changes in one year within a group of mature striped maples (*Acer pennsylvanica*) in a forest setting.

[after Hibbs & Fischer, 1979]

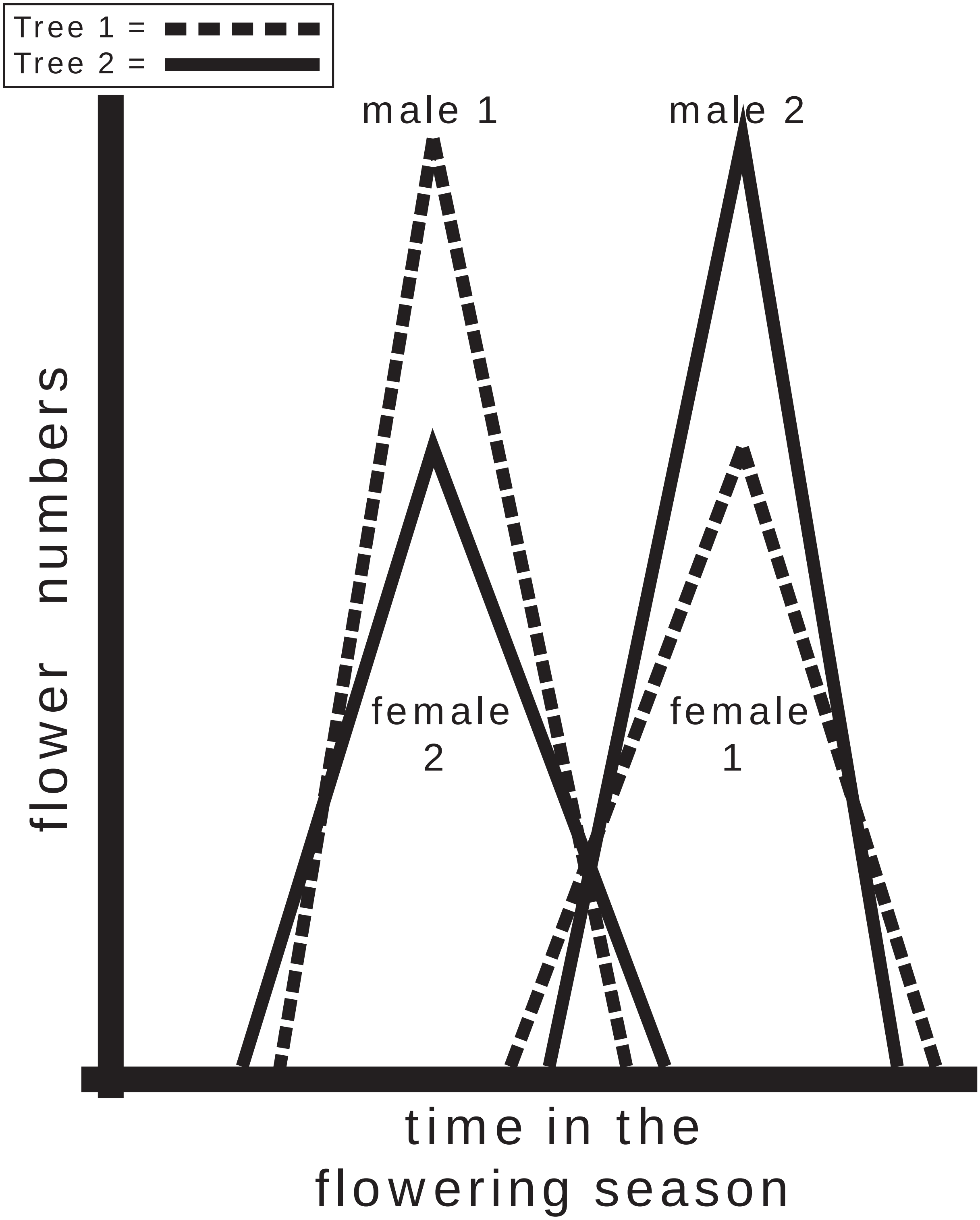

Figure 11: Example -- timing of flowering for *Juglans hindsii* trees growing in the same area. Tree 1 represents protandrous (male flowers first) trees and Tree 2 represents protogynous (female flowers first) trees. Peak flowering = ~15 days apart. (after Gleeson, 1982)

