

REVIEW

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The optimal balance between sexual and asexual reproduction in variable environments: a systematic review

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Abstract

Many plant species have two modes of reproduction: sexual and asexual. Both modes of reproduction have often been viewed as adaptations to temporally or spatially variable environments. The plant should adjust partitioning to match changes in the estimated success of the two reproductive modes. Perennial plants showed that favorable habitats in soil nutrients or water content tend to promote clonal growth over sexual reproduction. In contrast, under high light-quantity conditions, clonal plants tend to allocate more biomass to sexual reproduction and less to clonal propagation. On the other hand, plants with chasmogamous and cleistogamous flowers provides with a greater tendency of the opportunity to ensure some seed set in any stressful environmental conditions such as low light, low soil nutrients, or low soil moisture. It is considered that vegetative reproduction has high competitive ability and is the major means to expand established population of perennial plants, whereas cleistogamous reproduction is insurance to persist in stressful sites due to being strong. Chasmogamous reproduction mainly enhances established and new population. Therefore, the functions of sexual and asexual propagules of perennial or annual plants differ from each other. These traits of propagule thus determine its success at a particular region of any environmental gradients. Eventually, if environmental resources or stress levels change in either space or time, species composition will probably also change. The reason based on which the plants differ with respect to favored reproduction modes in each environmental condition, may be involved in their specific realized niche.

Keywords: Benefit, Chasmogamy, Cleistogamy, Cost, Fitness, Realized niche, Seccession, Trade-off

Background

Many plant species have two reproductive modes: sexual and asexual reproduction. For example, most of the perennial clonal plants possess the capacity for both sexual reproduction through seeds and asexual reproduction through vegetative propagation (Klimes et al. 1997). In clonal plants, vegetative reproduction produces new ramets by budding from roots, rhizomes, stems, storage organs such as tubers or (more rarely) leaves, or inflorescences (Silvertown 2008). Most of the clonal plants mainly rely on clonal propagation and exhibit lower rate of sexual reproduction (Eckert 2002). Some plant species can produce combinations of chasmogamous flowers

(sexual reproduction) and cleistogamous flowers (asexual reproduction) (Ronsheim and Bever 2000). Cleistogamous flowers are tiny, closed, and self-pollinating flowers, and chasmogamous flowers are showy, open, and often cross-pollinating flowers (Minter and Lord 1983). Especially, the phenomenon of amphicarp, where the same plant bears both aerial fruits (chasmogamy) and subterranean fruits (cleistogamy) has been recognized in quite a few species (Koller and Roth 1964; Kim et al. 2016). Both the modes of reproduction contribute to population persistence of plants (Chen et al. 2015). Clonal plants are widespread across all biomes and biogeographical regions, particularly in cold, wet, shaded, and nutrient-poor environments (Chen et al. 2015). Furthermore, chasmogamous and cleistogamous flowers are also relatively widespread (Lord 1981; Culley 2002) and are more likely to appear in short-lived fugitive species

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whose habitat varies with time and space (Harper 1977; Weiss 1980).

The trade-offs are a central concept of life history researches (Stearns 1989; Roff 1992; Cheplick 1995). For sessile plants, it is generally assumed that there is a trade-off in allocation among the competing functions or organs because available resources are frequently limited (Tilman 1988; Bazzaz and Ackerly 1992; Bazzaz 1997). For example, when such a trade-off is selected for increased resource allocation to sexual reproduction, allocation to asexual reproduction will be correspondingly reduced, and vice versa. Previous investigations on trade-offs between reproductive modes in plants have produced mixed results. Some have detected negative phenotypic correlations between sexual and asexual reproduction, while others have not (Thompson and Eckert 2004). The failure to detect negative phenotypic correlations between sexual and asexual reproduction is usually attributed to genetic or environmental variations in plant resource acquisition obscuring trade-offs between allocation components (Worley and Harder 1996). The variation in resource allocation to sexual reproduction versus asexual reproduction may be determined based on genetics, plant size, age, environmental conditions such as soil moisture, photoperiod, light intensity, grazing, disturbance, nutrient availability, and air temperature, and population density (Zhang and Zhang 2007).

Both the modes of reproduction have often been viewed as adaptations to temporally or spatially variable environments (Stebbins 1974; Venable 1985; Venable and Brown 1988). In response to environmental variation, it has been established that phenotypic plasticity and direct genetic change of the mixed reproductive system might have changed for optimization of reproductive response to local conditions (Lloyd 1984). Changes in partitioning to sexual and asexual reproduction depend on the detection of environmental cues by the plant, and the plant should adjust to partitioning to match with the changes in the estimated success of the two reproductive modes (Obeso 2002). As one mode of reproduction will likely have higher fitness as compared to other in any one environment, maintenance of these divergent reproductive modes is considered as an important mechanism for plants to adapt to a spatially and temporally heterogeneous environment (Bai et al. 2009).

Some researchers reported that under growth-limiting conditions, clonal plants tend to allocate more biomass to clonal propagation and less to sexual reproduction. However, other studies suggested that favorable habitats should promote clonal growth over sexual reproduction (Bai et al. 2009). There exist almost no studies explaining this perplexity. Also, although the balance between the two reproductive modes may vary widely among species according to environmental conditions (Zhang and Zhang 2007), little is known about the causes of the

various responses to environmental changes among species. The objectives of this paper are the following: (1) to review the nature of environmental conditions, which might favor individual mode of reproduction in plants capable of both sexual and asexual reproduction, and (2) to address the estimated factors leading to different responses to heterogeneous environments among species. Henceforth, we analyzed almost every research (related to our purposes) found in Google Scholar and written in English language. Moreover, we reviewed responses to only one environmental change, two mixed environmental factors, and interaction between environmental condition and plant density.

The benefits and costs of diverse propagations

Optimal balance between sexual and asexual reproduction of each environmental condition is determined by the integration of cost-benefit inputs, which mostly affects fitness, e.g., reproductive efficiency, genetic composition of offspring, and fecundity (Schemske 1978).

Benefits and costs of vegetative propagation

The major benefits associated with vegetative propagation are major contributors for local population growth through rapid, short-distance spread (Xiao et al. 2011), and high resilience following conditions of herbivory, drought, and other stresses (Chen et al. 2015). Also, clonal propagules are a sink for resources (Bazzaz et al. 1987) and have “foraging” behavior, i.e., the ability to respond to environmental quality by escaping from poor sites and proliferating in richer sites (Hutchings 1988). In addition, vegetative propagules, due to their relatively large size and their ability to photosynthesize and consume nutrients (Grace 1993), may have a greater potential than seeds for successful colonization and establishment (Boedeltje et al. 2008). Particularly, physiological integration between parents and daughter ramets may be beneficial due to the ability to share resources such as light, water, and soil nutrients (Callaghan 1984).

Yet, it is hypothesized that clonal growth can bring about costs. Connections among ramets result in reduction in genetic diversity in local populations. High density and genetic uniformity of clonal populations increases the susceptibility to diseases, disturbances, insect outbreak, and environmental upheaval than plant populations that are genetically diverse through sexual reproduction (Lei 2010). Compared with seed offspring, clonal ramets can only disperse within a much shorter distance and are usually clumped around the mother ramet, which inevitably leads to self-pollination resulting from transfer of pollen between flowers in an individual (Handel 1985; Vange 2002). These interactions between ramets reduce the benefits of clonal growth (Loehle 1987). In addition, compared to seeds,

vegetative propagules are generally more vulnerable to desiccation and are more short-lived (Boedeltje et al. 2008).

