Populations in clonal plants

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Contents

Abstract. Population phenomena in higher plants are reviewed critically, particularly in relation to clonality. An array of concepts used in the field are discussed.

In contrast to animals, higher plants are modular in structure. Plant populations show hierarchy at two levels: ramets and genets. In addition, their demography is far more complicated, since even the direction of development of a ramet may change by rejuvenation. Therefore, formulae concerning animal populations often require modification for plants. Furthermore, at the zygotic stage, higher plants are generally less mobile than animals. Accordingly, their population processes tend to be more local. Most populations of plants have a genetic structure: alleles and genotypes are spatially aggregated. Due to the short-ranged foraging behaviour of pollinators, genetically non-random pollination prevails.

A generalized formula for parent-offspring dispersal variance is derived. It is used to analyze the effect of clonality on genetic patchiness in populations. In self-compatible species, an increase in clonality will tend to increase the degree of patchiness, while in self-incompatible species a decrease may result. Examples of population structure studies in different species are presented. A considerable degree of genetic variation appears to be found also in the populations of species with a strong allocation of resources to clonal growth or apomictic seed production.

Some consequences of clonality are considered from the point of view of genetic conservation and plant breeding.

Index words: clonal plants, genetic patchiness, population structure, dispersal variance, plant breeding

1. The plant as a population

Botanists frequently emphasize the great *plasticity* of plant growth. The size and form of an individual plant are much more open to variation than are those of an animal. This variation results partly from differences in the availability of resources. HARPER (1978), however, states that the higher plant expresses its reaction to environmental stress mainly by varying the *number* of its modular units of construction rather than their size or form. According to this thinking, the individual *module* of plant growth should be *no more variable* or plastic than eg. the length of a rabbit's leg or a *Drosophila* wing.

Hence, in contrast to animals, one may regard an individual plant as a *population,* ie. a population of parts. The smallest module of organized structure in higher plants is the leaf with its axillary bud; larger modules (branches or *'ramets'*) are various aggregates of the smaller ones (HARPER 1978).

The modular approach has been applied eg. in *Carex arenaria* (NOBLE et al. 1979), in *Eichhornia crassipes* (WATSON and COOK 1982), and in *Dryas octopetala* (MCGRAW and ANTONOVICS 1983). Various workers have presented more or less general models of plant modular growth, branching and fecundity (eg. MCGRAW and ANTONOVICS 1983, PORTER 1983 a, b, FRANCO 1985).

The characteristic form of a plant is the result of a »reiteration» of the modular units, and depends on the arrangement of these units, their spacing and the angles of branching of the connecting structures. It also depends upon which of the modules develop, and which ones remain dormant or die (HARPER 1978).

PORTER (1983 a) points out that plant form is as likely to be constrained by developmental control of the population of meristems as by the carbon economy of the plant. He gives examples of differences in branching patterns resulting from different kinds of distributions of bud numbers in each branch order. Apical meristem utilization and growth form in *Potentilla anserina* was investigated by ERIKSSON (1985). If the phyllotaxy, ie. the angular position of lateral meristems around the parental axis is highly regular, the resulting plant may have a geometrically rather well defined structure, as in trees and even in some clonal species eg. *Eichhornia* (WATSON and COOK 1982).

A *clone* is defined by WEBBER (1903) as a population of cells or organisms derived from a single cell or common ancestor by mitoses. According to this definition, all the somatic cells of an individual plant should constitute a clone.

Hence, a plant might be regarded as a *population of cells.* However, in a higher plant, cells differentiate during the ontogenetic process; thus instead of a single population there exist an array of *functionally differentiated subpopulations* of cells.

In higher plants, therefore, the *smallest module* of repetitive structure, in the functional and morphological sense, should constitute a union of the various types of the differentiated cell types present. This reasoning yields a definition of modules equivalent to that presented by HARPER (1978) and cited above.

A final conclusion is that in contrast to animals, a population of a higher plant species is to be considered as a *hierarchical* one with at least two levels of hierarchy: genets and ramets.

Hence, many of the classical formulae of population biology, based on considerations in animal populations, should be *reformulated* to encompass plants as well. HARPER and WHITE (1974) argue that an adequate description of a population of plants must take account of two parameters: N, the *number of genets* resulting from individual zygotes and η, the *number of modular units* of that genet.

A pair of concepts sometimes in use (eg. WRIGHT 1976, HOLMES 1979) should be mentioned here. An *ortet* is the original single ancestor of a clone, while a *ramet* will be defined as an individual member of a clone.

2. Growth and reproduction

ASKER (1979) reviews the most well known definitions of *apomixis.* Different authors disagree over which forms of asexual reproduction should be included.

GUSTAFSSON (1946, 1947 a, b) and STEBBINS (1950) define *vegetative reproduction* (runners, layers, bulbils etc.) as a form of apomixis, while NOGLER (1978), RUTISHAUSER (1967) and ASKER (1979) himself do not.

All of the authors agree that *agamospermy* (seed formation without fertilization of the egg cell) should be included in apomixis, except that Nogler rules out nucellar embryony (= adventitious embryony; ie. embryos formed directly from somatic cells).

In an ecological and population genetical sense, there should be important differences eg. in gene flow, depending on the type of propagules (Table 1). The production of clones via seed is a special case, meriting a term of its own. Hence, in the present context, I prefer the terminology of Asker and Rutishauser who restrict the use of the term *apomixis* to be *synonymous with agamospermy.*

How, then, should one define *sexual reproduction?* RIEGER et al. (1968) define it as a regular alternation of meiosis and fertilization (karyogamy) in the life cycle. In addition, they present types of reproduction with some of the attributes of sexual processes. Examples of 'partial' or 'irregular' sexual reproduction have been termed as parasexual (PONTECORVO 1954) and subsexual (DARLINGTON and MATHER 1949).

