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Some life history strategies and population structure in asexually reproducing plants

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Abstract

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Asexual reproduction in higher plants comprises a) agamospermy and b) vegetative propagation. The paper deals with biological importance of these two processes and their bearing upon the population structure.

Strategies of dispersal and survival in asexually reproducing plants often comprise multiple tactics; they frequently involve seeds or units possessing seed-like features, e.g., carrying a nutrient reserve and/or exhibiting dormancy. Various forms of asexual reproduction may occur together; depending on a given combination, populations of asexually reproducing plants offer differences in size, density, age-structure and sometimes also in gender distribution within particular sectors.

The balance between sexual reproduction and vegetative propagation may not necessarily be essential in all plants; on the other hand, the balance between reproduction by seed/seed-like structures and clonal growth represents an important element both in sexual and asexual populations. Recent data suggest that local racial differentiation may occur not only in sexual taxa but also in asexually reproducing plants.

Key-words: reproduction – agamospermy – vegetative propagation – dispersal – survival

Introduction

Reproduction can be defined as propagation of parental genes in time and space; it results in formation of physiologically independent descendants representing a new generation in the demographic sense.

Occurrence of asexual reproduction in plants is well-known; however, the biological importance of particular forms of asexual reproduction as well as their bearing upon the population structure are frequently ignored. The aim of the present paper* is to examine some of these problems in the light of the available empiric evidence.

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* Paper partly based on the Invited Speaker's presentation at the Advanced Workshop on Plant Population Biology, Port-Camargue, France, May 21–25, 1984.

Remarks on terminology

Considerations on terminology may seem unnecessary to a non-involved scientist but to the students of plant reproduction in problem is, unfortunately, very real. In the course of time, very numerous terms have arisen that are rather arbitrarily used. For instance, Abrahamson (1975, 1980) distinguished between "seed reproduction" and "vegetative reproduction". Harper (1977) made a distinction between "reproduction" and "growth" and discarded the term "vegetative reproduction". Gustafsson (1946–47) used the general term "apomixis" for all kinds of asexual reproduction. On the other hand, numerous authors (e.g., Stebbins 1950, Nygren 1954, Bayer 1984) used the term "apomixis" solely for agamospermy; others opted the term "gametophytic apomixis" referring to agamospermy but excluding adventitious embryony (e.g. Asker 1980, Nogler 1984).

I suggested elsewhere (Urbanska 1981, 1984) that the terminology used in studies dealing with plant reproduction and specifically concerning asexual processes should be revised and co-ordinated. In the present paper two forms of asexual reproduction occurring in higher plants, viz. agamospermy and vegetative propagation, are briefly described in the respective paragraphs and some representative cases are discussed. No attempt is made to review the ample literature on the subject; for more information the reader is referred, e.g., to the recent textbook edited by Johri (1984) with an excellent chapter on gametophytic apomixis by Nogler (pp. 475–518).

Agamospermy

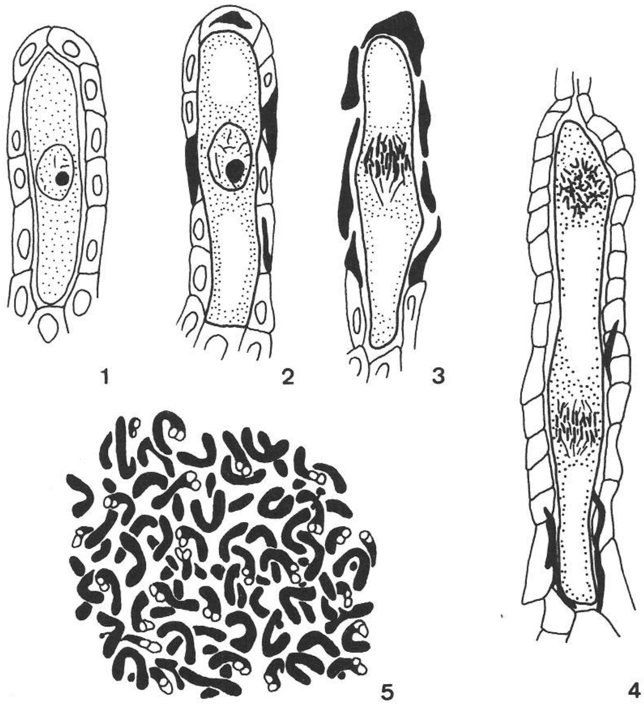
Agamospermy is asexual reproduction by seed that occurs fairly often in some families of the angiosperms. Except for adventitious embryony where the sporophyte, i.e. cell(s) of the ovule, gives rise directly to a new sporophyte (embryo), agamospermy is characterized by alternation of generations.

Agamospermy usually consists of two complementary phases viz. a) formation of an unreduced female gametophyte and b) seed development. An unreduced embryo sac may be formed through diplospory or apospory; in the former case, the female archesporial cell (EMC) or its derivatives are involved, whereas in the latter somatic cells of the ovule replace the archespore in its function. In seed development the embryo is most frequently formed as a result of female parthenogenesis; apogamy, i.e. embryo formation from a synergid or an antipodal cell, is exceedingly rare (e.g. Modilewski 1930). Androgenesis, i.e. male parthenogenesis, represents another exceptional process (e.g. Rao 1974). The development of endosperm may be autonomous or pseudogamous; in the former case, a secondary nucleus or polar nuclei develop spontaneously into endosperm, whereas in the latter, fertilization is the necessary prerequisite to the normal formation of the endosperm.