Benefits and costs of cleistogamous reproduction

Cleistogamous flowers exhibit obligate self-pollination are energetically less expensive due to reduced costs of inflorescence and floral parts and often produce large seeds than chasmogamous flowers (Corff 1993). Self-fertility is important in limiting the gene flow between populations and producing ecogenetic differentiation, preserving gene combinations that confer high fitness in a local environment, and permitting fruit to be set after long-distance dispersal or when conditions for pollination are adverse (Cheplick 1996). In addition, assuming no inbreeding depression, the seedlings arising from the larger cleistogamous propagules are larger and more tolerant to stress or competition (Choo et al. 2015). These cleistogamous seedlings have a higher probability of surviving to produce seeds (Cheplick and Quinn 1982). The adaptive advantages of large cleistogamous seedlings include well-developed competitive ability and low susceptibility to predator or pathogen attack. In case of species where seeds from chasmogamous and cleistogamous flowers are morphologically identical, empirical data have not shown a clear advantage for one seed type over the other (Mitchell-Olds and Waller 1985; Antlfinger 1986; Gara and Muenchow 1990). Moreover, the placement of cleistogamous seeds in favorable parental microhabitats provides protection from the risks of random dispersal. The strongly indurate cleistogamous propagules remain viable in the soil seed bank following the disappearance of plants in secondary succession and can give rise to “instant populations” upon subsequent vegetation removal and/or soil disturbance (McNamara and Quinn 1977). Additionally, the selective advantages of the subterranean seed production include not only the abovementioned advantages but also protection from microenvironmental extremes at the soil surface, protection from fire, and protection from herbivores or feeding by aboveground predators (Cheplick 1994).

On the other hand, evolutionary constraints on cleistogamous seed production include lack of gene exchange among cleistogamous flowers and the possibility of inbreeding depression, high costs associated with large cleistogamous reproductive structures, limitations on seed number if a seed size/number trade-off exists, limited dispersal, sibling competition among the offspring arising from a single, poorly-dispersed cleistogamous seed, and exposure to subterranean herbivores and/or seed predators (Cheplick 1994).

Benefits and costs of sexual reproduction

Sexual reproduction allows parents to promote genetically diverse offspring through recombination, mutation,

and gene flow from immigrants (Morain 1984). It is hypothesized that through sexual reproduction, genetic differentiation would decrease the susceptibility of a population to disturbances, competition, diseases, insect outbreaks, and locally adverse environmental conditions. In addition, sexual reproduction enables long-distance seed dispersal, easy colonization of new habitats (Lei 2010), and is generally considered a prerequisite for species persistence at a meta-population level (Olivieri et al. 1995; Husband and Barrett 1996). In addition, seeds gain an ability to tolerate more severe environmental conditions as compared to ramets and seedlings. Even if the habitat undergoes catastrophic changes, thanks to the seed bank, the population still has the opportunity to survive and flourish again (Bai et al. 2009). Therefore, seeds play the most important role at pioneer stages of vegetation by allowing the (re)establishment of genetically diverse stands (Alvarez et al. 2005; Nielsen et al. 2006; Pollux et al. 2007).

Although large quantities of seeds are often produced by most of the plant species and are usually dispersed for considerable distances, only a small proportion of these seeds get a chance to become mature plants (Kozłowski 1972). The greatest mortality occurs during the process of seed germination and seedling stages. High losses of seeds occur due to low viability, dormancy, or injury to seed by various animals, microbes, insects, and fungi (Kozłowski 1972). Seedlings are extremely fragile and tolerate a narrow range of environmental conditions. Seedlings are also highly susceptible to diseases, disturbances, herbivory, trampling, soil compaction, soil erosion, and environmental extremes than clonal ramets of the same species (Lei 2010). So, in many studies on long-lived plants, seedling recruitment has been reported to be of minor importance for population growth (Sarukhan 1974; Thomas and Dale 1975; Eriksson 1985; Damman and Cain 1998; Kiviniemi 2002).

Changes in reproductive modes in response to environmental variations

There are distinct trends in the variation in both soil water content and light intensity, but not in variation in content of soil nutrients. Based on the availability of fewer data on soil water level in perennial, more studies are necessitated to gain deeper insight on this topic.

A general trend on selection of reproductive modes in relation to soil nutrients level in perennial

Clonal plants increased allocation to clonal reproduction under good soil fertility in *Sanguinaria canadensis* (Marino et al. 1997), *Allium vineale* (Ronsheim 1996), *Leymus chinensis* (Bai et al. 2009), and *Penthorum sedoides* (Nicholls 2011) (see Table 1), probably because sexual reproduction is much more costlier than clonal reproduction (López-Almansa et al. 2003). The favorable soil reduces the needs

for progeny genetic diversity to be selected (Bai et al. 2009). This allows the plant to place its genetically identical offspring in an environment in which the parent plant has reproduced successfully. It is assumed that this phenomenon may be due to other functions of clonal propagules, such as storage, nutrient uptake and overwintering, and increased photosynthesis. Moreover, facilitation among genetically identical siblings growing together would favor clonal reproduction (Ronsheim and Bever 2000; Ronsheim 1996).

In nutrient-poor soils, plants may allocate more resources for sexual structures in *L. chinensis* (Bai et al. 2009), *P. sedoides* (Nicholls 2011), and *Trapella sinensis* (Liu et al. 2013) (see Table 1) because sexual reproduction has the potential to produce genetic variations, which could increase the survivorship of the plants in the future (Grant 1981; Philbrick and Les 1996). Moreover, seeds may serve as a potential escape mechanism for offspring (Choo et al. 2015; Nicholls 2011; van Kleunen et al. 2002). The increase in the sexual biomass indicates that the plant might favor from founding new populations instead of expanding the current population through seed dispersal and seed bank under conditions of scarcity of resources.

An occasional case in selection of reproductive modes in relation to soil nutrients level in perennial

Tussilago farfara (Ogden 1974) and *Chamaenerion angustifolium* (van Andel and Vera 1977) increased allocation to vegetative propagation in poor soils (see Table 1). The nature of causes for this effect is not known, but it might be related to a “preference” which *T. farfara* shows for open, unstable habitats, where surface soils are frequently deficient in plant nutrients. In such sites, *T. farfara* does not rapidly move towards competition for light and nutrients with other species. Thus, the tactical response of increased allocation to rhizomes in poor soils serves to maintain and expand the clone in situ, in an area, which is unfavorable to tall competitors (Ogden 1974).

Sexual reproductive allocation was less variable under conditions of different soil fertilities than vegetative reproductive allocation in *T. farfara* (Ogden 1974) and *S. canadensis* (Marino et al. 1997) (see Table 1). Unlike vegetative growth, sexual reproduction may not respond to elevated level of nutrients within short-term period. It would be impulsive to rule out differences in sexual reproduction based on the short-term nature of the reported study (Marino et al. 1997). Moreover, the response of this species to increased soil fertility will further ensure its egress as seeds from later seral communities. In such communities, the plants adapt to shade by increasing leaf area relative to leaf weight, but generally fails to maintain net assimilation rates at low

light intensities, so that the clones do not persist for long once they are overtopped (Ogden 1974).