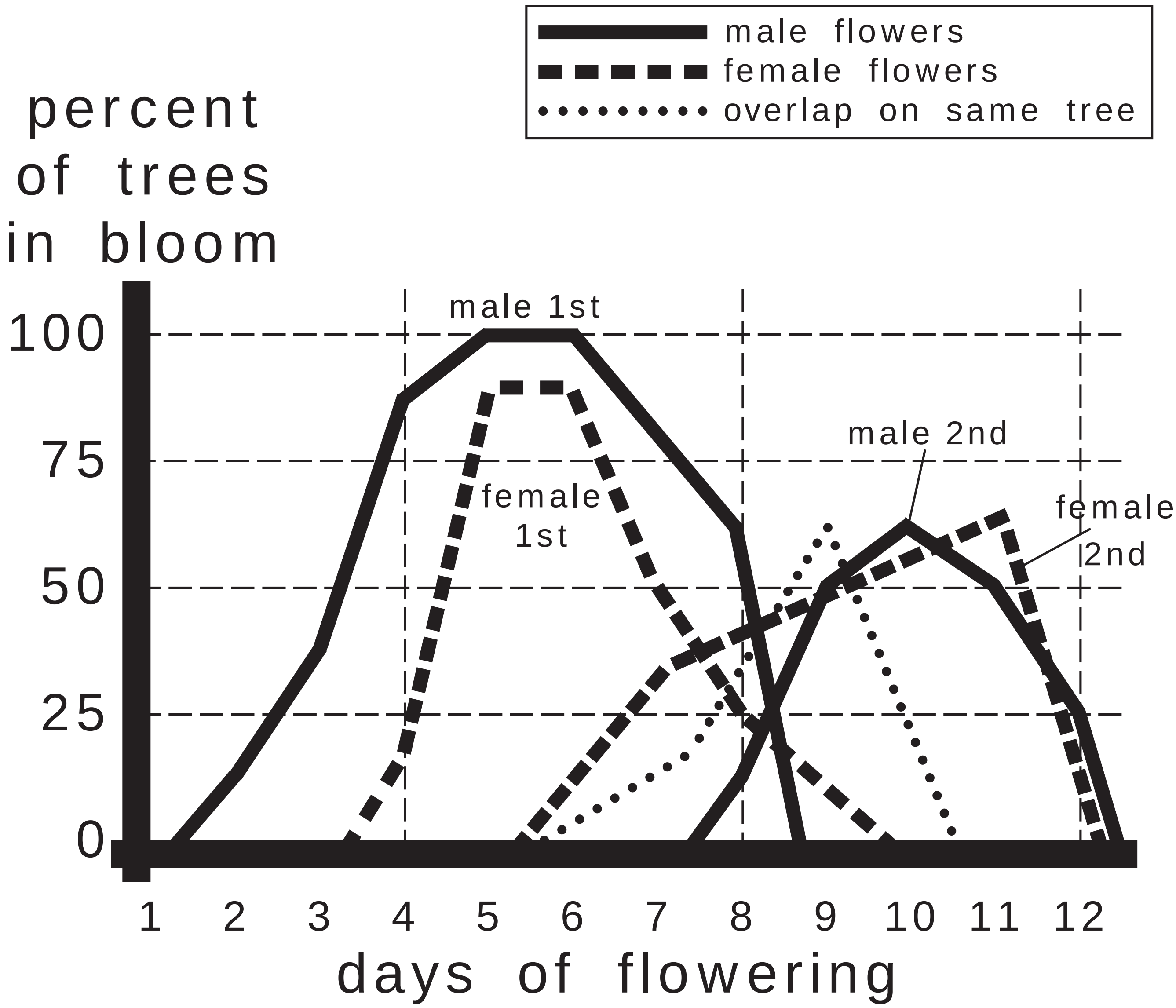

Figure 12: Example -- timing and duration of male and female flowers blooming on many different trees across several years in sugar maples (*Acer saccharum*). Note only the small dotted line represents both male and female flowering at the same time on the same tree. (after Gabriel, 1968)