The essential point in all cases of agamospermy is the absence of the sexual phase in the development of a viable embryo. For example, parthenogenetic development of the egg cell in an ovule that underwent meiosis should rightly be considered as agamospermy (see e.g., polyhaploid embryos in *Hieracium aurantiacum,* Skalińska 1971 a). Formation of an unreduced female gametophyte alone does not represent agamospermy; this should be stressed, as there is sometimes confusion on this point. If an egg cell, reduced or unreduced, does require fertilization to form an embryo, there is no agamospermy. For instance, an occasional formation of unreduced embryo sacs was noted in tetraploid ($2n=28$) *Antennaria dioica* by Bergman (1935) and also revealed in experimental crosses done by the present author (Urbanska 1962, 1965). However, female capitules did not produce achenes without fertilization and accordingly did not qualify as agamospermous. Unreduced embryo sacs in hexaploid ($2n=42$) *A. villifera* from North Scandinavia are sometimes formed as a result of highly disturbed macrosporogenesis (Bergman 1951, Urbanska 1967); however, the taxon is sterile on account of its mostly abnormal gametes (Urbanska 1967) and cannot be regarded as agamospermous (Urbanska 1970). In facultatively agamospermous taxa, i.e. those with both asexual and sexual seed production, fertilization of an unreduced egg cell may result in the offspring carrying a higher number of chromosomes than that of the mother plant (e.g. Nogler 1982, 1984); such cases obviously relate to sexual reproduction.

Asexual taxa of *Antennaria* Gaertn. and *Taraxacum* Zinn represent classic examples of autonomous agamospermy (Juel 1900, Stebbins 1932, Urbanska 1974, Gustafsson 1935, 1938, 1946–47). In *Antennaria alpina* s. l., the megaspore mother cell (EMC) develops directly into an unreduced embryo sac and the first division is wholly mitotic (Figs. 1–5). Egg cell and secondary nucleus in the mature diplosporous embryo sac develop autonomously into embryo and endosperm; curiously enough, polar nuclei sometimes do not even fuse.

Fecundity rates in agamospermous taxa of sect. *Alpinae* are usually high (Urbanska 1981, 1984). Achenes are most frequently dispersed by wind, and the dispersal is further influenced by runoff water and/or solifluxion. Achene dormancy is apparently enforced by a short vegetation season and harsh climatic conditions; innate dormancy seems to be rather rare. Achenes in *A. alpina* s. l. frequently remain viable for at least three years (Urbanska 1981, 1984) and the seed bank undoubtedly consists of various



Figs. 1–5. Diplospory in *Antennaria Porsildii* ($2n=70$). 1–4. The EMC forms the unreduced embryo cas. 315×. 5. Second mitosis in an embryo sac: metaphase with about 70 chromosomes. 2150×. (From Urbanska, 1974).

Fig. 6. *Antennaria stolonifera:* four-month-old plant. Greenhouse trial.

generations (Urbanska unpubl.). In subarctic and arctic sites seedlings were observed only at the beginning of the vegetation season; germination and seedling establishment seems to be density-dependent (Urbanska 1981, 1984 and unpubl.). Experiments in growth chamber and greenhouse reveal a high growth potential, leafy stolons and root-system being already well-defined in very young individuals (Fig. 6).

Antennaria alpina s. l. consists of high polyploids (2n = 56, 63, 70, 84) and is obligatory agamospermous, numerous taxa being known exclusively as female plants. Asexual representatives of sect. *Alpinae* have a circumpolar/cirumboreal distribution and apparently are very successful in a number of ecologically extreme niches.

Diplosporous embryo sacs in *Taraxacum* arise in a fundamentally different way. The first division in the EMC is characterized by nearly complete asyndesis with subsequent pseudohomeotypic metaphase or the formation of a restitution nucleus. The second meiotic division results in the formation of an unreduced dyad, and most frequently the chalazal macrospore gives rise to the diplosporous embryo sac. Seed development is autonomous and a multicellular embryo may sometimes be seen in a still unopened flower-bud.

The genus *Taraxacum* is cytologically differentiated (for ample information, see e.g. Fedorov 1969), and there is an important correlation between chromosome number and reproductive behaviour. Diploids (2n = 16) are sexual; in triploids (2n = 24), agamospermy is facultative or obligatory, whereas high polyploids are considered as obligatory apomicts. Not only the chromosome number but also pollen quality and size represent reliable criteria for a correct assessment of the genetic population structure in dandelions; they should be taken into consideration because sexual and agamospermous types may coexist in some lowland sites.

Achene output in *Taraxacum* may vary from one biotype and/or site to another but is frequently high. Achenes are dispersed by wind and are sometimes shifted locally by soil movement. An occasional formation of seedling clusters due to deposition of a whole capitulum was also reported (Ford 1981). Data on germination (e.g. Braun 1913, Schütz and Urbanska 1984) indicate only a limited innate dormancy. Greenhouse trials suggest a high growth potential in dandelions (Schütz und Urbanska 1984); on the other hand, formation of supplementary rosettes from the rootstock (Ford 1981) seems to represent a regeneration process rather than spontaneous clonal growth.