A general trend on selection of reproductive modes in relation to soil water level in perennial

Wet habitats favored relatively more vegetative propagation, while dry conditions favored sexual reproduction in *Cyperus esculentus* (Li et al. 2001b) (see Table 2). Consequently, wet conditions may favor invasion and range extension of *C. esculentus* because asexual reproduction is the major means of its multiplication and because this mode of reproduction has a number of advantages over sexual reproduction (Li et al. 2001b; Baker 1974; Turner 1988; Radosevich et al. 1996). Also, low soil water content as environmental stressors, have been reported to increase sexual reproduction in *C. esculentus* (Li et al. 2001b) and *Sinapis arvensis* (Mal and Lovett-Doust 2005) (see Table 2). Soil dryness may inhibit penetration of underground propagules, thereby increasing the energy cost per propagule produced, or increasing the chance of failure. Such factors should favor sexual reproduction (Loehle 1987). In addition, compared to seeds, vegetative propagules are generally more vulnerable to desiccation (Boedeltje et al. 2008).

A general trend on selection of reproductive modes in relation to light intensity in perennial

The allocation to sexual reproduction was obviously higher in canopy gaps or no-shading in *Aster acuminatus* (Pitelka et al. 1980), *Zamai skinneri* (Clark and Clark 1987), *Uvularia perfoliata* (Kudoh et al. 1999), *Astrocaryum urostachys* (Svenning 2000), *C. esculentus* (Li et al. 2001a), *Smilacina japonica*, *Cardamine leucantha* (Ida and Kudo 2009), and *Iris japonica* (Wang et al. 2013) (see Table 3). Increase in size of the plant in relation to high light intensity and probability of larger plants to flower more indicates that size is the proximal factor affecting sexual reproduction (Kudoh et al. 1999). Furthermore, light might restrict accumulation of photosynthate for sexual reproduction and differentiation of flower bud. Many understory plants in the forests adapt to low light and hardly reproduce sexually (Kawano et al. 1990). Flower production was more negatively affected than clonal production, indicating that sexual reproduction is suppressed under suboptimal conditions (Wang et al. 2013). Only when extra resources are available will *A. acuminatus* invest in much more risky sexual reproduction (Pitelka et al. 1980).

On the other hand, allocation to clonal structures was more under the shade conditions than under conditions of full natural irradiance in *Geonoma cf. aspidiifolia* (Svenning 2000), *Ligularia virgaurea* (Wang, Xu et al. 2008), and *I. japonica* (Wang et al. 2013) (see Table 3). A reduction in plant sizes might lead to a greater

Table 1 Selection of reproductive modes according to soil nutrients level

Species	Life historical strategy	Response of reproductive propagules according to soil nutrient level (when soil nutrients level are increased)		Estimates by plant size covariance	Main habitat	References
		Sexual propagules	Asexual propagules			
<i>Tussilago farfara</i>	Perennial plant	N.S	Decreased	Not used	Snow-patch in sand dune	(Loehle 1987; Ogden 1974)
<i>Chamaenerion angustifolium</i>	Perennial plant	Increased (But one variable: N.S)	Decreased	Not used	Open and semi-open habitats of the boreal forest	(Loehle 1987; van Andel and Vera 1977)
<i>Silene latifolia</i> Poiret	Perennial plant	(Nitrogen addition): increased (Phosphorus addition): N.S (Potassium addition): increased		Not used	Open disturbed habitats like fallow fields, field margins, and roadsides	(Gehring and Linhart 1993)
<i>Sanguinaria canadensis</i>	Perennial plant	N.S	(In the potting and the reciprocal transplant study): increased (In the permanent plot experiments): N.S	Not used	Moist temperate forest understory	(Marino et al. 1997)
<i>Allium vineale</i>	Perennial plant		Increased (Only three of the 16 genotypes, but the others: N.S)	Not used	Roadsides and highly fertilized agricultural fields	(Ronsheim and Bever 2000)
<i>Leymus chinensis</i>	Perennial plant	(Nitrogen addition): decreased	(Nitrogen addition): increased (But one variable: N.S)	Not used	Steppe zone	(Bai et al. 2009)
<i>Penthorum sedoides</i>	Perennial plant	Decreased (Only in 2007, but in 2004: N.S)	Increased	Used	Ditches and near streams	(Nicholls 2011)
<i>Trapella sinensis</i>	Perennial plant	Decreased	N.S	Not used	50-cm water depth in rich sediment.	(Liu et al. 2013)
<i>Calathea micans</i>	Perennial plants with chasmogamy and cleistogamy	Increased	N.S	Not used (CH: positively correlated with plant size)	Lowland tropical rain forests	(Corff 1993)
<i>Impatiens capensis</i>	Annual plants with chasmogamy and cleistogamy	N.S	N.S	Used (CH: positively correlated with plant size, CL: independent of plant size)	Floodplains	(Waller 1980)
<i>Triplasis purpurea</i>	Annual plants with chasmogamy and cleistogamy	Upper nodes (CH spikelets and some CL spikelets): more increase (CH mass/CL mass: N.S)	Lower nodes (the other CL spikelets): Less increase	Not used	Coastal dune	(Cheplick 1996, 2007)
<i>Emex spinosa</i>	Amphicarpic annual plant	(High nitrogen): increased	(High nitrogen): N.S	Not used (CH: positively correlated with plant size, CL: independent of plant size)	Semi-arid region, roadside, vineyards, cereal crops, and pastures	(Weiss 1980)
<i>Amphicarpum purshii</i>	Amphicarpic annual plant	CH mass/CL mass: N.S			Disturbed habitats on the coastal plain	(Cheplick 1989, 2007)

Table 1 Selection of reproductive modes according to soil nutrients level (*Continued*)

<i>Polygonum thunbergii</i>	Amphicarpic annual plant	(High nitrogen): N.S	(High nitrogen): N.S	Not used (CH: independent of plant size, CL: independent of plant size)	Riversides	(Kawano et al. 1990)
<i>Emex spinosa</i>	Amphicarpic annual plant	Increased (CH mass/CL mass: increased)	Decreased	Used (CH: positively correlated with plant size, CL: independent of plant size)	Semi-arid region, roadside, vineyards, cereal crops and pastures	(Sadeh et al. 2009)
<i>Persicaria thunbergii</i>	Amphicarpic annual plant	1. CH mass: increase 2. CH number: decrease	N.S	Not used	Riparian zones and lakesides	(Kim et al. 2016)

