

Alternative Strategies for Clonal Plant Reproduction®

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INTRODUCTION

Pick up any biology textbook and there will be a description of the typical sexual life cycle for plants. In higher plants, the life cycle starts with seed germination followed by vegetative growth leading to flower and gamete formation with the ultimate goal of creating genetically diverse offspring through seed production. The fern life cycle is more primitive but follows a similar progression from spore germination to the gametophytic generation leading to sexual union of gametes resulting in the leafy sporophyte, which in turn creates the spores.

Interestingly, plants have evolved unique alternative life cycles that bypass typical seed production in favor of clonal reproduction systems. This may seem counter-intuitive because sexual reproduction should lead to greater genetic diversity in offspring compared to clonal plants. These sexual offspring should have a higher potential to adapt to new or changing environments, i.e., be more successful. However, investing in clonal reproduction seems to increase the likelihood that a species can colonize specific environmental niches. It has been observed that many of the perennial species in a given ecosystem tend to combine both sexual and clonal forms of reproduction (Ellstrand and Roose, 1987). Additionally, unique clonal propagation systems tend to be more prevalent in plants adapted to extreme environments like arctic, xerophytic, and Mediterranean climates.

Mini-Review Objectives. The objective of this mini-review is to describe some of the ways plants have evolved clonal reproduction strategies that allow unique plants to colonize extreme environments.

CLONAL REPRODUCTION ADOPTED BY PLANTS

There are two basic forms of clonal reproduction adopted by plants. Flowering plants and ferns can reproduce by modifications of vegetative structures (shoot, leaf, and root). Additionally, flowering plants can produce clonal seeds via apomixis. It is interesting that cycads and gymnosperms that are intermediate in their evolution between ferns and flowering plants do not display alternative clonal propagation strategies. It is possible that morphological adaptations in cycads and gymnosperms did not permit the plasticity needed for clonal reproduction.

Vegetative reproductive systems are incredibly unique, and their diversity is listed in Table 1 and illustrated in Figure 1. These reproductive structures can be aerial or subterranean modifications of stems, leaves, inflorescences, and roots. They range from basal stem modifications that slowly colonize local areas (like off-set production in geophytes) to the production of detachable vegetative plantlets (like aerial bulbils) that can be disseminated much like true seed.

Unlike the structural anomalies obvious in vegetative clonal reproduction, there are no obvious outward signs that clones formed through apomixes differ from their sexual counterparts. Apomixis is the production of an embryo that bypasses the usual process of meiosis and fertilization (Hartmann et al., 2002). The genotype

Table 1. Clonal propagation strategies as alternatives to sexual seed production.

1.	Modified stems (basal)			
	a. Bulbs (offsets)	tulip lily	<i>Tulipa</i> <i>Lilium</i>	
	b. Tubers	potato wind flower	<i>Solanum tuberosum</i> <i>Anemone</i>	
	c. Corms (cormels)	crocus gayfeather	<i>Crocus</i> <i>Liatris</i>	
	d. Rhizomes	iris bamboo	<i>Iris</i> <i>Bambusa</i>	
	e. Stolons (runners)	strawberry red stem dogwood	<i>Fragaria</i> <i>Cornus sericea</i> (syn. <i>C. stolonifera</i>)	
2.	Modified stems (above ground)			
	a. Aerial bulbs (bulbils)	European bittercress lily monkey flower	<i>Cardamine bulbifera</i> (syn. <i>Dentaria bulbifera</i>) <i>Lilium</i> <i>Mimulus gemmiparus</i>	
	b. Aerial tubers (tubercles)	meadow saxifrage devil's tongue hardy begonia rosary vine winged yam	<i>Saxifraga granulata</i> <i>Amorophallus bulbifer</i> <i>Begonia grandis</i> subsp. <i>evansiana</i> <i>Ceropegia linearis</i> subsp. <i>woodii</i> <i>Dioscorea alata</i>	
3.	Plantlets on leaves	mother of thousands piggy-back plant hen and chick fern walking fern bulblet fern button fern	<i>Kalanchoe daigremontiana</i> (syn. <i>Bryophyllum daigremontiana</i>) <i>Tolmiea menziesii</i> <i>Asplenium bulbiferum</i> <i>Asplenium rhizophyllum</i> (syn. <i>Camptosorus rhizophyllum</i>) <i>Cystopteris bulbifera</i> <i>Tectaria cicutaria</i>	

4. Plantlets on roots	pawpaw blackberry	<i>Asimina triloba</i> <i>Rubus</i>
5. Plantlets on inflorescence	century plant wild garlic spiderplant orchard grass walking iris meadow grass alpine bistort	<i>Agave americana</i> <i>Allium vineale</i> <i>Chlorophytum comosum</i> <i>Dactylis glomerata</i> <i>Neomarica caerulea</i> <i>Poa bulbosa</i> <i>Polygonum viviparum</i>
6. Roots on stems	English ivy figs	<i>Hedera helix</i> <i>Ficus</i>
7. Apomixis		
a. Gametophytic	grasses dandelion crabapple	<i>Poa</i> , <i>Pennisetum</i> <i>Taraxacum</i> <i>Malus</i>
b. Sporophytic (adventive embryony)	orange mango	<i>Citrus</i> <i>Mangifera</i>