Asexual or *agamic reproduction* RIEGER et al. (1968) define as the development of a new individual in the absence of any sexual process.

Reproduction is defined by RIEGER et al. (1968) as the production (self-propagation) of an organism, a cell, or a cell organelle by one like itself.

HARPER (1977, 1978), however, does not accept such a definition. He distinguishes sharply between growth and reproduction. He argues that the process of *growth* is the result of meristematic activity. It is always the result of development from an *organised body of cells,* interconnected by plasmodesmata and, for a time, integrated by hormonal control. In contrast to this, *reproduction,* says Harper, involves the »re-production» (the production again) of an entirely new organization from a *single cell,* formed with renewed and cleaned cytoplasm, lacking protoplasmic continuity with other cells (and usually following some process of genetic recombination). The isolation of the new individual from the mother is remarkably complete.

In the terminology of RIEGER et al. (1968), the latter phenomenon (Harper's 'reproduction') is called, in this asexual context, *agamogony,* and the former (Harper's 'growth') is called *vegetative reproduction* — a term which, according to Harper, has done great harm to the population biology of perennials.

Harper's terminology gives support to the concept of apomixis given by Rutishauser and Asker and presented above; »vegetative reproduction» should not be included there since it is not reproduction but growth.

What, then, might one understand by a

Table 1. Influence of plant breeding systems and seed dispersal mechanisms on levels of genetic differentiation among populations (After LOVELESS and HAMRICK 1984; as GREGORIUS (1987) suggests, 'differentiation' has been substituted for 'diversity', however).

	Number of studies	Mean differentiation among populations (G_{ST})
Breeding system		
Autogamous	39	.523
Annual	31	.560
Perennial	8	.329
Mixed Mating	48	.243
Outcrossed	76	.118
Animal	32	.187
Wind	44	.068
Dispersal mechanism of seeds		
Gravity	59	.446
Animal-Attached	18	.398
Animal-Ingested	14	.332
Explosive	24	.262
Winged/Plumose	48	.079

clonal plant? The definition by WEBBER (1903), given above, implies that an individual higher plant is to be considered as a clone at the cellular level. The same applies at higher organizational levels, too, since higher plants are repetitive, ie. modular, in structure. Thus, HARPER (1978) considers a tree as an interconnected branched clone of shoots.

However, not all species of higher plants are generally referred to as clonal. The term clonal often seems to take on quite another sense for which, as is all too common in biology, explicit definition is lacking. HARPER himself (1977, 1978), unfortunately, has used the term in this undefined manner. To clarify the definition of a 'clonal plant', I shall present a small argument.

The interpretation of whether or not a particular tree is 'clonal' might depend on the direction of growth. For the tree not to be 'clonal' should the ramets grow away from the growth medium (ground, water or host) not conquering new resources (except light, CO_2 or water from the air)?

Supposing the connections between the modules were less perpendicular to the medium, allowing a more lateral or 'sprowling' growth habit? Is the plant then a clonal one? Or do we still demand that the modules have an independent, local root system?

HARPER (1977, p. 215) states that »it is sometimes convenient to take the establishment of its own root system as the point at which a branch has become a tiller or ramet». Then »wheat is to be regarded as a clonal annual», which seems odd to him.

Should the modules perhaps be capable of following an independent existence if severed from the mother plant (cf. HARPER 1977, p. 24; though he redefines 'ramet' via 'clonal growth'). Or should the plant break up spontaneously, or even by natural mechanisms, into disconnected, physiologically independent parts?

For most purposes, the implicit meaning of the term might be covered by the following *definition.* A higher plant is called *clonal* if a genotype is capable of changing its place of resource utilization within the growth medium by adding new modules via growth or via apomictic seed.

This definition poses some difficulties eg. with water plants, which take up nutrients largely through their leaves from the water. Perhaps 'utilization' should be replaced by 'utilization through the roots', or the growth medium should be understood to mean bottom sediments for water plants, excepting the freely floating species.

Bearing in mind the genetically-oriented definition of a clone by Webber, presented above, it might have been better originally to introduce a distinct term for »clonal growth» and »clonal plants», for instance 'wandering growth' and '*wandering plants*'.

To sum up, in higher plants, there should be two ways of producing a clone (at a higher level of organization): via growth or via asexual reproduction (ie. apomictic seed).

HARPER himself (1977, p. 27), though, claims that »clones are formed by growth — not reproduction»; with respect to the higher level of organization this is, of course, a lapse.

3. Growth forms of perennial plants

Growth forms of perennial plants represent (HARPER 1977) a continuum with two extremes: 1) one dominated in its evolution by selective pressures to attain height and shade out its neighbours, leading almost inevitably to a woody habit, and 2) one dominated by pressures to expand laterally to pre-empt limited water and nutrient reserves. This latter »strategy» leads to a lateral branching, nodal rooting or suckering habit of clonal plants (Fig. 1). Mixed growth forms also exist; e.g. clonal trees such as *Populus* exhibit a combined »strategy».

A *genet* is defined (KAYS and HARPER 1974, HARPER 1977 p. 26, 1978) as a genetic individual, representing a product of an original zygote; such units represent independent colonizations.