Taraxacum alpinum s. l. occurs in mountains of Central, Western and Southern Europe. In the Swiss Alps it frequently grows in ecologically extreme sites at high altitudes where it is considered as a pioneer element. The material we studied from scree slopes was uniformly tetraploid (2n = 32); the exceedingly high pollen sterility was a further indication of obligatory agamospermy (Schütz and Urbanska 1984). Populations of *T. alpinum* on alpine scree slopes are rather small, with individual rosettes scattered over some distance. Emergence of seedlings was noted only within the first week after the snow had melted (Schütz unpubl.). An optimal adaptation of *T. alpinum* to harsh and unpredictable life conditions was reflected in its excellent reproductive performance. Differences in germination and development of young plants from two alpine substrata strongly suggested local racial differentiation (Fig. 7, Schütz and Urbanska 1984).

The seed production in autonomously agamospermous taxa represents a low-risk strategy, plants being independent of male partners and pollinators. On the other hand, hazards involved in seed* dispersal, germination and seedling establishment (Grime

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* Achenes are functional equivalents of seeds.

1979) are apparently independent of sexual or asexual seed formation, the biological function of survival and dispersal being the same in any kind of seed. The population dynamics patterns in agamospermous plants are thus generally similar to those occurring in sexually reproducing taxa as illustrated, e.g., by the sexual stoloniferous *Antennaria dioica* from the alpine tundra and the asexual *A. stolonifera* from the arctic tundra (Urbanska 1984). Comparison between, e.g., sexual diploid *Taraxacum pieninicum* from mountain habitats in Poland (Małecka 1958) and asexual tetraploid *T. alpinum* from high altitude sites in Switzerland (Schütz and Urbanska 1984) does not reveal any essential differences either, populations of both taxa being apparently at carrying capacity.

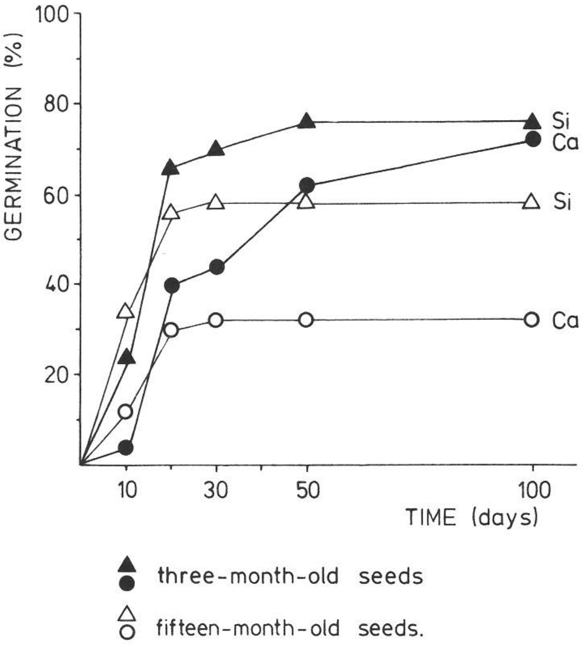


Fig. 7. *Taraxacum alpinum* (2n = 32): germination of achenes originating from alpine scree slopes. Si = acidic silicate; Ca = dolomite. Laboratory trial. (From Schütz and Urbanska, 1984).

The characteristic similarity in seed biology and a similar population appearance of agamospermous and sexual plants requires a rather thorough analysis of reproductive system(s). Our comment does not seem to be superfluous, as rather inquieting interpretations are beginning to appear in the literature dealing with population dynamics and genetic structure. For instance, Thomas and Dale (1974, 1975) automatically associated the reproduction by seed in *Hieracium floribundum* with sexuality and opposed it to "vegetative reproduction" without any data supporting their assessment. *H. floribundum* was previously reported as triploid (2n = 27) and agamospermous (Skalińska 1967, 1968). Also Stergios (1976) characterized the achene production in *H. aurantiacum* as "sexual reproductive output", contrary to his own vague reference to agamospermy in this taxon. Cytological differentiation and the complex agamospermous phenomena in *H. aurantiacum* are well-known (Ostenfeld and Rosenberg 1906, Ostenfeld 1910, Gustafsson 1935, 1946–47, Christoff 1942, Skalińska 1971, 1971a, 1973). Recently, Ford (1981, 1981a) characterized his material of *Taraxacum* spp. "in toto" as agamospermous. It is unfortunate that he neither provided any information on the taxonomy of his material nor gave any clues concerning chromosome number and pollen quality and made only a rather general remark on the wide distribution of agamospermy in British dandelions. In four species-groups of *Taraxacum* in Great Britain diploid sexual as well as polyploid agamospermous types occur and various hybrids have also been found (Richards 1972, Stace 1975).

Population size, density and age-state structure (*sensu* Rabotnov) in agamospermous plants may offer aspects similar to those occurring in sexual taxa; on the other hand, the gender structure of population may be affected. Many agamospermous taxa of *Antennaria* consist exclusively of females; male individuals in other asexual populations of the group are exceedingly rare, manifest diminished vigour and nearly complete pollen sterility (Urbanska 1967, 1974, 1981, 1984 and unpubl.). The female-biased population structure is a rather constant feature in apomictic *Antennarias* and the sex ratio has been used by some authors (e.g. Bayer and Stebbins 1983) to distinguish between sexual and agamospermous populations in the wild. Also other agamospermous genera e.g. *Cortaderia* and *Lamprothyrsus* may comprise only female individuals (Connor 1979).

Vegetative propagation

Vegetative propagation refers to clonal growth accompanied by spontaneous and obligatory clone fragmentation resulting in the appearance of physiologically independent modules. The term can be used both for the production of non-specialized propagules as well as for the formation of reproductive units that are morphologically quite distinct from the mother plant.