CH chasmogamy, *CL* cleistogamy, *N.S* not significantly different

Table 2 Selection of reproductive modes according to soil water level

Species	Life historical strategy	Response of reproductive propagules according to soil water level (when soil water level is increased)		Estimates by plant size covariance	Main habitat	References
		Sexual propagules	Asexual propagules			
<i>Silene latifolia</i>	Perennial plant	Increased		Not used	Open disturbed habitats like fallow fields, field margins, and roadsides	(Gehring and Linhart 1993)
<i>Cyperus esculentus</i>	Pseudoannual	Decreased	Increased (But not one clone)	Not used	Moist fields, in heavily irrigated crops, along riverbanks and roadsides, and in ditches	(Li et al. 2001b)
<i>Lythrum salicaria</i>	Perennial plant	Decreased		Not used	Wetlands	(Mal and Lovett-Doust 2005)
<i>B. carinatus</i>	Perennial plants with chasmogamy and cleistogamy	Increased	Decreased	Not used	Forest	(Harlan 1945)
<i>Stipa leucotrich</i>	Perennial plants with chasmogamy and cleistogamy	Increased	Decreased	Not used	Grasslands, prairies, and brushy areas	(Brown 1952)
<i>Dichanthelium clandestinum</i>	Perennial plants with chasmogamy and cleistogamy	N.S (CH mass/CL mass: increased)	Decreased (But one population on one variable: N.S)	Not used	Open or frequently disturbed and early successional habitats	(Bell and Quinn 1987; Cheplick 2007)
<i>Calathea micans</i>	Perennial plants with chasmogamy and cleistogamy	(Many rainfall): increased	(Many rainfall): N.S	Not used (CH: positively correlated with plant size)	Lowland tropical rain forests	(Corff 1993)
<i>Bromus unioloides</i>	Annual plants with chasmogamy and cleistogamy	Increased (when only short photoperiods)		Statistical method not reported	Prairie	(Langer and Wilson 1965)
<i>Impatiens capensis</i>	Annual plants with chasmogamy and cleistogamy	Increased (not with covariates) N.S (with covariates)	N.S	Used (CH: positively correlated with plant size, CL: independent of plant size)	Floodplains	(Waller 1980)
<i>Collomia grandiflora</i>	Annual plants with chasmogamy and cleistogamy	Increased	Decreased	Used	Disturbed and open sites within or immediately adjacent to forest and shrub communities.	(Minter and Lord 1983; Wilken 1982)
<i>Gymnarrhena micrantha</i>	Amphicarpic annual plant	(Many rainfall): increased	(Low soil moisture): increased	Statistical method not reported	Steppe and desert regions	(Koller and Roth 1964)
<i>Amphicarpaea bracteata</i> L.	Amphicarpic annual plant	(Many rainfall): N.S	(Many rainfall): increased	Not used (CH: positively correlated with plant size, CL: positively correlated with plant size, not in 1983)	Moist woods	(Trapp and Hendrix 1988)
<i>Polygonum thunbergii</i>	Amphicarpic annual plant	N.S	N.S	Not used (CH: positively correlated with plant size)	Riversides	(Kawano et al. 1990)
<i>Commelina benghalensis</i>	Amphicarpic annual plant	More increased	Less increased	Not used	The ditch-banks at the field margins and low areas within a field	(Webster and Grey 2008)

CH chasmogamy, CL cleistogamy, N.S not significantly different

Table 3 Selection of reproductive modes according to light intensity

Species	Life historical strategy	Response of reproductive propagules according to light intensity (when light intensity is increased)		Estimates by plant size covariance	Main habitat	References
		Sexual propagules	Asexual propagules			
<i>Aster acuminatus</i>	Pseudoannual	Increased	N.S	Not used	Open and slightly disturbed sites such as tree falls, abandoned logging roads, or other small clearings within the forest	(Loehle 1987; Pitelka et al. 1980)
<i>Zamai skinneri</i>	Perennial plant	Increased		Not used	Shaded understory of a tropical rain forest	(Clark and Clark 1987)
<i>Silene latifolia</i>	Perennial plant	N.S		Not used	Open disturbed habitats like fallow fields, field margins, and roadsides	(Gehring and Linhart 1993)
<i>Sanguinaria canadensis</i>	Perennial plant	N.S	Increased	Not used	Moist temperate forest understory	(Marino et al. 1997)
<i>Circaea lutetiana</i>	Pseudoannual	N.S	Increased	Not used	The darkest spots on the forest floor.	(Verburg and During 1998)
<i>Uvularia perfoliata</i>	Pseudoannual	1. Flowering individual: occurred 2. Clonal diversities: increased			Temperate deciduous woodland	(Kudoh et al. 1999)
<i>Astrocaryum urostachys</i>	Perennial plant	Increase	N.S	Not used (seeds: positively correlated with plant size)	Riversides	(Svenning 2000)
<i>Phytelephas tenuicaulis</i>	Perennial plant	N.S	N.S	Not used (seeds: positively correlated with plant size)	Forest	(Svenning 2000)
<i>Geonoma cf. aspidiifolia</i>	Perennial plant	N.S	1. Increased (in case the genet had many large ramets) 2. Decrease (in case the genet had few large ramets)	Not used (seeds: positively correlated with plant size, clonal: positively correlated with plant size)	Forest	(Svenning 2000)
<i>Cyperus esculentus</i>	Pseudoannual	Increased	N.S	Not used	Moist fields, in heavily irrigated crops, along riverbanks, and roadsides, and in ditches	(Li et al. 2001a)
<i>Ligularia virgaurea</i>	Perennial plant		Decreased	Not used (clonal: positively correlated with plant size)	Alpine grasslands	(Wang et al. 2008)
<i>Smilacina japonica</i>	Perennial plant	Increased		Not used	Deciduous forests	(Ida and Kudo 2009)
<i>Cardamine leucantha</i>	Pseudoannual	Increased		Not used	Deciduous forests	(Ida and Kudo 2009)
<i>Iris japonica</i>	Perennial plant	Increased	1. Allocation of coarse rhizome, fine rhizome, and new ramets biomass: N.S	Not used	Forest understory, forest gap, forest edge, and moist grassland	(Wang et al. 2013)

Table 3 Selection of reproductive modes according to light intensity (*Continued*)

			2. The number of daughter ramets : Decreased			
<i>Dichantheium clandestinum</i>	Perennial plants with chasmogamy and cleistogamy	N.S (CH mass/CL mass: different among populations)	N.S	Not used	Open or frequently disturbed and early successional habitats	(Bell and Quinn 1987; Cheplick 2007)
<i>Calathea micans</i>	Perennial plants with chasmogamy and cleistogamy	Increased	N.S	Not used (CH: positively correlated with plant size)	Lowland tropical rain forests	(Corff 1993)
<i>Viola pubescens</i>	Perennial plants with chasmogamy and cleistogamy	Increased	Decreased	Not used	Deciduous forests	(Culley 2002)
<i>Impatiens pallida</i>	Annual plants with chasmogamy and cleistogamy	Increased	Decreased	Not used	Moist forest	(Schemske 1978)
<i>Impatiens biflora</i>	Annual plants with chasmogamy and cleistogamy	Increased	Decreased	Not used	Adjoining lakes or rivers	(Schemske 1978)
<i>Impatiens capensis</i>	Annual plants with chasmogamy and cleistogamy	1. Increased (no covariates) 2. Increased (with covariates)	N.S	Used (CH: positively correlated with plant size, CL: independent of plant size)	Floodplains	(Waller 1980)
<i>Impatiens noli-tangere</i>	Annual plants with chasmogamy and cleistogamy	Increased	Decreased	Not used	Wet areas along forest margins, stream margins, and roadsides	(Masuda and Yahara 1994)
<i>Microstegium vimineum</i>	Annual plants with chasmogamy and cleistogamy	Decreased (CH mass/CL mass: Decreased)		Used	Beneath the completely closed, shady forest interior, and along the periphery of the forest	(Cheplick 2005, 2007)
<i>Amphicarpaea bracteata</i>	Amphicarpic annual plant	Increased		Not used (CH: positively correlated with plant size, CL: positively correlated with plant size, not in 1983)	Moist woods	(Trapp and Hendrix, 1988)
<i>Polygonum thunbergii</i>	Amphicarpic annual plant	Increased	N.S	Not used (CH: positively correlated with plant size)	Riversides	(Kawano et al. 1990)

CH chasmogamy, CL cleistogamy, N.S not significantly different

proportion of photosynthetic organs (leaves) as compared to non-photosynthetic ones and clonal components (Wang et al. 2013). These morphological changes could be an adaptation to maintain the carbon balance of the individuals under shaded conditions and to achieve clonal expansion by new ramets (Wang et al. 2013). On the forest floor, weak interspecific competition due to low coverage of herbs and adequate growth space was in favor of clonal propagation. Therefore, clonal propagation strongly enhanced population stability and adaptations to habitat with limited resources (e.g., light and temperature) by physiological integration. In addition, through clonal reproduction, plants could expand their populations to colonize the habitats under condition of full natural irradiance. Clonal reproduction was thought to enable plants to forage for light-rich microsites to facilitate the establishment of genets and decrease the mortality risk under shade conditions (Maurer and Zedler 2002; Chu et al. 2006; Wang et al. 2008).