Each genet is composed of modular units of construction — the convenient unit may be

a shoot on a tree, the ramet of a clonal plant, the tiller of a grass or the leaf with its bud in an annual (HARPER 1977, p. 26). An individual genet may be a tiny seedling or it may be a clone extending in fragments over a kilometre.

A clonal plant might be envisaged as a *horizontal tree,* the branches representing the ramets. However, the modules of a clonal plant should have their own roots. Rhizomatous herbs grow horizontally through the extension of a system of serial shoot/rhizome/root modules instead of branch modules as in trees.

In the case of rhizomatous plants, in contrast to trees, one *cannot identify* the genets visually as a rule, since the connections between parts of a single genet are usually hidden below ground. Furthermore, the connections between the ramets are often fragmented (NOBLE et al. 1979), even in stoloniferous herbs (SARUKHAN 1974), leaving the genotype to be expressed as a fragmented phenotype with independent, wandering parts (HARPER 1978). This situation reaches its extreme in those species which produce clones via detaching propagules (eg. bulbils) or even via reproduction (apomictic seed), there existing no connections at all between the ramets.

4. Evolution of clonality

Apomixis, ie. agamospermy has been reported in about 250 plant species representing

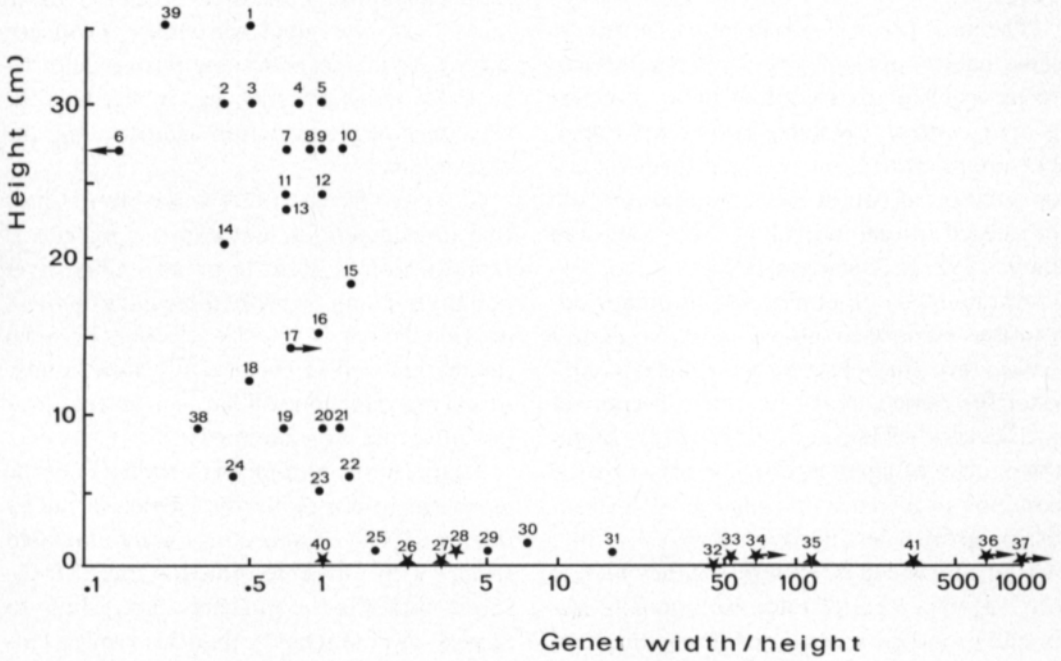

Fig. 1. Genet height and width in perennial plants (point denotes woody species, asterisk denotes herbaceous species). 1. *Pseudotsuga douglasii* Carr., 2. *Picea abies* (L.) Karst., 3. *Sequoia gigantea* Lindl. et Gord, 4. *Gingko biloba* L., 5. *Cedrus libani* Barrel., 6. *Populus nigra* L. var. *italica* Du Roi, 7. *Ulmus procera* Salisb., 8. *Fraxinus excelsior* L., 9. *Aesculus hippocastanum* L., 10. *Fagus sylvatica* L., 11. *Pinus sylvestris* L., 12. *Ailanthus glandulosa* Desf., 13. *Acer pseudoplatanus* L., 14. *Betula pendula* Roth., 15. *Quercus petraea* Lieb., 16. *Salix babylonica* L., 17. *Populus tremuloides* Michx., 18. *Ilex aquifolium* L., 19. *Eucalyptus gunnii* F.v.M. not Hook.f., 20. *Crataegus monogyna* Jacq., 21. *Magnolia denudata* Desrouss., 22. *Laburnum anagyroides* Medicus., 23. *Arctostaphylos glauca* Lindl., 24. *Eucalyptus porrecta* S. T. Blake, 25. *Calluna vulgaris* (L.) Hull., 26. *Plechtrachne schinzii* Hent., 27. *Triodia basedowii* Pritzel, 28. *Spartina townsendii* H. & J. Groves, 29. *Arctostaphylos glauca* Lind., 30. *Nitraria billardieri* DC., 31. *Vaccinium myrtillus* L., 32. *Holcus mollis* L., 33. *Cirsium arvense* (L) Scop., 34. *Carex arenaria* L., 35. *Trifolium repens* L., 36. *Pteridium aquilinum* (L.) Kuhn, 37. *Festuca rubra* L., 38. *Banksia serrata* L., 39. *Eucalyptus obliqua* L'Hérit., 40. *Hypochaeris maculata* L., 41. *Rubus arcticus* L. Species No 41 according to TAMMISOLA (1987), other species after NOBLE et al. (1979).