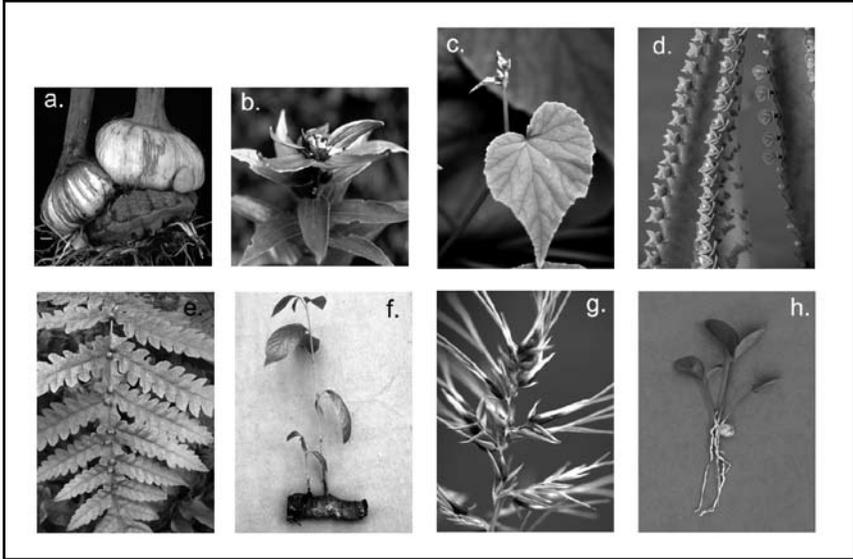


Figure 1. Examples of clonal reproduction systems. (A) Corm and cormel production in gladiola; (B) Aerial bulbils in lily; (C) Aerial tubers in hardy begonia; (D) Plantlets along the leaf margin in mother-of-thousands (*Kalanchoe*); (E) Aerial bulblets on the frond of bulblet fern; (F) Root suckers in pawpaw; (G) Aerial bulbils in the inflorescence of meadow grass; (H) Multiple apomictic embryos in citrus.

of the embryo and resulting plant will be the same as the seed parent. Seed production via apomixis is clonal. Some species or individuals produce only apomictic embryos; however, the majority of apomictic species produce both apomictic and sexual embryos.

Apomixis can be further divided into gametophytic versus sporophytic apomixis. In gametophytic apomixis, the megaspore mother cell fails to initiate or complete meiosis. However, the unreduced ($2n$) mother cell goes on to form an otherwise normal embryo sac. The egg cell divides to form an embryo but it was never fertilized by a male gamete. The result is clonal seed production.

In sporophytic apomixis, the megaspore mother cell does complete meiosis and forms an egg sac with reduced ($1n$) female gametes. These are fertilized and form normal endosperm and a sexual embryo. However, in addition to this single sexual embryo multiple clonal embryos spontaneously develop from nucellar ($2n$) tissue surrounding the sexual embryo sac but still inside the developing seed (ovule). The seed usually contains one sexual embryo and multiple asexual embryos. This type of apomixis is a form of polyembryony and is termed adventive embryony.

An obvious question for biologists to ponder is whether reliance on vegetative propagation with its inherent reduction in genetic diversity allows the flexibility for a species to adapt to a changing environment and avoid extinction. There are few cases where a species relies on vegetative propagation as its predominant means of propagation. For example, the Minnesota trout lily (*Erythronium propullans*) reproduces by means of a dropper (propagation bulb) produced at the end of a stolon. This general vegetative strategy allows trout lily species to colonize relatively large

areas. However, the Minnesota trout lily appears incapable of significant sexual reproduction to supplement vegetative propagation. It only rarely produces seeds and these seeds are thought to be hybrids with white fawnlily (*E. albidum*) (Banks, 1980). The result is significantly less genetic diversity in Minnesota trout lily compared to white fawnlily colonies (Pleasants and Wendel, 1989). Currently, this genetic bottleneck leaves the Minnesota trout lily an endangered species found only in two southeastern Minnesota counties.

In contrast to the Minnesota trout lily, there are numerous species that reproduce predominately by vegetative means, but still are capable of seed production. Genetic studies indicate that there is reduced genetic diversity found within local colonies of clonal species and that this diversity increases with geographic distance as the number of dominate clones also increases (Ellstrand and Roose, 1987). The mother plant (genet) can dispense both genetic (seedlings) and clonal progeny (ramet). When the clonal progeny is very adaptive to a particular environment, it becomes the dominant reproduction unit (Eriksson, 1997). An extreme example is in aspen (*Populus tremuloides*) populations that can have over 1000 clonal offspring (ramets) from a single dominant mother plant (genet) covering over 30 acres (Kemperman and Barnes, 1976). However, even in species where clonal propagation is dominant, sexual progeny from the mother plant provides the genetic flexibility to allow the species to adapt to a changing environment. Sexual reproduction provides essential genetic drift in a species that leads to greater adaptive capacity observed in clonal populations.

Some violet species may take the prize for combining the most genetic and clonal strategies for plant reproduction within an individual plant. Violets can produce two types of flowers. Chasmogamous flowers are produced in the spring or summer when pollinators are plentiful and active. Chasmogamous flowers open to permit cross-pollination between flowers and produce offspring (seeds) with generous genetic diversity. They also produce subterranean cleistogamous flowers in the autumn that never open and self-pollinate. Although this restricts genetic diversity, it does not require the same level of plant resources for seed production and provides insurance against poor seed production from earlier out-crossing flowers. Finally, these same violets produce stolons that serve to clonally reproduce successful mother plants. The result is mixed populations of violets that combine two levels of genetically diverse seedling populations and a means for local clonal colonization.

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