There are also many cases of unaffected allocation to vegetative propagation. The relative allocation to vegetative propagation was unaffected by light conditions in *A. acuminatus* (Pitelka et al. 1980), *A. urostachys* (Svenning 2000), and *C. esculentus* (Li et al. 2001a) (see Table 3). For *A. acuminatus* existing in low light availability due to canopy development or other types of interspecific competition, by devoting a fixed percentage of its energy to vegetative reproduction, each plant almost insures its survival for another year because *A. acuminatus* has low seed and high rhizome survivorship (Pitelka et al. 1980).

An occasional case in selection of reproductive modes in relation to light intensity in perennial

S. canadensis (Marino et al. 1997) and *Circaea lutetiana* (Verburg and During 1998) exhibit rapid vegetative spread in response to increased levels of light; whereas, sexual reproduction did not respond to increase in light intensity (see Table 3). As *S. canadensis* grows much more vigorously in high-light habitats, individual plants that have persisted at low densities in the shaded understory may respond through rapid vegetative spread and multiple branching or rhizomes when disturbances such as tree falls provide an elevated light environment (Marino et al. 1997). Unlike vegetative growth, sexual reproduction may not respond to elevated light within one growing season. Therefore, it would be impulsive to rule out differences in sexual reproduction because of the short-term nature of the reported study (Marino et al. 1997).

In certain other cases, an explanation for the absent or rather weak influence of light availability on sexual and clonal fecundity in *Phytelephas tenuicaulis*, understory palms (see Table 3), are so shade-tolerant that their responses to light availability were more

subtle than what was captured by the measures used in the study (Svenning 2000).

A general trend on selection of reproductive modes in relation to soil nutrients level in plants with chasmogamy and cleistogamy

High nutrient treatments generally increased the allocation of chasmogamous propagation, compared to low-nutrient treatments in *Calathea micans* (Corff 1993), *Triplasis purpurea* (Cheplick 1996), *Emex spinosa* (Weiss 1980; Sadeh et al. 2009), and *Persicaria thunbergii* (Kim et al. 2016) (see Table 1). A plant invests in larger numbers of long-range dispersing propagules along with an opportunity to colonize new patches when it perceives the habitat as nutrient-rich (Sadeh et al. 2009). The production, under favorable conditions, of numerous, small chasmogamous achenes provides efficient means of dispersal to suitable germination sites and possible establishment in new areas. Additionally, production of chasmogamous achenes may also be necessary to maintain genetic diversity through outcrossing before their dispersal, which would be unlikely in cleistogamous achene production (Weiss 1980; Keeton 1967). Moreover, dispersible seeds, produced higher up on emergent terminal panicles are able to escape from the negative consequences of crowding (sibling competition) that are likely to occur for seedlings arising from seeds that are not dispersed in space or time (Cheplick 1995, 1996; Venable and Brown 1993). Other explanations of this phenomenon are decrease in the cost of sexual reproduction (Bai et al. 2009; Loehle 1987) and the effects of nutrient availability on plant growth (Corff 1993; Cheplick 1994) with subsequent increase in chasmogamous seed output.

On the other hand, in *C. micans* (Corff 1993), *E. spinosa* (Weiss 1980), and *Persicaria thunbergii* (Kim et al. 2016), varying levels of nutrients affect cleistogamous seed production to a lesser extent than chasmogamous seed production (see Table 1). In poor soil, production of the cleistogamous achenes would be advantageous for such species to encompass a mechanism of ensuring persistence in situ (Weiss 1980).

The reproductive strategy observed in *T. purpurea* (Cheplick 1996) and *E. spinosa* (Sadeh et al. 2009) was the increase in reproductive success in the form of cleistogamous achenes under strenuous nutrient conditions (see Table 1). In a nutrient-poor environment, where the risk of dispersal is high, a plant growing in a sparsely inhabited patch invests more in cleistogamous achenes. By doing so, the plant increases the probability of its descendants dominating the patch. Since a small fraction of the propagules usually make it to successful germination, the plant is required to produce extremely high numbers of them to attain some success, thus rendering

the “escape” strategy economically unfeasible under strenuous conditions (Sadeh et al. 2009). If resources are available, additional seeds are matured on chasmogamous panicles (Cheplick 1996).

A general trend on selection of reproductive modes in relation to soil water level in plants with chasmogamy and cleistogamy

Wet habitats favored more chasmogamous propagation in *Bromus carinatus* (Harlan 1945), *Stipa leucotricha* (Brown 1952), *Dichanthelium clandestinum* (Bell and Quinn 1987), *C. micans* (Corff 1993), *Bromus unioloides* (Langer and Wilson 1965), *Impatiens capensis* (Waller 1980), *Collomia grandiflora* (Minter and Lord 1983; Wilken 1982), *Gymnarrhena micrantha* (Koller and Roth 1964), and *Commelina benghalensis* (Webster and Grey 2008) (see Table 2). In benign soil, chasmogamous reproduction is more beneficial than cleistogamous reproduction because chasmogamous flowers will produce numerous light-weight seed that are readily dispersed from the parent plant and there exists possibility of cross-pollination, which encourages adaptability and plasticity within the population (Cheplick 1994; Webster and Grey 2008; Kaul et al. 2000). Furthermore, since chasmogamous seeds germinate on the soil-surface and only after some delay, relative to the cleistogamous seeds, a favorable combination of environmental factors is a prerequisite for their formation as well as for their subsequent germination and establishment. And this fits in well with the relatively low tolerance which their seedlings exhibit towards unfavorable soil-moisture regimes (Koller and Roth 1964). In addition, in years with low rainfall, the plant can wither and die without any formation of chasmogamous inflorescences after production of cleistogamous seeds (Koller and Roth 1964).

Meanwhile, cleistogamous reproduction was favored over chasmogamous reproduction as soil moisture became more limited in *B. carinatus* (Harlan 1945), *S. leucotricha* (Brown 1952), *D. clandestinum* (Bell and Quinn 1987), *C. grandiflora* (Minter and Lord 1983; Wilken 1982), *G. micrantha* (Koller and Roth 1964), and *C. benghalensis* (Webster and Grey 2008) (see Table 2). This increased proportion of cleistogamous flowers in response to water stress may serve as an adaptation to increase the probability of reproductive success during unusually dry years (Minter and Lord 1983). The cleistogamous fruits are a very safe investment. They start to germinate relatively soon after imbibitions, and their germination is relatively less sensitive to variations in the environment. The seedlings from cleistogamous achenes survived to a much larger extent than did those from the chasmogamous achenes. In addition, seedlings produced by the larger cleistogamous seed are more vigorous and have a greater ability to compete and to

withstand adverse soil-moisture conditions than those produced by chasmogamous seeds (Webster and Grey 2008; Kaul et al. 2000). All these characteristics tend to increase the probabilities for germination and completion of the life cycle. In addition, since cleistogamous seeds typically have limited dispersal than chasmogamous seeds, they germinate exactly in the conditions, which sufficed for their parent to complete their life-cycle and the process is most likely to be duplicated (Koller and Roth 1964). Furthermore, the plants give priority to cleistogamous flowers under stressful conditions because cleistogamous flowers are cheaper to make, and thus the plant can produce some cleistogamous offspring under conditions that may not permit production of the more costly chasmogamous offspring (Bell and Quinn 1987). Additionally, if increased humidity surrounds the stigma and germinating pollen as a result of the closed corolla of cleistogamous flowers, then excessive desiccation under arid conditions may be prevented (Minter and Lord 1983). There is a possibility that the changes in chasmogamy/cleistogamy across the moisture gradient were simply indirect effects of plant size because biomass is significantly lower whenever soil moisture is limited (Bell and Quinn 1987; Cheplick 2007).