22 families (MARSHALL and BROWN 1981). One might expect agamospermy to be far more prevalent, since it offers '*automatic advantage*' over sexual reproduction. At the group level, advantage arises because no resources need be expended on producing male gametes. At the individual level, an agamospermous parent confers on its progeny a genetic complement twice as large as does a sexually maternal parent.

In a one locus model, a mutation to agamospermy should have a clear initial advantage over sexual alleles, irrespective of dominance. Hence, once introduced, agamospermy should eventually become *fixed* in a population, unless it radically reduces the fitness of its carriers (MARSHALL and BROWN 1981).

The most plausible explanation for the relative paucity of agamospermy in plants seems to be that apomixis is often under *complex genetic control,* involving two or more loci. For apomixis to become established, the accumulation of two or more mutations would be needed in one individual (MARSHALL and BROWN 1981, cf. NOGLER 1984).

Another way of gaining the automatic advantage mentioned above is by *vegetative spread* (growth). Here we are obliged to consider the ramets as the progeny, in contrast to the view of HARPER (1977, 1978). Might the paucity of agamospermy be offset by the common occurrence of clonal growth (wandering growth habits) in plants?

Clonality will in effect *lengthen* the *life span* of a genotype, thus offering exceptionally successful genotypes a chance of conquering very large areas. Hence it provides the plant with a means of exploiting 'sisyphean' fitness (WILLIAMS 1975), which results from the very high selection intensities present in some long-lived plant communities.

There are, however, some general reasons *favouring sexuality* which may prevent clonality from becoming universal or even far more prevalent.

BERNSTEIN et al. (1985) suggest that *repair* and *complementation* are the selective forces maintaining sex. Outcrossing is maintained because it promotes complementation, ie. the masking of deleterious mutations. Furthermore, the reparation of double-strand injuries to DNA molecules is possible during sexual reproduction, due to the pairing of homologous chromosomes. Asexual cell lineages, on the contrary, cannot avail themselves of the injury removal system offered by recombination and natural discrimination against unfit genotypes.

As will be explained later (chapter 8., eg. LEVIN and KERSTER 1971, LEVIN and WILSON 1978), the populations of facultatively clonal organisms should not be as quick in adapting to a very rapid change in the environment as are those of obligately sexual ones. The *more rapid adaptation* of a sexual population, based largely on the great variability produced during sexual reproduction, may render it essentially more effective eg. in keeping the resistance of a population against plant diseases high.

MAYNARD SMITH (1977) was able to show that *sib competition* may confer upon sexual reproduction a short-term advantage over apomixis. In an *unpredictable environment,* provided there is intense selection between families as well as between sibs in a family, sexual reproduction will have an advantage of upto twofold over apomixis.

A large number of understorey herbs of the temperate forests of North America spread by rhizomes. The existence of several unrelated species with the same growth pattern in the forest understorey indicates, according to SCHELLNER et al. (1982), that this growth pattern is especially well suited to the forest environment. The *rhizomatous habit* in these species may be considered an adaptation to the *paucity* and *uneven distribution of resources* in and on the forest floor. Such a habit also offers the genotype a way of extending its life span in an environment where seedling establishment is infrequent and unpredictable (SCHELLNER et al. 1982, cf. MAYNARD SMITH above).

Plant taxa that are able to produce seeds

asexually display some distinct *geographical and ecological patterns.* Such taxa have a greater tendency to colonize once-glaciated areas, tend to have larger ranges, to extend into higher latitudes and upto higher elevations than do their sexual relatives.

This kind of data has been interpreted to support the hypothesis that sexuality is favoured by biotic selection: in areas where *biotic interactions* are especially important, sexuals should enjoy advantages over apomicts (GLESENER and TILMAN 1978).

Still further proposals have been put forward to explain the observed patterns. For example, the apomicts should be better *able to colonize* new areas, since they have the potential to found a new population with a single individual (STEBBINS 1950). This explanation implies that the observed patterns should be only *temporary:* in the course of time the »young» habitats with clonal plants will be conquered by their sexual relatives.

However, since experimental evidence is lacking, BIERZYCHUDEK (1985) considers it *premature* to regard observed distribution patterns as evidence to support hypotheses about what forces maintain sexual reproduction. He points out that all of the interpretations presented have ignored the positive correlation that exists between ploidy level and breeding system: asexual plant (and animal) taxa are generally polyploid while their sexual relatives are generally diploid. Furthermore, he presents evidence that *high ploidy levels alone* could (independent of the breeding system) endow individuals with the *ability to tolerate* these 'extreme' environments.

In clonal plants, genets often fragment into separate entities rather early. There is at least one apparent advantage of the *fragmentation* of a genet, which may have favoured it over physical coherence during the evolution of clonal growth and reproduction habits. Diseases, particularly viruses, spread rapidly through the parts of an interconnected plant. If the connections between the ramets are nonexistent, as in the clones of agamospermous apomicts, or if they tend to decay rather rapidly, as in many rhizomatous or stoloniferous species (SARUKHAN 1974, NOBLE et al. 1979), the *spread of diseases* in the plant populations may be retarded (HARPER 1978).

5. Wandering via growth or via reproduction

There are two main types of clonal plants. The first type wanders via clonal growth (eg. stolons, rhizomes, suckers, bulbils, nodal rooting). The second type wanders, or rather is dispersed via clonal reproduction (ie. apomictic seed); these are the agamosperms.