The duckweed family *(Lemnaceae)* is well-known for its characteristic vegetative propagation by means of daughter fronds (e.g. Hegelmaier 1868, Landolt 1980, Landolt, in prep.). The clonal growth in duckweeds follows a consistent rhythm and the separation of fronds occurs very regularly; the resulting populations may consist of innumerable ramets.

Spirodela polyrrhiza constitutes a model example of the vegetative propagation in the Lemnaceae. Its daughter fronds mature within 3–4 days from the bud emergence (Das and Gopal 1969) and their morphology is identical to that of the "mother" frond. *S. polyrrhiza* is dispersed by fronds; they may be transported by water fowl, sometimes over distances of several kilometers (Landolt 1957). Apart from its aggressive growth, *S. polyrrhiza* has a relatively high potential for regeneration after some mechanical frond damage (Das and Gopal 1969). The fast recovery undoubtedly represents an element in the survival strategy of the taxon. However, if and when the habitual tolerances are not sufficient to cope with environmental changes, *S. polyrrhiza* forms turions as survival units. Turions are smaller and more pigmented than normal fronds and carry starch as a nutrient reserve. They have plastids but are not photosynthetically active, their stomata staying closed (Landolt, pers. comm.). Turions sink to the bottom of the water basin and stay dormant until the life conditions improve; they are also able to survive embedded in clay, even if it subsequently dries out (Gopal, pers. comm.). Sprouting of turions begins when they rise to the water surface; daughter fronds of the typical morphology are then produced in the usual way. "Germination" of turions is controlled by exceedingly complex factors, not only the actual change in life conditions, but also circumstances accompanying the turion formation being relevant (e.g. Jacobs 1946, Das and Gopal 1969, Lacor 1969, Sibasaki and Oda 1979, Malek and Oda 1980).

Population structure in *S. polyrrhiza* is very uniform, save for the turion formation and/or the turion sprouting phase. Most frequently, very numerous frond groups occur; however, a reliable assessment of population size or density is not possible, large fluctuations being unpredictable. Populations of *S. polyrrhiza* are continuously rejuvenated and no flowering occurs, so age-state structure also cannot be studied; only dying fronds are recognizable but they may represent quite different generations.

S. polyrrhiza has a worldwide distribution and is apparently successful under a wide range of ecological conditions (Landolt 1982, Landolt, in prep.). The taxon is rather flexible as far as various tolerances are concerned; on the other hand, physiological studies reveal an occasional racial differentiation (Landolt 1957, Landolt and Dann 1983). Also a racial differentiation in chromosome number was sometimes observed (Urbanska 1980, Tab. 1).

Tab. 1. Cytological variation within the genus *Spirodela.* (Urbanska 1980).

Taxon	Intraindividual variation		Variation populations		Racial variation		N of the studied samples
	Aneusomaty	Mixoploidy	Aneuploidy	Polyploidy	Aneuploidy	Polyploidy	
S. intermedia	–	–	–	–	–	+	16
S. biperforata	+	–	–	–	–	+	7
S. polyrrhiza	+	+	+	+	–	+	187
S. punctata	+	–	+	–	+	+	83

The low-risk life history strategy of *S. polyrrhiza* is exclusively based upon vegetative propagation but apparently comprises some finely balanced tactics. Differential turion dormancy suggests that responses towards environmental changes involve various physiological mechanisms whereas the morphology of the survival unit is not differentiated. It should be most interesting to gather more information about the actual physiology of dormancy in survival structures produced by other aquatic plants differing in behaviour, e.g., *Potamogeton crispus* (Sculthorpe 1967, Sahai and Sinha 1969).

Another type of vegetative propagation occurs in plants that form specialized propagules within their inflorescence or in the axils of cauline leaves. A representative example of the former group is *Allium Grayi* ($2n = 32$) where bulbils evidently possess a function comparable to seeds (Kawano and Nagai 1975). Also in *Lilium bulbiferum* representing the latter category, the propagules play an essential rôle in dispersal and survival because populations of this taxon often consist of single self-incompatible clones (Sokołowska-Kulczycka 1965).

The formation of bulbils is known in numerous plants; on the other hand, detailed studies on their dispersability, survival and germinability are as yet rare. Of special interest in this respect are data on viviparous taxa where small plantlets often develop from propagules while still on the mother plant. *Poa alpina* var. *vivipara* and *Polygonum viviparum* which belong to this group are familiar vegetation components both in the high mountains as well as in subarctic/arctic tundra.

In the Swiss Alps, propagules of *Poa alpina* begin to appear within inflorescences soon after the snow has melted and are produced until October (Braun 1913, Zollikofer 1930, Urbanska unpubl.). The number of propagules varies from one inflorescence to another, but total propagule output in a given clonal unit is high (Tab. 2).

Propagules in *P. alpina* usually are non-dormant. The aerial biomass is accumulated rather rapidly, whereas the development of roots is slow (Fig. 8). Dispersal of propagules is mostly local: the flowering shoot gradually bends under the weight of numerous plantlets, eventually touches the soil surface and the propagule cluster takes root. Some plantlets may fall off separately and their dispersal is enhanced by wind.

Survival and further development of propagules in the wild is influenced by climatic conditions, dry and hot weather being unfavourable; the soil texture also seems to play a rôle (Bachmann 1980). In experimental conditions, on the other hand, 100% survival rates were observed (Urbanska unpubl.).