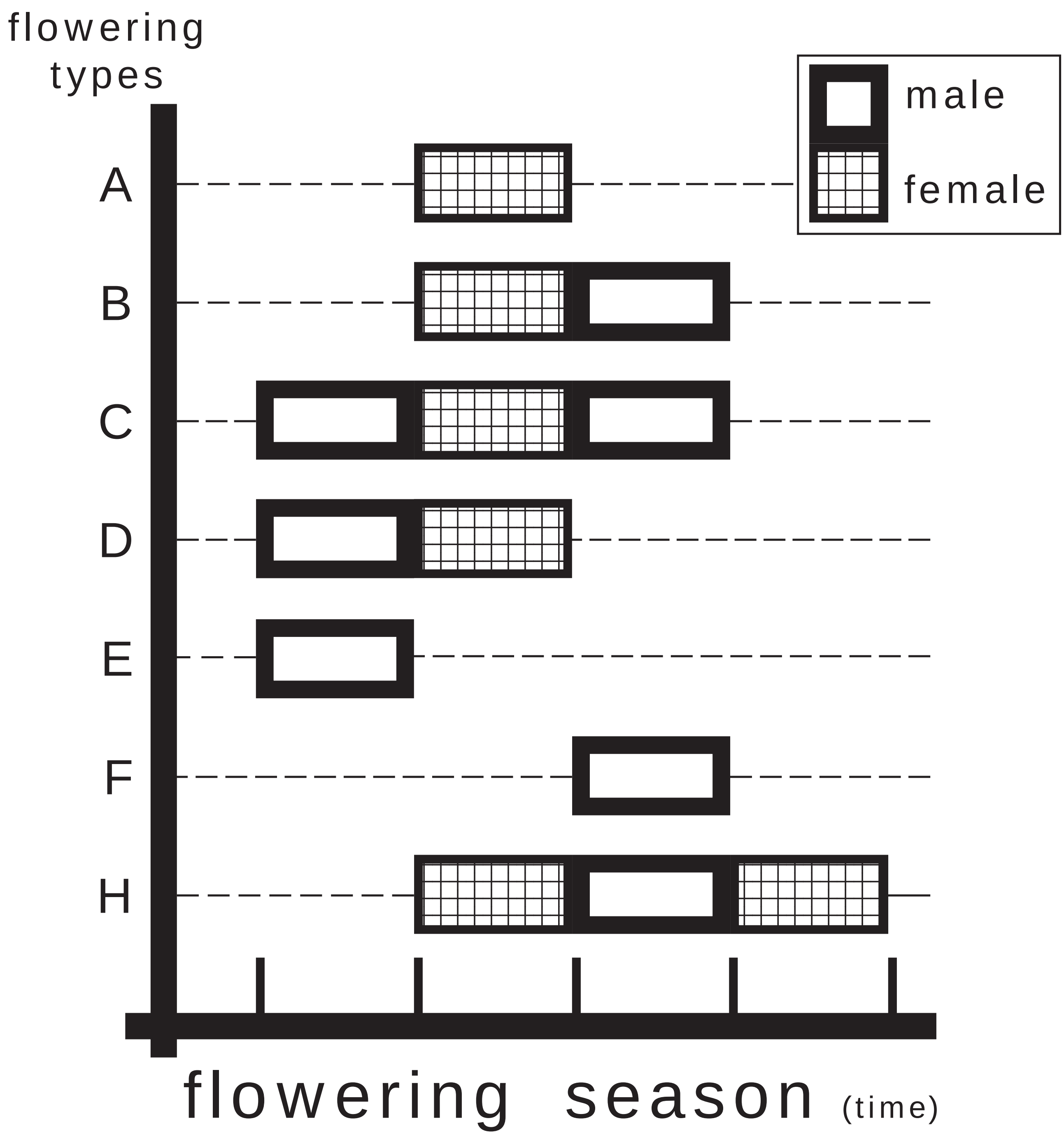

Figure 13: Example -- standard types of male and female flowering phases seen in different species of *Acer* (maples). Note *Acer saccharum* in one study used flowering types B & D.
(after de Jong, 1976)

Table 1: An outline of tree sexual classifications based on flower appearance generated and sexual function.