At the level of gene flow via propagules, there exists an important difference between these two types. As a rule, seed should be much more amenable to *distant colonization* than, for example, rhizomes. Considering only asexual propagules, this results in a more extensive gene flow between the populations of an apomict than between the populations of a rhizomatous or stoloniferous plant.

Further, the *mechanism of seed dispersal* exerts a great influence on the gene flow and hence on the genetic differentiation among populations (Table 1). On average, by far the smallest differentiation among populations is found in the plant species with winged/plumose seed, (eg. dandelion) (LOVELESS and HAMRICK 1984), capable of travelling far.

If we consider local spread, clonal growth should be much *more economical* than seed dispersal in removing the daughter plant from the competitive influence of its parent (SCHELLNER et al. 1982). The *death rate* is usually much lower in new ramets than in seedlings. One reason for this might well be the ability of plants to *translocate assimilates* and inorganic matter effectively. Hence, new ramets are not necessarily dependent for their survival on the availability of local resources, as are seedlings (SCHELLNER et al. 1982, LOVETT DOUST 1981).

Hence, might not wandering via clonal growth be more suitable for K-strategists while that via apomictic seed would be more amenable for the colonization situation encountered by r-strategists?

The germination of seeds or the primary *establishment of seedlings* is often controlled by the density of the vegetation. Successful establishment occurs in local bare patches (HARPER 1978). For example in the genus *Viola,* seed germination or seedling establishment is negatively affected by the density of ramets while the emergence of new ramets from stolons is independent of density (SCHELLNER et al. 1982, cf. WATSON and COOK 1982).

On the other hand, KAYS and HARPER (1974) reported that in *grasses* the final density of tillers is independent of sowing density. The genets that establish are eliminated according to the common 3/2 thinning law of YODA et al. (1963). There is an overproduction and subsequent density-dependent mortality of tillers and genets.

In *Ranunculus repens,* SARUKHAN and HARPER (1973) have shown that for ramets the death risk is rather constant over time while for seedlings the risk is extremely high during the juvenile stage. This difference may be partly attributable to the translocation of assimilates between ramets. In addition the *recombinational load* of seedlings will augment the risks of juvenile establishment, while for ramets, the death rate is that of already proven genotypes (HARPER 1978). Since there cannot be any recombinational load in apomictic seedlings, these should have a more constant risk of mortality than sexual ones. Comparative studies are, however, lacking.

Regarding the establisment phase, translocation of nutrients to the new ramet may lessen the competition the ramet incurs from its close relatives. Such behaviour might increase the 'inclusive fitness' (HAMILTON 1964 a, b) of ramets and thus provide an instance of *kin selection* in plants (NAKAMURA 1980).

6. Age, state and vitality

A plant population may be characterized according to the distribution of its ramets in different age classes. Clonal plants are perennials, as a rule, though conceptually 'clonal annuals' might exist (eg. wheat, see above) (HARPER 1977). Hence, ramets of different ages coexist.

Characterization by age distributions is not, however, as informative in plants (RABOTNOV 1978) as in animals.

The *rate of development varies* greatly among different ramets, depending heavily on the microenvironment of a particular ramet. Ramets of similar ages may be of strikingly different sizes and developmental stages. One might be a sterile dwarf with a juvenile habitus while another develops a large flowering stem with a mature habitus.

This phenomenon is very typical of the perennials, especially of the clonal ones, since their young ramets exist under conditions of intense competition, develop slowly and their *virginal period* is usually *prolonged.* Ramets are able to persist for a long time in the pregenerative states, attaining the mature state as soon as appropriate ecological niches become vacant (RABOTNOV 1978).

The situation in plants is complicated further by the ability of certain herbs (eg. grasses) to enter a *long-term* state of *dormancy,* lasting sometimes for several years. A transition to dormancy may be caused eg. by competitive relationships, as in *Taraxacum koksagyz* seedlings sown too densely (ZAVADSKII 1954).

Hence, age structure is not adequate to characterize plant populations. RABOTNOV (1978) has preferred classifying the life of plants reproducing by seeds into four main *states* (periods): primary dormancy, virginal, generative and senile states. An important phenomenon is the *state reversal* which often occurs in clonal plants: the sequence of development may involve more or less frequent reversals of direction. For instance, a grassland farmer can *rejuvenate* a suppressed population of white clover by appropriate management quite regardless of the age of the genets in the sward (HARPER 1978).

Viable seeds are considered as individuals in a state of *primary dormancy* (RABOTNOV 1978). An analogy in clonal plants which

wander via growth might be their dormant buds. There is often a vast population of dormant rhizome buds underground; in numbers it may exceed tenfold the size of the ramet population (NOBLE et al. 1979).

While primary dormancy in seeds may last many decades, resting buds will likely tolerate a time-lag of only a few years. However, not all plant species are able to retain the germinability of their seed for years. As a rule, viable seeds of plants with vigorous clonal growth are absent in the soil. The species with large quantities of viable seeds in the soil have evolved under an alternation of conditions favourable for germination of their seeds, as well as establishment of their seedlings, with long periods without such conditions.

This pattern is characteristic of *'meadow explerents'*, such as *Ranunculus repens* and *Agrostis stolonifera,* and also of some plants occurring in burned and felled areas. Explerents are plants that have a very low competitive ability but are able to invade vacant territories quickly, filling the gaps between strong plants, although being easily displaced by the latter (RABOTNOV 1978). Accordingly, the soils of forests carry a pool of viable seeds belonging chiefly to plants of the formerly open areas (burning and felling, old fields etc.) subsequently overgrown by the forest (RABOTNOV 1978).