Tab. 2. *Poa alpina* var. *vivipara:* propagule output in two small tussocks (diameter of about 10 cm) originating from different alpine substrata.

Substratum	N of propagules per shoot					Total
Shoot No.	1	2	3	4	5	
Silicate	33	13	19	34	27	152
Dolomite	13	27	6	29	69	144

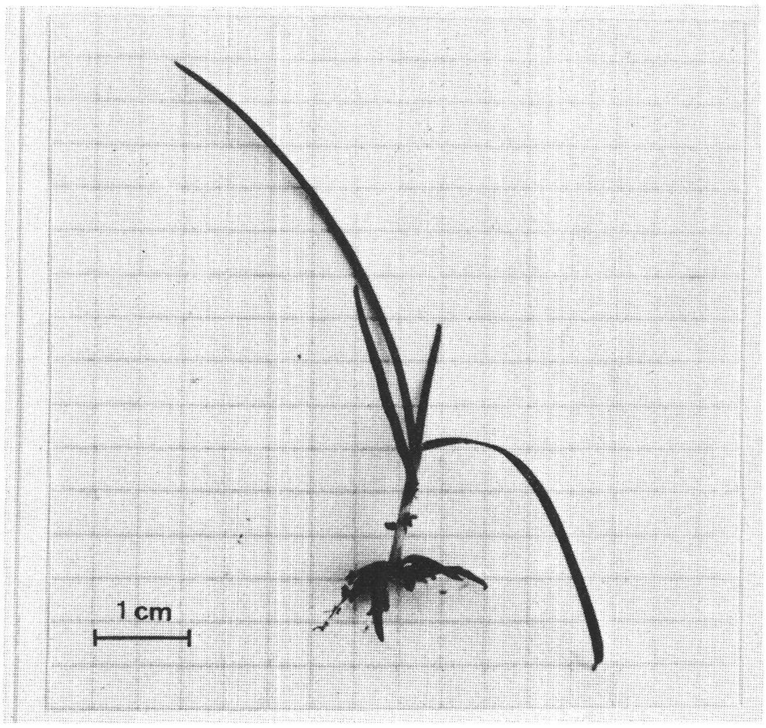


Fig. 8. *Poa alpina* var. *vivipara:* two-week-old plantlet. Experimental garden trial.

The precise background of vivipary in *P. alpina* is not yet clearly understood, but ecological factors are undoubtedly important. It seems that vivipary and reproduction by seed are environmentally cued at least in some individuals (Bachmann 1980). It is also interesting to note that calcium carbonate in the soil may enhance the production of propagules (Zollikofer 1930). Further studies in the latter subject are worthwhile because *P. alpina* occurs upon various alpine substrata.

Large semi-continuous populations of *P. alpina* at higher altitudes have a rather complex structure, clusters of young individuals that form a ring around the mother unit being a characteristic feature. *P. alpina* var. *vivipara* frequently occurs in pioneer sites up to about 3300 m a. s. l. and is considered as an excellent colonizing taxon. It tolerates well a wide range of niche conditions, being equally successful, e.g., in sites that stay snow-free in winter and in stations that remain under snow for a long time. According to Braun (1913), *P. alpina* in wind-exposed sites may show a temporary photosynthetic activity even in winter.

The distribution area of *P. alpina* var. *vivipara* is very large; it was reported also from high northern latitudes (e.g., Greenland, 81°40′ N. Lat.).

In *Polygonum viviparum,* flowering shoots appear in early summer and bulbils are produced throughout the vegetation season. They are small, shiny-brown, and contain starch as a nutrient reserve. The propagule output, related to the length of inflorescence and the occurrence of flowers, is very variable (8–76) bulbils per shoot, Urbanska unpubl.); it might be influenced by local niche conditions but no precise pattern was so far revealed.

Dispersal of propagules in *P. viviparum* may be limited or occurs over large distances, not only wind but also some animals being involved (Hartmann 1957). According to Schröter (1926), snow grouse *(Lagopus mutus)* play a particularly active part in the dispersal of edible bulbils. The present author observed also an occasional accumulation of propagules in habitations of *Marmota marmota.*