1. **cosexual** (hermaphrodite, bisexual)
   -- flowers with both functional male and female parts

   "sequential cosexual" – an individual tree changes sex as it ages or reaches some size threshold (usually starts out male and can be confused as a dioecious tree)

2. **monoecious** (unisexual)
   -- separate male and female flowers on the same tree

   2a. andromonoecius
   -- separate cosexual & male flowers on the same tree

   2b gynomonoecius
   -- separate cosexual & female flowers on the same tree

3. **polygamous** (trimonoecious, polygamomonoecious)
   -- separate cosexual, female and male flowers on the same tree

4. **dioecious**
   -- male and female flowers on different trees

   3a. androdioecious
   -- one tree cosexual (primarily female) & one tree male

   3b. gynodioecious
   -- one tree cosexual (primarily male) and one tree is female

   "paradioecious" — an individual tree switches sex depending upon environmental conditions (can be confused as a dioecious tree)

5. **polygamodioecious** (subdioecy)
   -- cosexual and male flowers, and cosexual and female flowers, on different trees

6. **trioecious**
   -- cosexual, male, and female flowers each on different trees

Table 2: Percentages for various sexual reproduction strategies in tree species across the globe. Values are composite estimates from multiple studies and will not sum to 100%.

tree sexual strategies	percent	number of sources
cosexual	80%	n=4
monoecious	8.5%	n=7
andromonoecious	4.5%	n=2
gynomonoecious	2.0%	n=2
polygamous	10%	n=1
dioecious	8.0%	n=7
gynodioecious & androdioecious	7.0%	n=1
gynodioecious	0.5%	n=1
androdioecious	0.1%	n=1

Table 3: Sexual system distribution in a natural population within a species traditionally considered dioecious, *Populus tremuloides*. (averaged from three authors) (after Lester, 1963)

sexual system	percent of trees	
dioecious	83.4	
male		53.1
female		30.3
monoecious	16.6	
gynomonoecious		9.3
andromonoecious		7.3

Table 4: Dominant sexual strategies of major tree genera and species, and their age in years when reaching sexual maturity, by scientific name.

Note: This list was compiled from many published sources, a number of which disagreed with each other as to sexual strategies of various species. All sexual strategies cited are listed. The age of sexual maturity in years value was derived from an average of multiple ages cited and / or a mid-point value from a cited range.

Table coding: C = cosexual; D = dioecious; M = monoecious; P = polygamous; T = trioecious; a = male dominant.

tree species scientific name	sexual strategy	sexual maturity age (years)
Abies spp.		
Abies alba	-M-	25
Abies balsamea	-M-	15
Abies concolor	-M-	40
Abies fraseri	-M-	15
Abies grandis	-M-	20
Abies lasiocarpa	-M-	25
Abies procera	-M-	
Acacia spp.	-C--P-	4
Acer spp.		
Acer barbatum	-D--P-	
Acer campestre		10
Acer ginnala	-C-	20
Acer japonicum	-Da--M-	
Acer macrophyllum		10
Acer negundo	-D-	
Acer palmatum	-M-	
Acer pennsylvanicum	-C--M-	
Acer platanoides	-M-	
Acer rubrum	-C--M--P-	4
Acer saccharinum	-D--M-	11
Acer saccharum	-C--M--P-	30
Acer spicatum	-M-	
Aesculus spp		
Aesculus flava	-Ca--P-	
Aesculus glabra	-Ca-	8
Aesculus hippocastanum		10
Aesculus parviflora	-C-	
Aesculus pavia	-C-	
Aesculus sylvatica	-Ca-	8
Ailanthus altissima	-Ca–D-	16
Aleurites fordii	-M-	
Alnus spp.		
Alnus glutinosa	-M-	10
Alnus incana	-M-	22
Alnus rubra	-M-	9
Alnus serrulata	-M-	
Amelanchier arborea	-C-	
Amorpha spp.	-C-	
Aralia spinosa	-C--P-	
Araucaria spp.	-P-	17
Arbutus spp.		
Arbutus menziesii	-C-	4
Arbutus unedo	-C-	
Arctostaphylos spp.	-C-	
Aronia spp.	-C-	2
Asimina triloba	-C-	
Baccharis halimifolia	-D-	
Betula spp.		
Betula alleghaniensis	-M-	25
Betula lenta	-M-	40
Betula nigra	-M-	
Betula papyrifera	-M-	15
Betula pendula	-M-	15
Betula populifolia	-M-	8
Betula pubescens	-M-	15
Broussonetia papyrifera	-D-	
Bumelia langinosa	-C-	
Calocedrus decurrens	-M-	
Carpinus spp.		
Carpinus betulus	-M-	18
Carpinus caroliniana	-M-	15
Carya spp.		
Carya aquatica	-M-	20
Carya avellana	-M-	
Carya cordiformis	-M-	30
Carya glabra	-M-	30
Carya illinoensis	-M-	15
Carya laciniosa	-M-	40
Carya myristicaeformis	-M-	30
Carya ovata	-M-	40
Carya tomentosa	-M-	25