The *virginal state* (RABOTNOV 1978) is the state of plants from germination up to the beginning of flowering and fructification. The period is a long one, and virginal plants are subdivided into four sub-states: seedling, juvenile, immature and mature virginal plants.

Thereafter, provided no state reversals occur, the states which follow will be the *generative state,* covering reproduction by seeds, and the *senile state,* when due to senescence plants lose their ability to reproduce by seeds (RABOTNOV 1978).

In the composition of age groups of mature individuals, there is another source of heterogeneity, ie. *vitality.* Foresters have long since distinguished vitality classes. In Kraft's scale there exist five classes of vitality among mature trees: I = exceptionally well-developed, II = dominant, III = codominant, IV = suppressed and V = strongly suppressed (MOROZOV 1925). Between the classes there are often remarkable differences not only in vigour but also in the order of their seed production.

Hence, a population of plants, especially a population of clonal plants, constitutes a *highly heterogeneous system* of individual ramets with very *diverse age-state-vitality* combinations (RABOTNOV 1978).

7. Breeding system

A term *'breeding system'* is used to cover all those variables apart from mutation which affect the genetic relations of the gametes that fuse in sexual reproduction (RIEGER et al. 1968). According to LEWIS and JOHN (1964), two main groups of such variables may be distinguished. 1. Those variables which affect the *ability* of particular gametes to fuse or parents to mate (ie. the variables comprising the *'mating system'),* and 2. those variables which affect their *probability* within the limits set by the first. The breeding system controls the extent of outbreeding which may take various forms: exclusive or predominant outcrossing (due to eg. self-incompatibility), predominant selfing, and a mixture of selfing and crossing.

According to HARPER (1978), the *clonal growth* habit is usually tightly linked with strict *outbreeding* (dioecy or self-incompatibility). The same should apply to the clonal reproductive habit, ie. the ancestors of apomicts (agamosperms) will usually be strongly outcrossing perennials (MARSHALL and BROWN 1981). This linkage is so tight that LEVIN and KERSTER (1971) utilize it in characterizing a clone. According to them, a clone may be characterized as a group of organisms having a strong correlation in space, but being incapable of sexual reproduction inter se.

Changes in the size and structure of a plant and the consequent *number* and *position of flowers* will cause a change in the processes

of pollen transport and fertilization. As the wandering of a genet proceeds, its structure will change. There is often — though not always — an increase in the number of its ramets, or at least an increase in the genet's total extent. Hence, clonal growth patterns may exert an influence on the effective breeding system of the plant population (HANDEL 1985).

Provided the genets of the population are separated widely enough, *'large'* clones, ie. clones with numerous fertile ramets, will always have a greater proportion of endogenous ('own') pollen on their stigmas than will smaller clones (HANDEL 1985).

With the same presumption as to widely separated genets, the more *aggregated* is the distribution of ramets, the greater should be the proportion of endogenous pollen on the stigmas (GLEAVES 1973).

In a population of clones of *Carex platyphylla,* a self-compatible (hence exceptional) and wind-pollinated species, the average load of endogenous pollen on the stigmas increased sharply with the size of the clone upto a clone size of about 10 'culms' (ie. reproductive spikelet complexes) (HANDEL 1985).

Similar phenomena have been recorded in the populations of insect-pollinated plants, since *short flight intervals* from flower to flower predominate in the foraging trips of most pollinating insects. In bees, the average flight interval from one flower to the next is linearly related to the *density* of the target species; the denser is the population, the shorter on average are the flight intervals. Foraging by lepidopterans, flies, beetles, bees and hummingbirds is economic in terms of energy expenditure; most flights are from a plant to one of its nearest neighbours (LEVIN and KERSTER 1969 a).

In a »realistic» simulation study (LEVIN and WILSON 1978), the alien pollen influx appeared to be a function of both *patch size* and *form.* Elongate patches received relatively more alien pollen than square-shaped ones, and large patches received relatively less alien pollen than small ones.

Hence, one consequence of *large clones* may have been *increased inbreeding.* In clonal plants, however, inbreeding may not offer any advantages, since there already exist good (though asexual) means of fixing superior genotypes. Thus, in clonal species, there might have arisen an evolutionary tendency to favour mechanisms *discouraging self-fertilization,* eg. self-incompatibility, heterostyly, dichogamy or even dioecy.

An example of a dioecious species is aspen, *Populus tremula* (an anemophilous tree with vigorous clonal reproduction through root suckers). Clonal patches of this species are usually 'large' and 'widely separated' in effect, as it makes a big tree with numerous flowers and usually grows at low population densities in mixed stands (HANDEL 1985, NOBLE et al. 1979). Hence, without any mechanism preventing self-fertilization, inbreeding would heavily predominate in aspen populations.

In self-incompatible or dioecious plants, the amount of *seed set* may depend strongly on the size and relative vicinity of the clones. Provided the clones are separated widely enough from each other, an increase in the number of ramets in a clone will cause a decrease in the average number of seeds produced per ramet.

Furthermore, in a plant species pollinated by insects, the breeding system is always basically influenced by the distribution, variation in numbers and *foraging habits* of the pollinators. When insect visitation patterns show *density dependence,* the density of flowers in the clones should have an effect on the seed set. Thus, in a bee-pollinated species, the denser are the (widely separated) clones, the less seed should be set per ramet.