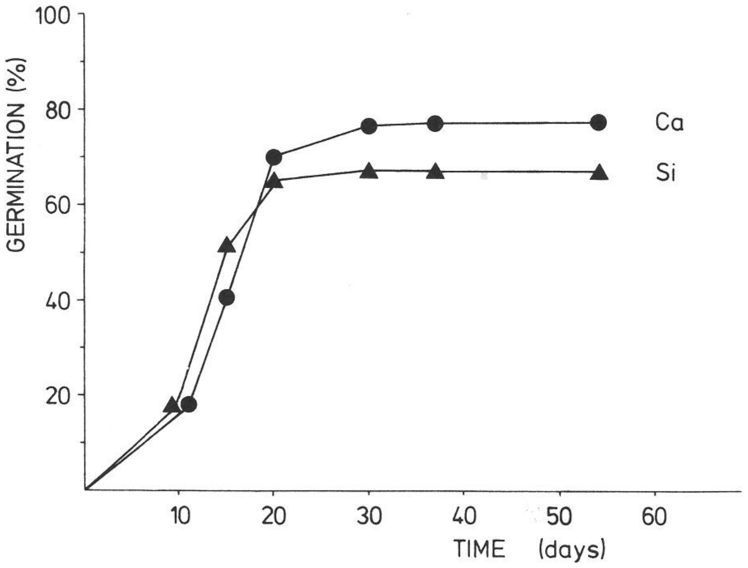
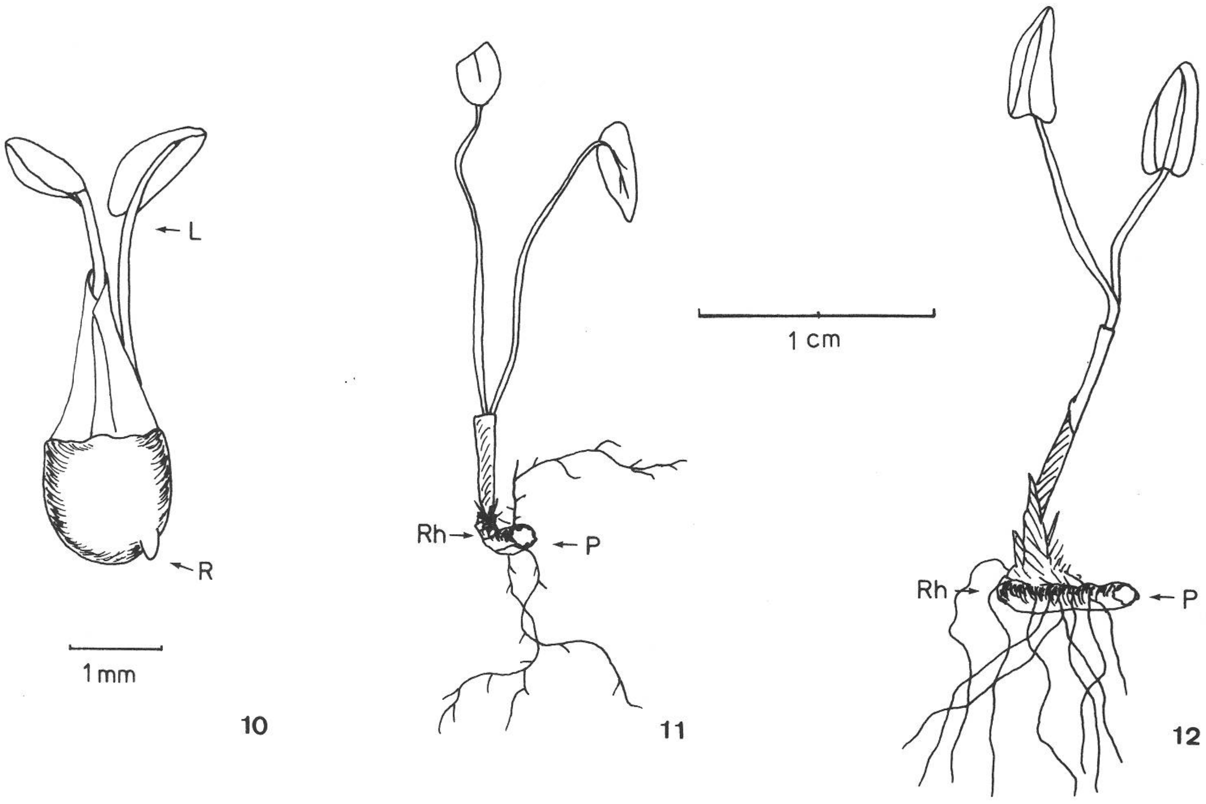


Fig. 9. *Polygonum viviparum:* germination of two months old propagules from alpine sites. Si = acidic silicate; Ca = dolomite. Laboratory trial.

It seems that the dormancy in propagules of *P. viviparum* may be to some extent influenced by environmental conditions. In some previous reports (e.g., Hartmann 1957), only a transient dormancy period prior to plantlet development was noted; on the other hand, the present author observed in 1984 mostly dormant propagules dispersed in high altitude sites near Davos, E. Switzerland. Innate dormancy was observed in about 15% of propagules (Braun 1913, Urbanska unpubl.); in controlled laboratory conditions, bulbils that were previously dry-stored for two months at 20 °C germinated well and rather rapidly (Fig. 9).

Development of plantlets in *P. viviparum* usually begins with the formation of two small leaves followed by root development (Fig. 10). In experimental conditions, individuals grow rather rapidly (Fig. 13); in the wild, however, development is slow. Accumulation of below-ground biomass is characteristic, whereas only two leaves occur even in three-year-old plants (Figs. 11–12). Remains of a propagule attached to the rhizome are frequently visible for a rather long time (Hartmann 1957). Reproduction occurs for the first time when the plant is at least six years old (Linkola 1935).

Populations of *P. viviparum* are large and semi-continuous, particular sectors showing pronounced differences as to density and sex structure. As yet, we observed only male or female sub-populations (Urbanska unpubl.); however, *P. viviparum* may be monoecious, dioecious, or produce hermaphroditic flowers, and further studies on gender distribution in alpine populations are of interest.



Figs. 10–12. *Polygonum viviparum:* propagule development. 10. Propagule from an inflorescence. 11. One-year-old plantlet. 12. Three-year-old plantlet. L = leaf; Rh = rhizome; P = remaining part of a propagule. (Redrawn and modified from Hartmann, 1957).