Table 4: (continued)

tree species scientific name	sexual strategy	sexual maturity age (years)
Castanea spp.		
Castanea dentata	-M-	
Castanea mollissima	-M-	
Castanea pumila	-M-	
Castanopsis spp.	-M-	
Casuarina spp.	-D--M-	4
Catalpa spp.		
Catalpa bignonioides	-C-	20
Catalpa speciosa	-C-	20
Ceanothus spp.	-C-	3
Cedrus spp.		32
Cedrus atlantica	-M-	
Cedrus deodara	-M-	
Cedrus libani	-M-	
Celtis spp.		
Celtis laevigata	-M--P-	15
Celtis occidentalis	-M--P-	
Cephalanthus occidentalis	-C-	
Cephalotaxus harringtonia	-D-	
Cercidiphyllum japonicum	-D-	
Cercis canadensis	-C-	5
Cercocarpus spp.	-C-	11
Chamaecyparis spp.		
Chamaecyparis lawsoniana	-M-	9
Chamaecyparis thyoides	-M-	8
Chionanthus virginicus	-C--D--P-	6
Cinnamomum camphora	-C-	
Cladrastis kentukea	-C-	
Clethra acuminata	-C-	
Cliftonia monophylla	-C-	
Cornus spp.		
Cornus alternifolia	-C-	
Cornus amomum	-C-	5
Cornus drummondii	-C-	
Cornus florida	-C-	6
Cornus nuttallii	-C-	10
Corylus spp.	-M-	
Cotinus spp.		
Cotinus coggygria	-D--P-	
Cotinus obovatus	-D--P-	
Crataegus spp.	-C-	
Cryptomeria spp.	-M-	
Cunninghamii spp.	-M-	
Cupressocyparis leylandii	-M-	
Cupressus spp.	-M-	10
Cyrilla racemiflora	-C-	
Davidia involucrata	-Ma-	
Diospyros virginiana	-D-	10
Elaegnus spp.		
Elaegnus angustifolia	-C-	4
Elaegnus umbellata	-C-	6
Elliottia racemosa	-C-	
Eucalyptus spp.	-C-	10
Euonymus spp.		
Euonymus alatus	-C-	
Euonymus atropurpureus	-C-	
Fagus spp.		
Fagus grandifolia	-M-	40
Fagus sylvatica	-M-	50
Forestiera acuminata	-D--P-	
Frangula caroliniana	-C-	
Franklinia alatamaha	-C-	
Fraxinus spp.		
Fraxinus americana	-D-	20
Fraxinus caroliniana	-D-	
Fraxinus dipetala	-C-	
Fraxinus excelsior	-P--T-	15
Fraxinus nigra	-P-	
Fraxinus ornus	-P-	20
Fraxinus pennsylvanica	-D-	
Fraxinus profunda	-D-	10
Fraxinus quadrangulata	-C--D-	25
Fraxinus velutina	-D-	
Ginkgo biloba	-D-	23
Gleditsia spp.		10
Gleditsia aquatica	-P-	
Gleditsia triacanthos	-P-	
Gordonia lasianthus	-C-	
Gymnocladus dioicus	-D--P-	
Halesia spp.		
Halesia carolina	-C-	
Halesia diptera	-C-	
Halesia monticola	-C-	
Halesia tetraptera	-C-	
Hamamelis virginiana	-C-	
Ilex spp.		
Ilex ambigua	-D-	
Ilex amelanchier	-D-	
Ilex aquifolium	-D-	7
Ilex cassine	-D-	
Ilex coriacea	-D-	
Ilex decidua	-D-	
Ilex myrtifolia	-D-	
Ilex opaca	-D-	5
Ilex vomitoria	-D-	
Illicium floridanum	-C-	
Idesia polycarpa	-D-	
Juglans spp.		
Juglans ailantifolia	-M-	10