The effects of these factors on the breeding system are exemplified in a study by HANDEL (1985) on *Trifolium repens,* a stoloniferous, self-incompatible and bee-pollinated pasture plant. He utilized estimates from several sources to model the foraging behaviour and pollen transport of bees and the clonal growth of white clover.

There are three ways in which one white

clover clone can invade a greater area than another: by the production of more internodes, of longer internodes, or of both.

If the plant produces *more internodes,* there will be an increase in the number of inflorescences per clone. Provided the clones are separated widely enough from each other, the probability that any one inflorescence receives compatible pollen will accordingly decrease. In large but separate clones, exogenous pollen is deposited mainly on the first few inflorescences during a visit, with the result that the average efficiency of pollination will decrease sharply with increasing clone size and the seed set will become more concentrated on relatively fewer inflorescences.

If the plant produces *longer* rather than more numerous *internodes,* the number of inflorescences will not change but the inflorescences will be set further apart.

In such a clone, it should occur more frequently than in a clone with similar numbers of shorter ramets, that a pollinator now visiting an inflorescence has just arrived from another clone, not from another inflorescence of the same clone. Namely, in the less dense (part of a) population, the bees will on average fly longer intervals from one flower to the next on their foraging trips.

Furthermore, the sparse clones with the longest internodes will *interdigitate* with neighbouring clones more quickly (and thoroughly?); thus they are able to turn the negative effect of clone size on their seed set into a positive one earlier in their life than can the compact clones (HANDEL 1985).

In the populations of self-incompatible clonal plants, the *degree of asexuality* in the breeding system is greatly affected by the *number* and *relative distances* of the clones. Populations consisting of large clones with no or negligible intermixing should possess reduced fertilization rates, most new ramets being produced by asexual means.

Extreme cases are populations consisting of *one clone* only. In such populations, provided the self-incompatibility is strong enough, the breeding system becomes *effectively asexual.*

In spite of profuse flowering in the very dense, elongated populations of *Cardamine amara* (a self-incompatible cruciferous plant with vigorous vegetative reproduction via runners), sexual reproduction is totally suppressed, due to monoclonality (URBANSKA-WORYTKIEWICZ 1980).

In North America, seed set is lacking in most natural populations of *Rorippa sylvestris,* a self-incompatible and rhizomatous species. This has been regarded by MULLIGAN and MUNRO (1984) as indicating that plants within most sites are genetically members of one clone each.

To be exact, the breeding system and its degree of asexuality are not determined solely by the number and reproductive characteristics of the clones but rather by the number and pattern of different *incompatibility genotypes.* In theory, a population may hold essentially fewer incompatibility genotypes than clones. Investigations often reveal, however, a remarkable array of incompatibility alleles constituting polymorphisms in plant populations (CAMPBELL and LAWRENCE 1981, RAMULU 1982, YOKOYAMA and HETHERINGTON 1982, MULCAGHY and MULCAGHY 1985). Hence, in practice, the number of clones and that of incompatibility genotypes may often coincide rather well in populations of clonal plants.

A facultative apomict and an outbreeder spreading predominantly via clonal growth possess breeding systems that at first sight appear very similar. Both of them are *mixed* 'open' and 'closed' breeding systems in the sense of HANDEL (1985), thus providing the population with both long term genetic flexibility and a short term ability to utilize the high immediate fitness of well-adapted genotypes.

It is also worth noticing that on the one hand the *degree of sexual reproduction* in the facultative apomict (MARSHALL and BROWN 1981, BAYER and STEBBINS 1983), and on the other the relative allocation of resources into reproduction versus clonal growth in the clonal outbreeder (DOUGLAS 1981, LOVETT DOUST 1981, SANO and MORISHIMA 1982,

TERAMURA 1983, WATSON 1984, ERIKSSON 1985). are under both genetic and environmental control.

8. Population structure

8.1. Concepts and measures

Clumping, patchiness or aggregation

Natural plant populations are usually not perfectly homogeneous: the *density* of ramets *varies* from place to place in the population (CLARK and EVANS 1954, BARKHAM and HANCE 1982). Thinking in discontinuous terms: one often encounters small scale clumping.

One would also expect clumping to arise in a totally *randomly* (Poisson-)*distributed* population of ramets (ROUGHGARDEN 1979, see later). A population with no clumping would be a totally non-random one and might be achieved only artificially, by planting the ramets in a regular net design. Hence, clumps or patches will usually be found in a population, and the *degree of clumping* (patchiness, level of aggregation etc.) may be classified as being either less than, equal to or *more than random*.

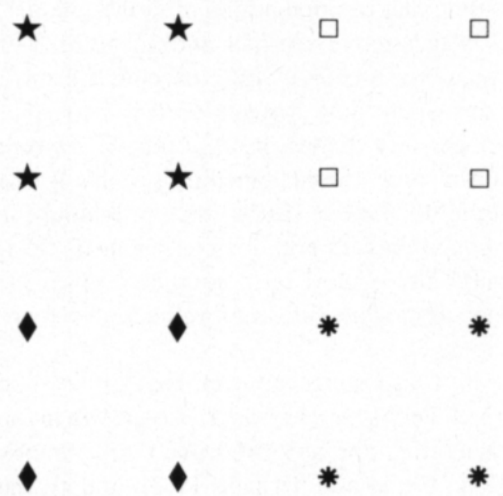

Fig. 2. Strict genetic patchiness underlying an apparently homogeneous (non-patchy) population of ramets. Different symbols indicate the genotype of a ramet.