An occasional case in selection of reproductive modes in relation to soil water level in plants with chasmogamy and cleistogamy

Amphicarpaea bracteata quantitatively reduced the subterranean seed production under dry soil (Trapp and Hendrix 1988) (see Table 2). The drought resulted in the death of most of the runners and greatly reduced the number of subterranean flowers and seeds on the runners. Since subterranean flowering is initiated in advance of aerial flowering, the loss of the runners and/or a large number of the subterranean flowers may have freed resources that were then used in the production of aerial flowers. This might have prevented a reduction in chasmogamous flower number in response to the drought, as well as increased the number of aerial cleistogamous flowers.

In another case, under soil with low water content, the maintenance of the more expensive chasmogamous seed production in *D. clandestinum* (Bell and Quinn 1987) and *Polygonum thunbergii* (Kawano et al. 1990) (see Table 2) may be a result of a multiple dispersal strategy in which, the seeds with the potential for greater variability are dispersed through space (or time via dormancy) into new environments (Bell and Quinn 1987).

A general trend on selection of reproductive modes in relation to light intensity in plants with chasmogamy and cleistogamy

The allocation to sexual reproduction was higher under high light levels in *C. micans* (Corff 1993), *Viola*

pubescens (Culley 2002), *Impatiens pallida*, *Impatiens biflora* (Schemske 1978), *I. capensis* (Waller 1980), *Impatiens noli-tangere* (Masuda and Yahara 1994), *A. bracteata* (Trapp and Hendrix 1988), and *P. thunbergii* (Kawano et al. 1990) (see Table 3). In elevated light environments during early spring, chasmogamous flowers can easily be detected and air temperatures are high enough (Motten 1986) for maximum pollinator activity (Culley 2002; Schemske et al. 1978). High light availability may lead to increased photosynthetic rates, resulting in more resources for production of the costly chasmogamous flowers (Culley 2002; Waller 1980; Schemske et al. 1978). Besides, production of genetically variable progeny should be avoided in small plants, which are already facing the variability of low fecundity, whereas large plants, assured of less variation in their mean fitness by means of greater numbers of progeny, can better afford the risks of outcrossing. In addition, the offspring of larger plants face high levels of competition more frequently than the offspring of smaller plants. Under conditions of low competition, maximum fecundity as derived from efficient cleistogamy would be favored, but under high competition, outcrossed progeny expressing heterosis would dominate in achieving success (Waller 1980). Furthermore, higher light intensity appears to increase outcrossing both by enhancing growth and by directly increasing the production of outcrossing flowers in larger plants. The chasmogamous flowers are located in the axils of the upper nodes, indicating that the production of these flowers depends on plant size. Smaller plants never produce these many nodes and chasmogamous flowers. The placement of chasmogamous flowers within the plant does appear to be an adaptation to pollinator availability. They are produced on the periphery of the top branches where they are conspicuous and easy to reach. Greater production of the chasmogamous flowers under sunny conditions could likewise be interpreted as adaptive if the pollinators preferentially visit sun-lit flowers (Waller 1980; Beattie 1971).

A facultative cleistogamy as a conditional strategy has been demonstrated to be affected by changes in light condition in *V. pubescens* (Culley 2002), *I. pallida*, *I. biflora* (Schemske 1978), and *I. noli-tangere* (Masuda and Yahara 1994) (see Table 3). It has been reported that cleistogamous flowers appeared under low light levels after the overstory trees had leafed out and pollinators had virtually disappeared. Cleistogamous flowers, which lack petals and other attractive features, may subsequently appear under low light levels because they are less costly to produce. And in this case, self-pollinated cleistogamous flowers would be favored in shaded environments because they do not depend on insect pollinators (Culley 2002).

In *C. micans* (Corff 1993), *I. capensis* (Waller 1980), and *P. thunbergii* (Kawano et al. 1990), plants increased

the production of chasmogamous inflorescences, whereas there was no significant effect on the production of cleistogamous inflorescences in response to increase in light intensity (see Table 3). By lowering the cost of reproduction, cleistogamy allows the plant to assure some seed set even in conditions unfavorable for plant growth and chasmogamous flower production (Corff 1993). Also, cleistogamous seeds possessing higher fitness may be crucial for population maintenance (Kawano et al. 1990).

An occasional case in selection of reproductive modes in relation to light intensity in plants with chasmogamy and cleistogamy

In the case of *Microstegium vimineum*, the majority of reproduction appears to be by cleistogamy when conditions are relatively benign; in the shaded habitat, there is relatively more chasmogamous reproduction (Cheplick 2005) (see Table 3). These results do not support the generalization that environmental conditions that are “not optimal for growth and reproduction may favor a higher proportion of cleistogamous flowers” (Campbell et al. 1983). As the development of axillary racemes along a tiller is basipetal, light availability presumably determines the number and mass of seeds that ultimately can be matured on axillary cleistogamous racemes under conditions of low light under a forest canopy, and seeds set in chasmogamous spikelets on terminal racemes may be the primary method of reproduction (Cheplick 2005).

In another case, there were no significant differences among light treatments for mean percentage biomass allocation to either chasmogamous or cleistogamous reproduction in *D. clandestinum* (Bell and Quinn 1987) (see Table 3). The lack of a pronounced chasmogamous-cleistogamous response to light may be because light has no consistent or triggering effect on *D. clandestinum* on biomass allocation to chasmogamous and cleistogamous reproduction (Bell and Quinn 1987).

A general trend on selection of reproductive modes according to environmental variations in plants

Different reproductive modes might suggest different adaptive strategies in plants in response to varying environments (Wang et al. 2008). Perennial plants showed that favorable habitats in soil nutrients or water content tend to promote clonal growth over sexual reproduction. In contrast, under high light quantity conditions, clonal plants tend to allocate more biomass to sexual reproduction and less to clonal propagation (Fig. 1). In addition, in some cases, clonal reproduction is less variable than sexual reproduction in environmental conditions.