Table 4: (continued)

tree species scientific name	sexual strategy	sexual maturity age (years)
Juglans californica	-M-	6
Juglans cinerea	-M-	20
Juglans cordiformis	-M-	
Juglans hindsii	-M-	9
Juglans microcarpa	-M-	20
Juglans nigra	-M-	8
Juglans regia	-M-	8
Juniperus spp.		
Juniperus communis	-D-	
Juniperus monosperma	-D--M-	12
Juniperus occidentalis	-D--M-	
Juniperus pinchotii	-D-	12
Juniperus scopulorum	-D--M-	12
Juniperus virginiana	-D-	10
Kalmia latifolia	-C-	
Koelreuteria spp.		
Koelreuteria bipinnata	-C--P-	
Koelreuteria paniculata	-C--P-	
Lagerstroemia indica	-C-	
Larix spp.		
Larix decidua	-M-	10
Larix laricina	-M-	40
Larix occidentalis	-M-	25
Laurus nobilis	-D-	
Leitneria floridana	-D-	
Libocedrus decurrens	-M-	
Lindera benzoin	-D--P-	
Liquidambar styraciflua	-M-	22
Liriodendron tulipifera	-C-	15
Lithocarpus densiflorus	-M-	
Lyonia ferruginea	-C-	
Maclura pomifera	-D-	10
Magnolia spp.		10
Magnolia acuminata	-C-	
Magnolia fraseri	-C-	
Magnolia grandiflora	-C-	10
Magnolia macrophylla	-C-	
Magnolia tripetala	-C-	
Magnolia virginiana	-C-	
Malus spp.		
Malus angustifolia	-C-	
Malus coronaria	-C-	
Melia azedarach	-C--D--P-	
Metasequoia glyptostroboides	-M-	
Morus spp.		
Morus alba	-D--M-	5
Morus rubra	-D--M--P-	10
Myrica cerifera	-D--M-	
Nyssa spp.		
Nyssa aquatica	-C--D--P-	6
Nyssa ogeche	-C--D--P-	
Nyssa sylvatica	-C--D--P-	
Olea europaea	-C-	5
Osmanthus americanus	-P-	
Ostrya virginiana	-M-	25
Oxydendrum arboreum	-C-	
Paulownia tomentosa	-C-	
Persea spp.		
Persea borbonia	-C-	
Persea palustris	-C-	
Phellodendron amurense	-D-	
Picea spp.		
Picea abies	-M-	35
Picea engelmannii	-M-	18
Picea glauca	-M-	30
Picea pungens	-M-	20
Picea rubens	-M-	35
Picea sitchensis	-M-	20
Pinckneya bracteata	-C-	
Pinus spp.		
Pinus banksiana	-M-	6
Pinus clausa	-M-	5
Pinus contorta	-M-	6
Pinus echinata	-M-	
Pinus edulis	-M-	35
Pinus elliottii	-M-	8
Pinus glabra	-M-	
Pinus monticola	-M-	8
Pinus nigra	-M-	20
Pinus palustris	-M-	25
Pinus pungens	-M-	5
Pinus radiata	-M-	7
Pinus resinosa	-M-	15
Pinus rigida	-M-	7
Pinus serotina	-M-	6
Pinus strobus	-M-	7
Pinus sylvestris	-M-	8
Pinus taeda	-M-	7
Pinus virginiana	-M-	5
Pistacia chinensis	-D-	
Planera aquatica	-P-	
Platanus spp.		
Platanus occidentalis	-M-	6
Platanus x acerifolia	-M-	
Podocarpus macrophyllus	-D-	
Poncirus trifoliata	-C-	
Populus spp.		
Populus acuminata	-D-	5
Populus alba	-D-	10
Populus balsamifera	-D-	9