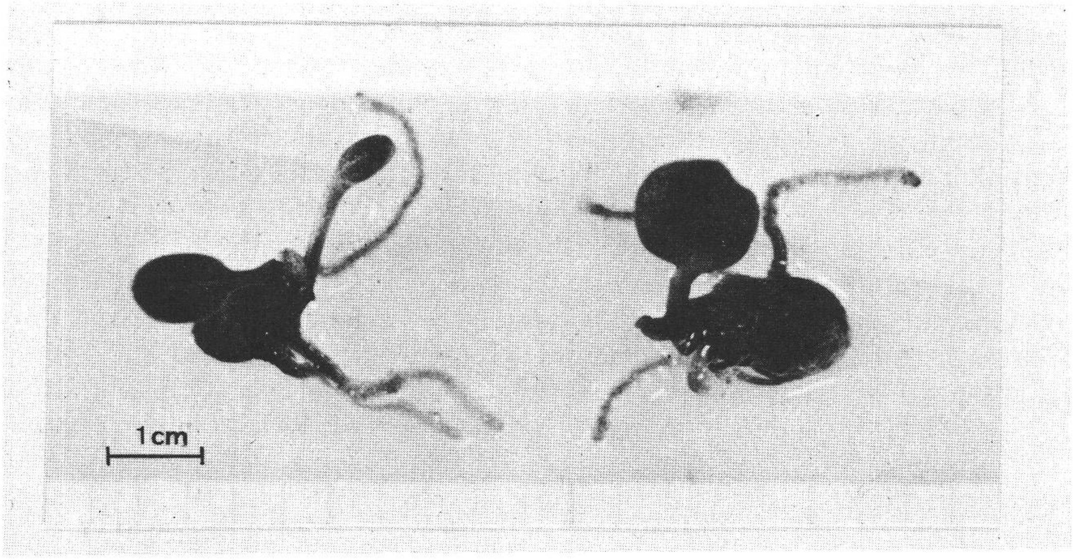


Fig. 13. *Polygonum viviparum:* two-week-old plantlet in a laboratory trial.

P. viviparum is a well-known species at high altitudes. In the Alps, it occurs up to 3000 m a. s. l. (Braun 1913); in the Himalayas, it has been recorded from Mt. Everest at 4830 m. (Salisbury 1942); in Yukon, it is known to occur up to 2200 m. (Hultén 1968). *P. viviparum* is also successful in high northern latitude sites: it was found, e.g., in Greenland at about 83° N Lat.

The behaviour of *Poa alpina* var. *vivipara* and *Polygonum viviparum* shows that life history strategies of viviparous/bulbiferous plants do not follow a single pattern. In *Poa alpina,* vigorously developing plantlets are initially supported by the mother plant but are soon photosynthetically active, and their energy input to the clonal module budget is undoubtedly considerable. In *Polygonum viviparum,* on the contrary, development of plantlets is slow; however, propagules own an initial capital of complex carbohydrates and may perhaps afford limited photosynthetical activity. As far as the actual survival of propagules in the wild is concerned, the propagule dormancy in *P. viviparum* might represent an advantage; it should be remembered, however, that *Poa alpina* may sometimes produce seeds under conditions that are unfavourable to propagule formation. Facultative agamospermy in *P. alpina* is widely distributed (see e.g. Müntzing 1940, 1966); for the time being, it is impossible to distinguish between sexually and asexually produced seeds (Cook, pers. comm.).

Concluding remarks

The present paper shows that mechanisms of asexual reproduction in plants are greatly varied, the resulting differences in population structure being sometimes very pronounced. Distinction between agamospermy and vegetative propagation should therefore be maintained; the two forms of asexual reproduction might be opposed to "clonal growth" (Harper 1977). These concepts seem to be helpful in demographic studies (evaluations of population density, survivorship or studies on distribution of variants); they may also be useful in phytosociology (assessment of abundance).