On the other hand, plants with chasmogamy and cleistogamy provide with a greater tendency the opportunity

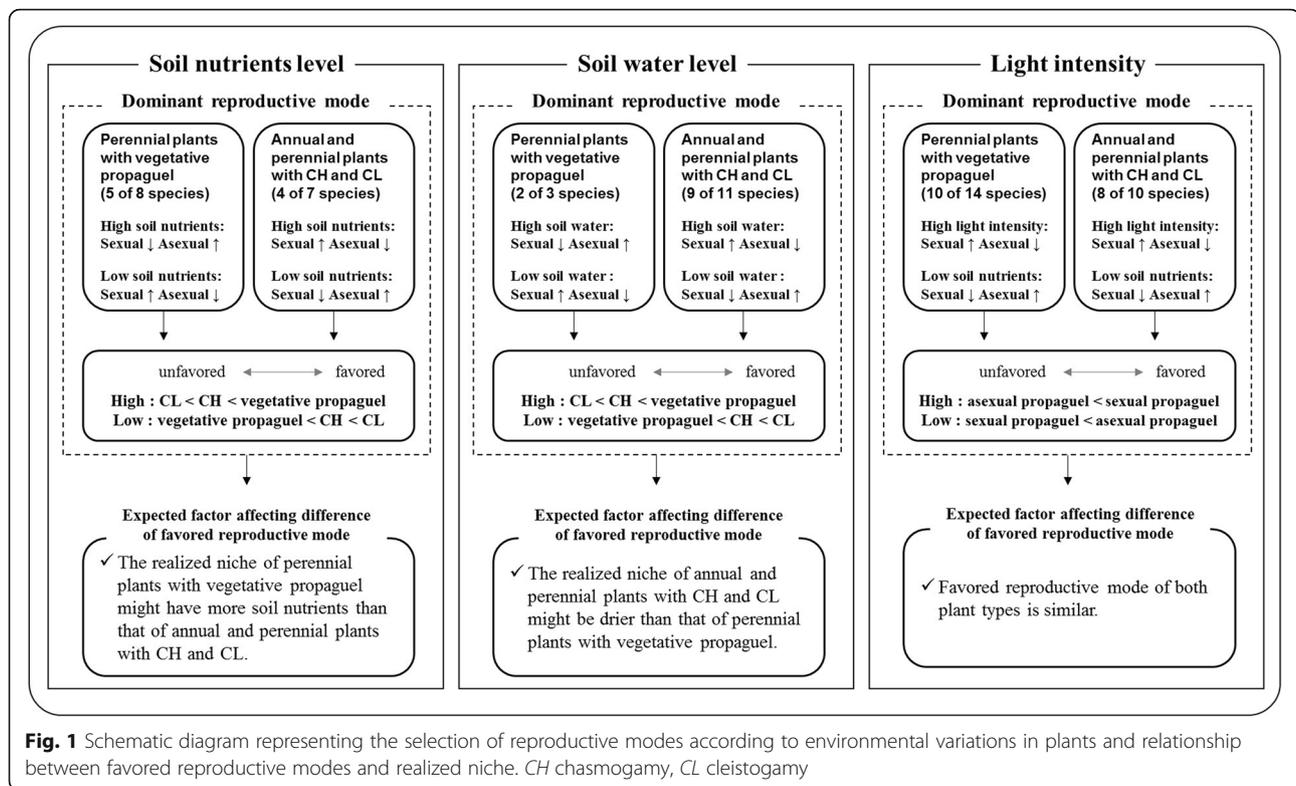


Fig. 1 Schematic diagram representing the selection of reproductive modes according to environmental variations in plants and relationship between favored reproductive modes and realized niche. CH chasmogamy, CL cleistogamy

to ensure some seed set under any stressful environmental conditions such as low light, low soil nutrients, or low soil moisture (“reproductive insurance” hypothesis) (Fig. 1). This seems to be related with the prediction that progeny from chasmogamous flowers have higher fitness in environments differing from the maternal environment while progeny from cleistogamous flowers would be more successful at establishing in the parental habitat (Corff 1993; McCall et al. 1989; Schmitt and Gamble 1990). Because the genetic attributes of chasmogamy outweigh the energetic disadvantages in favorable habitats, the relative advantage of cleistogamy should increase in habitats and seasons where time and energy become critical resources (Schemske 1978). Moreover, in some cases, allocation to cleistogamous reproduction tends to be less plastic than allocation to chasmogamous reproduction.

Allometric relationships and allocation of propagules

Plant size could alter the life history trade-offs (Kawano et al. 1990). Size-dependency in sexual fecundity is the rule, while size-dependency in asexual reproduction can be present or absent depending on the species (Svenning 2000; Wilken 1982). As can be seen in the Tables 1, 2, and 3, most of the sexual propagules production and plant size were positively correlated (8 of 9 species), but the majority of cleistogamous propagules production was not correlated with plant size (3 of 4 species). Clonal reproduction

was positively related to plant size (2 of 2 species) even though the number of data was small. Thus, in many cases, the reproductive mode is dependent on local environmental conditions through their effects on plant growth and eventual size (Corff 1993).

Therefore, it is necessary that investments in sexual reproduction or asexual propagation are tested using plant size variable as a covariable rather than using a ratio to correct for this size-effect (Jasienski and Bazzaz 1999; Mony et al. 2010). For example, a size covariate in *I. capensis* was very significant in accounting for variation in the proportion of outcrossing branches, thus soil nutrients and soil water level indirectly influenced sexual reproduction through their influence on plant size (Waller 1980). However, higher light intensity appears to increase outcrossing both by enhancing growth and by directly increasing the production of outcrossing flowers in larger plants (Waller 1980). When controlling for the effect of size in *C. grandiflora* (Wilken 1982), *M. vimineum* (Cheplick 2005), *E. spinosa* (Sadeh et al. 2009), and *P. sedoides* (Nicholls 2011) (see Table 1, 2 and 3), true plasticity of investments in sexual reproduction or asexual propagation was still evident.

Relationship between favored reproduction modes and realized niche

Why do plants differ with respect to favored reproduction modes in varying environmental conditions? Specific

realized niche may account for differences in reproductive allocation patterns among diverse plants.

Perennial plants with vegetative propagule tend to have more asexual reproduction in fertile soil. Conversely, annual and perennial plants with chasmogamy and cleistogamy tend to have more sexual reproduction in rich soil. Thus, it is considered that vegetative propagule might be more beneficial than chasmogamy, and chasmogamy might be more favored than cleistogamy in soil with high nutrients. On the contrary, in soil with low nutrients, cleistogamy might be the most favorable (Fig. 1). It is hypothesized that this notation has connection with tendency that the niche of perennial plants with vegetative propagule might have more soil nutrients than that of annual and perennial plants with chasmogamy and cleistogamy. The general trends of plant succession are always the same with the following: from bare soil to plant cover, from annual to perennial, from herbaceous to woody, from smaller plants to larger plants, from short-lived to long-lived, from light-demanding to shade-tolerant, and from pioneers to stayers (Whitefield 2009). During the initial phases of succession in nutrient-poor condition, mineral substrates, and dead plant material accumulates rapidly in the soil. The accumulation of soil organic matter can result in increase in nitrogen mineralization (Berendse 1998; van Breemen 2013). Accordingly, perennial plants as species of later succession stage, distribute in more rich soil which supports our suggestion.

Smillay, perennial plants with vegetative propagule tend to have more sexual reproduction in drier soil. However, annual and perennial plants with chasmogamy and cleistogamy tend to have more asexual reproduction in drier soil. Therefore, it is considered that cleistogamy might be more beneficial than chasmogamy, and chasmogamy might be more favorable than vegetative propagule in soil with low water potential. On the contrary, in soil with high water potential, vegetative propagule might be the most favorable (Fig. 1). Possibly, this is related to tendency that the niche of annual and perennial plants with chasmogamy and cleistogamy might be drier than that of perennial plants with vegetative propagule. Soil water infiltration generally increases with soil development in primary succession as plant roots and burrowing animals increase infiltration and developing organic horizons lead to water retention (Walker and Moral 2003). On this account, annual plants as species of early succession stage, distribute in drier soil; this fact also support our suggestion. Additionally, vegetative reproduction is an important process for amphibious species since most are unable to germinate in flooded habitats (van der Valk 1981; Lenssen et al. 1998). Because vegetative reproductive organs usually function as perennating organs and store carbohydrates, the ability to form rhizomes is crucial for

expansion and persistence at flooded sites (Lenssen et al. 2000). Hence, the capacity of vegetative propagule to amphibious species might be more beneficial for soil with high water potential (Fig. 1).