Table 4: (continued)

tree species scientific name	sexual strategy	sexual maturity age (years)
Populus deltoides	-D-	10
Populus fremontii	-D-	8
Populus grandidentata	-D-	12
Populus heterophylla	-D-	10
Populus lasiocarpa	-M-	
Populus nigra	-D-	9
Populus tremula	-D-	
Populus tremuloides	-D-	12
Populus trichocarpa	-D-	10
Prosopis juliflora	-C-	
Prunus spp.		
Prunus americana	-C-	
Prunus angustifolia	-C-	
Prunus avium	-C-	6
Prunus caroliniana	-C-	
Prunus cerasus	-C-	6
Prunus ilicifolia	-C-	3
Prunus pensylvanica	-C-	2
Prunus persia	-C-	5
Prunus pumila	-C-	5
Prunus serotina	-C-	5
Prunus tomentosa	-C-	3
Prunus virginiana	-C-	5
Pseudolarix amabilis	-M-	
Pseudotsuga menziesii	-M-	7
Ptelea trifoliata	-M--P-	
Pterocarya fraxinifolia	-M-	
Pyrus communis	-C-	
Quercus spp.		
Quercus acutissima	-M-	5
Quercus agrifolia	-M-	15
Quercus alba	-M-	20
Quercus arkansana	-M-	
Quercus bicolor	-M-	20
Quercus coccinea	-M-	20
Quercus falcata	-M-	25
Quercus geminata	-M-	
Quercus georgiana	-M-	
Quercus hemisphaerica	-M-	
Quercus ilicifolia	-M-	
Quercus imbricaria	-M-	25
Quercus incana	-M-	
Quercus kelloggii	-M-	30
Quercus laevis	-M-	
Quercus laurifolia	-M-	15
Quercus lyrata	-M-	25
Quercus macrocarpa	-M-	35
Quercus margaretta	-M-	
Quercus marilandica	-M-	
Quercus michauxii	-M-	20
Quercus montana	-M-	
Quercus myrtifolia	-M-	
Quercus nigra	-M-	20
Quercus nuttallii	-M-	5
Quercus oglethorpensis	-M-	
Quercus pagoda	-M-	
Quercus palustris	-M-	20
Quercus petraea	-M-	40
Quercus phellos	-M-	20
Quercus plaustris	-M-	
Quercus prinus	-M-	20
Quercus robur	-M-	20
Quercus rubra	-M-	25
Quercus shumardii	-M-	25
Quercus sinuata	-M-	
Quercus stellata	-M-	25
Quercus suber	-M-	12
Quercus texana	-M-	
Quercus velutina	-M-	20
Quercus virginiana	-M-	25
Rhamnus spp.		
Rhamnus caroliniana	-C--D--M-	6
Rhamnus carthartica	-C--D--M-	
Rhamnus frangula	-C--D--M-	
Rhododendron sp.		
Rhododendron catawbiense	-C-	
Rhododendron macrophyllum	-C-	
Rhododendron maximum	-C-	
Rhododendron nudiflorum	-C-	
Rhus spp.		
Rhus aromatica	-D--P-	
Rhus copallina	-D--P-	
Rhus glabra	-D--P-	
Rhus laurina	-D--P-	
Rhus typhina	-D--P-	
Robinia pseudoacacia	-C-	6
Sabal palmetto	-C-	
Salix spp.		
Salix alba	-D-	
Salix bebbiana	-D-	4
Salix caroliniana	-D-	
Salix discolor	-D-	2
Salix nigra	-D-	10
Sambucus canadensis	-C-	
Sapindus spp.		
Sapindus drummondii	-D--P-	
Sapindus saponaria	-P-	
Sapium sebiferum	-M-	
Sassafras albidum	-D-	10
Sciadopitys verticillata	-M-	
Sequoia sempervirens	-M-	7
Sequoiadendron giganteum	-M-	20
Serenoa repens	-C-	