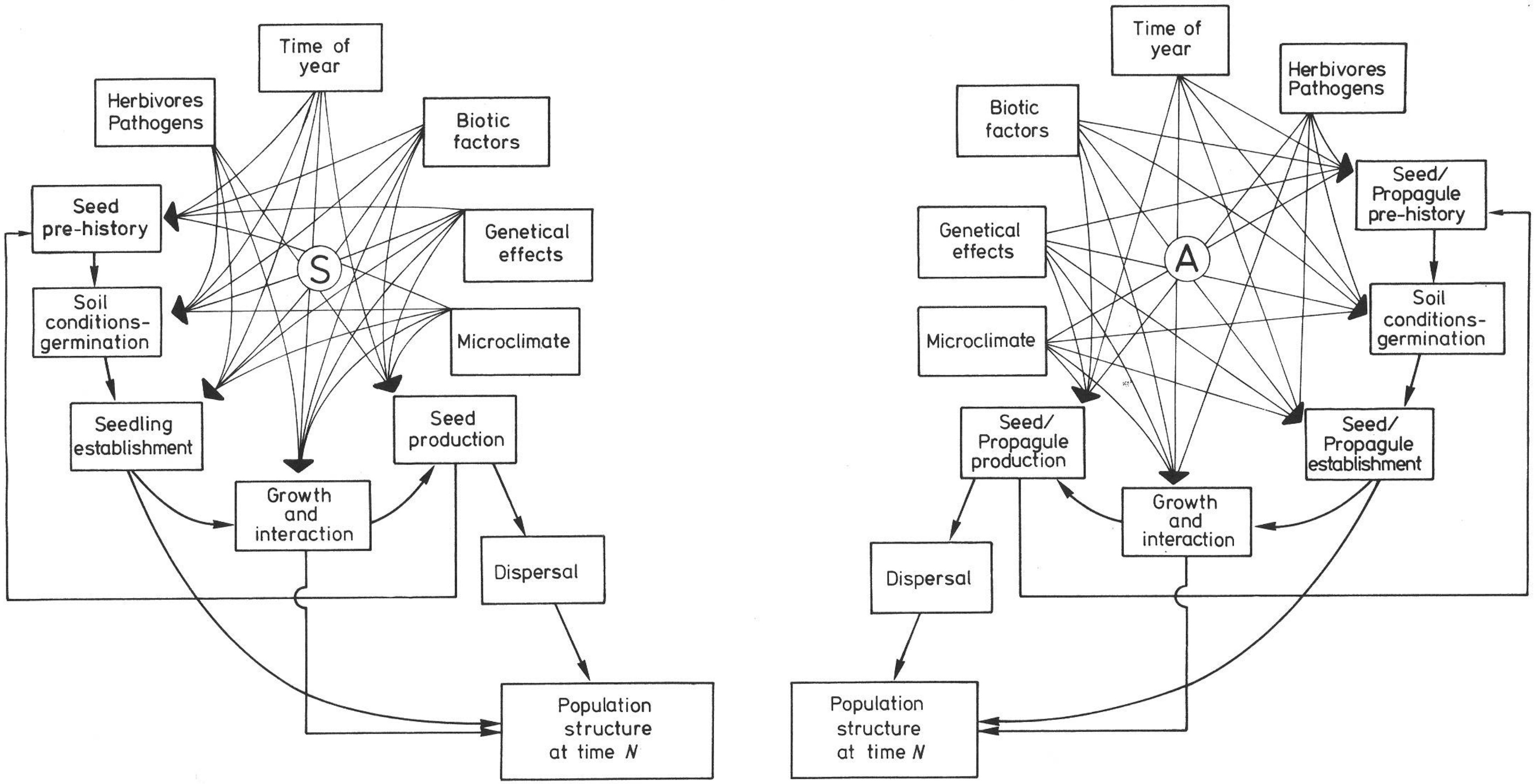


Fig. 14. Life history and population dynamics in sexual (S) and asexual (A) plants.

Dispersal and survival strategies in asexual plants often comprise multiple tactics either used in habitual conditions or reserved for occasions when the situation becomes precarious for the population. It is interesting that these tactics frequently involve seeds or units possessing seed-like features, e.g., carrying nutrient reserves and/or exhibiting dormancy. In this respect, asexual and sexual plants have a very similar population biology (Fig. 14).

The concept of a "favourable habitat" does not really apply to arctic and high-alpine ecosystems where life conditions are harsh and notoriously unpredictable. The sexual-vegetative reproduction balance (Williams 1975) may therefore not necessarily be most important in all arctic/alpine taxa; on the other hand, the balance between reproduction *by seed* (or seed-like structures) and clonal growth represents an essential element both in sexual and asexual populations.

The genetic uniformity of asexual populations is usually pronounced (e.g. Grant 1975, 1981) and should obviously be taken into consideration in any serious study. It seems, however, that asexual plants, traditionally considered as unalterable ("blind alley of evolution", Stebbins 1950), may undergo microdifferentiation and form local races.

The formation of local races represents one of maximizing fitness processes; it is influenced by small neighbourhood size, in-breeding system resulting in a limited gene-pool, high reproductive output, and intense local selection (Wright 1943, 1948, Levin and Kerster 1971, Levins 1968). Local races may indeed have a very restricted distribution (Bradshaw 1971, Antonovics et al. 1971) and may arise rapidly (e.g. Wu and Antonovics 1976). Asexually reproducing plants have zero neighbourhood size, frequently a high reproductive output, a limited gene-pool, and selection is sometimes exceedingly strong. Formation of genetically diversified offspring is admittedly rare but not excluded; in fact, some data on the Lemnaceae (e.g. Landolt 1957, Landolt and Dann 1983, Landolt, in prep., Urbanska 1980) as well as our recent results on *Taraxacum alpinum* (Schütz and Urbanska 1984) strongly point to a racial differentiation.

Further studies dealing with local adaptation patterns in asexually reproducing taxa should be of a special interest, ecologically extreme sites being particularly promising. It is not quite certain that only sexual reproduction constitutes the difference between survival and extinction.

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Résumé

La reproduction asexuée chez les plantes supérieures comprend a) l'agamospermie et b) la propagation végétative. Sont discutées l'importance biologique des deux procès ainsi que leur influence sur la structure des populations végétales.

Stratégies de dispersion et de survie chez les plantes se reproduisant par voie asexuée embrassent fréquemment de tatiques multiples. Elles employent souvent les graines ou des unités dont les cractéristiques sont celles de graines (p. ex. réserve des substances nutritives et/ou dormance). Des formes variées de reproduction asexuée se

rencontrent fréquemment ensemble. Pour une combinaison donnée, les populations des taxons à reproduction asexuée montrent des différences en effectif, densité, structure d'âges et parfois également pour ce qui concerne la distribution des sexes au sein de secteurs particuliers.

Il ne semble pas que l'équilibre entre la reproduction sexuée et la propagation végétative soit essentiel chez tous les végétaux; en revanche, l'équilibre entre la reproduction par graines (ou structures comparables aux graines) et la croissance clônale représente un élément important aussi bien pour les populations sexuées que pour celles dont la reproduction est asexuée. Des données récentes indiquent que la différenciation raciale locale peut se manifester non seulement chez les plantes à reproduction sexuée mais aussi chez les taxons qui se reproduisent par voie asexuée.

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