Both perennial and annual plants exhibit more sexual reproduction in high light condition and more asexual reproduction in low light condition. In conclusion, traits of vegetative, chasmogamy, and cleistogamous propagules are different from each other, and the properties of each reproduction modes might affect determination of its realized niche. This fact is in disagreement with previous statement that cleistogamous strategy could be a substitute for vegetative reproduction (Cheplick 1994).

Responses on two mixed environmental factors

When one environmental factor is more intense as compared to another, the intense factor might only affect trade-off. For example, plants in drier areas developed no chasmogamous flowers despite condition of good light (Waller 1980). Otherwise, two environmental factors might make a mixed response.

In *S. canadensis*, there was a significant two-way interaction between light and fertilization on the change in rhizome dry weight, and the plants responded vegetatively more strongly to light than to nutrient conditions (Marino et al. 1997). In *C. micans*, nutrient availability and light had a significant effect on the total number of chasmogamous inflorescences per plant, and there was a significant interaction between light and nutrients (Corff 1993). Variations in *P. thunbergii* in soil nitrogen and moisture appear to have smaller effects on the growth, allocation patterns, and population structures, and thus variations in the population structure here can be explained primarily by spatio-temporal changes in light conditions (Kawano et al. 1990).

Responses on interaction between environmental conditions and plant density

Differences in environmental tolerances among species and changes in the nature of species interactions result in shifts in the species present and their relative abundance (Smith and Smith 2015). Previous studies showed interaction in some cases and absence of interaction between environmental factor and plant density in certain other cases.

In *E. spinosa*, the interaction terms of five variables between nutrient availability and plant density were not significant. However, both total aerial achene mass and the total number of aerial achenes were positively affected by nutrient availability and negatively affected by density but the positive effect of nutrients weakened in high density treatments (Sadeh et al. 2009). In *I. capensis*, in the low density-grown plants, light intensity still enhanced outcrossing significantly even after adjustment for the effects of size. However, in the high density-grown plants,

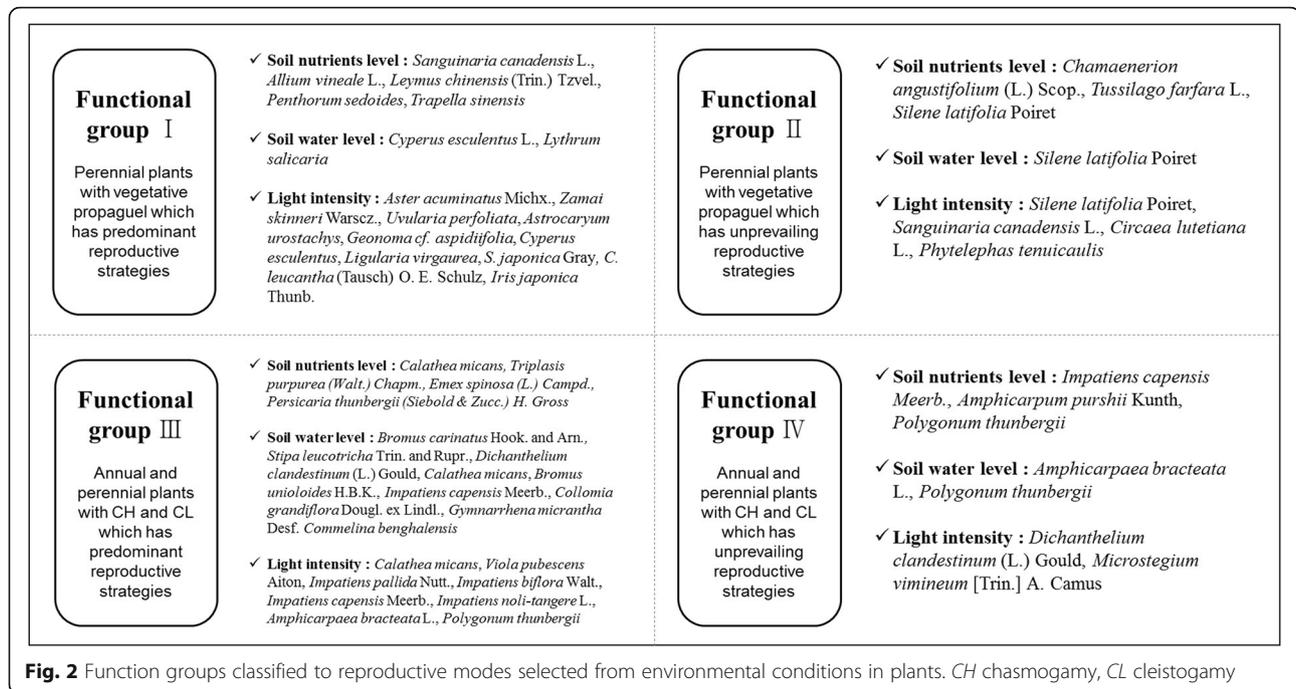


Fig. 2 Function groups classified to reproductive modes selected from environmental conditions in plants. CH chasmogamy, CL cleistogamy

adjusting for the effects of size removed all significant differences between the treatments (Waller 1980).

Conclusions and promising directions for future research

It is considered that vegetative reproduction has high competitive ability and is main means to expand established population of perennial plants, whereas cleistogamous reproduction is an insurance to persist in stressful sites due to being strong. Chasmogamous reproduction mainly enhances established and new population. These traits of propagule thus determine its success at a particular region of any environmental gradients. Eventually, if environmental resource or stress levels change in either space or time, species composition will probably also change. In this way, the functions of sexual and asexual propagules of perennial or annual plants differ from each other.

The balance between both the types of reproduction is one of the most important life-history characteristics of plants (Chu et al. 2006) because of its effects on demography (Eriksson 1986), population genetic structure (Chung and Epperson 1999; Ceplitis 2001), dispersal (Winkler and Fischer 2001), and meta-population processes (Piquot et al. 1998). We suggest that this concept should be considered as a useful framework that will potentially improve the general understanding on life-history strategies of plants inhabiting variable and changeable environments. Furthermore, this framework will help to select appropriate reproductive mode for transplanting and predict successional process at the time of restoration in any landscape.

Until now, it is not clear as why some species differ from general trends of favored reproductive mode in any environmental condition, and how this fact is connected with realized niche of species. More field and manipulating experiments are needed to test our hypotheses. Obviously, when trying to compare species or different experimental treatments within a species, investigators must be careful to compare only the data recorded at equivalent phenological stages and plant size to know whether environmental variable directly influences each propagule or not (Cheplick 2007). Moreover, the list of functional group according to favored reproductive mode (Fig. 2) needs to be updated continuously, which will further broaden understanding about life-history strategies and successional process of plants.

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Authors' contributions

All authors declare their roles in the manuscript as follows: JGK and YYY designed the project, YYY performed the research and wrote the first version of the manuscript, and JGK supervised the project, revised the manuscript, and secured research funding. All authors read and approved the final manuscript.

Competing interests

The authors declare that they have no competing interests.

Consent for publication

Not applicable.

Ethics approval

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