Table 4: (continued)

tree species scientific name	sexual strategy	sexual maturity age (years)
Sideroxylon spp.		
Sideroxylon lanuginosum	-C-	
Sideroxylon lycioides	-C-	
Sophora japonica	-C-	
Sorbus spp.		
Sorbus americana	-C-	
Sorbus aucuparia	-C-	15
Staphylea trifolia	-C-	
Stewartia spp.		
Stewartia malacodendron	-C-	
Stewartia ovata	-C-	
Styrax spp.		
Styrax americanus	-C-	
Styrax grandifolius	-C-	
Symplocos tinctoria	-C-	
Taxodium spp.		
Taxodium ascendens	-M-	
Taxodium distichum	-M-	
Taxus spp.		
Taxus baccata	-D--M-	30
Taxus brevifolia	-D--M-	
Taxus canadensis	-M-	
Taxus cuspidata	-D--M-	
Taxus floridana	-D--M-	
Tectona grandis	-C-	4
Thuja spp.		
Thuja occidentalis	-M-	22
Thuja plicata	-M-	18
Tilia spp.		
Tilia americana	-C-	15
Tilia cordata	-C-	25
Torreya taxifolia	-D-	
Toxicodendron vernix	-D--P-	
Tsuga spp.		
Tsuga canadensis	-M-	22
Tsuga caroliniana	-M-	22
Tsuga heterophylla	-M-	25

tree species scientific name	sexual strategy	sexual maturity age (years)
Ulmus spp.		
Ulmus alata	-C-	
Ulmus americana	-C-	15
Ulmus crassifolia	-C-	
Ulmus glabra	-C-	35
Ulmus laevis	-C-	35
Ulmus minor	-Da-	
Ulmus parvifolia	-C-	
Ulmus pumila	-C-	8
Ulmus rubra	-C-	15
Ulmus serotina	-C-	
Ulmus thomasii	-C-	20
Umbellularia	-C-	25
Vaccinium spp.		
Vaccinium arboreum	-C-	
Vaccinium corymbosum	-C-	
Vaccinium ovatum	-C-	
Vaccinium parvifolium	-C-	
Viburnum spp.		
Viburnum lantana	-C-	5
Viburnum lentago	-C-	8
Viburnum nudum	-C-	
Viburnum prunifolium	-C-	9
Viburnum rufidulum	-C-	
Yucca spp.	-C-	6
Zanthoxylum spp.	-D-	
Zanthoxylum americanum	-D-	
Zanthoxylum clava-herculis	-D--P-	
Zelkova serrata	-P-	

Table 5: A summary of Table 4 tree list.

Remember this review states percentages of trees listed in Table 4, not all tree species, as only more common trees are listed and many species with consistently identifiable sexual strategies are represented only by their genus name. Combination strategies are counted in all strategies with which they are identified. Combination strategies could represent both actual tree reproductive processes and / or ignorance of observers to correctly identify functional sexual strategies.

sexual strategy	number of trees with a sole strategy	percentage of all species with sole strategy	number of trees with combination strategies	percentage of all species in table
cosexual (C)	122	37%	+18	32%
dioecious (D)	51	15%	+37	20%
monoecious (M)	151	45%	+22	39%
polygamous (P)	9	3%	+31	9%
trioecious (T)	0	0%	+1	0.2%

combination sexual strategies	number of trees
D P	14
D M	12 (1)
C D P	5 (2)
C P	5
C D M	3 (1, 2, 3)
M P	3
C D	2 (2)
C M P	2 (3)
C M	1 (3)
D M P	1 (1)
P T	1

D + M = (1); C + D = (2); C + M = (3)

sexual strategy	average age at sexual maturity	number of trees
C	11.3 years	n= 49
D	9.6	n= 24
M	18.8	n= 99
P	15.7	n= 3