A population apparently homogenous in respect to the distribution of ramets in space, may still display any degree of patchiness if we take into consideration the *genetic constitution* of each ramet (Fig. 2). Conversely, a population may consist of patches of ramets and still be genetically more or less homogeneous. That is to say, the patches are not genetically differentiated, at least no more so than expected on the basis of a random distribution of ramets into exploitable patches (Fig. 3).

Furthermore, at the level of *ramets* a population may be genetically patchy even though at the level of *genets* (clonal entities) a distribution less than randomly patchy were found (Fig. 2).

In a clonal species, a *disjointed pattern* of clonal entities in space will be displayed as genetic uniformity among ramets within a patch, while ramets from different patches will often belong to different genotypes. Such a pattern might be the result eg. of the dispersal history of a (rather recent) population. In apomicts and in plants with the »guerilla»-type of clonal growth, this kind of genetic patchiness is likely to be only *transient*. However, in clonal plants with the »phalanx»-type of growth, a disjointed distribution of clones may be more common and persistent (cf. HANDEL 1985).

The *phalanx*-type of clonal growth is defined by Clegg (HARPER 1978) as a growth type where a clone forms a tight, uniform mass of invading shoots. Respectively, the *guerilla*-type refers to an intermingling, exploring type of growth.

When the clones become well intermixed, the possibly existing clumps will often be of mixed origin genetically and may no longer contribute greatly to genetic patchiness.

Another probable reason for the clumping of ramets is the *lateral heterogeneity of environments* in a multi-species plant community (HARPER 1977). In fact, environmental heterogeneity often provides a more plausible explanation for patchiness than does growth habit. This is especially the case in plants re-

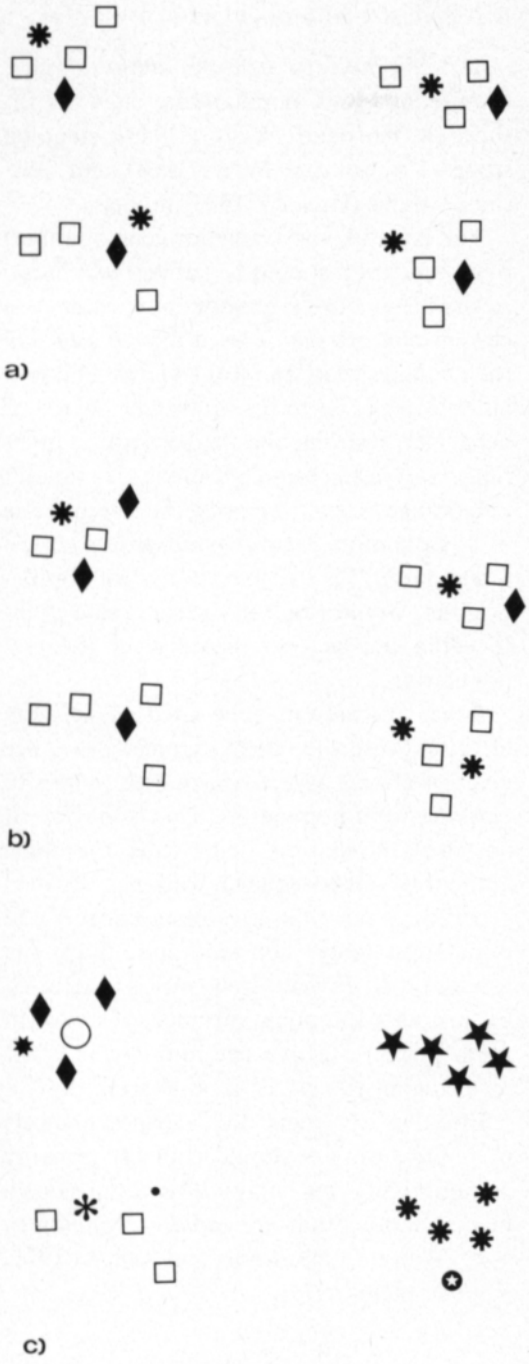

Fig. 3. A patchy population of ramets (different symbols refer to different genotypes): a) genetically totally homogeneous over patches (ie. no genetic differentiation among patches), b) genetically »randomly homogeneous» over patches (ie. »random» genetic differentiation among patches), c) genetically totally non-homogeneous over patches (ie. »full» genetic differentiation among patches).

producing via seed, since seed germination and seedling establishment are more strictly controlled by environment than the establishment of new ramets via clonal growth.

In a theoretical treatise, ROUGHGARDEN (1979) considers patchiness as a function of environment. He defines (p. 372) a *patch* as an area within the species range where the organisms are *more abundant than average.*

Even in a uniform environment, though, organisms are not uniformly distributed. A random distribution *does* lead to patches, but there is *no* preferred patch length. The pattern of variation can be viewed as a wave, and the definition of the *patch length* is simply half the wavelength of the wave pattern (ie. half the distance between adjacent peaks of abundance).

When the environmental *resources fluctuate* in that both the intrinsic rate of increase, r, and the carrying capacity, K, of the population vary with time, then populations will attain an *equilibrium distribution* of population sizes. This should apply on a smaller scale, for the distribution of patch size within a population as well, provided sufficient environmental variation exists therein.

ROUGHGARDEN (1979) points out that the *scale* of the patchiness is set largely by the *dispersal distances* of the organisms involved. The qualitative effect of *increasing* the dispersal distance is to produce *longer* but *less distinct patches* of population abundance. On the other hand, the qualitative effect of decreasing the intrinsic rate of increase, r, is to produce shorter and less distinct patches.

The overall picture that emerges (ROUGHGARDEN 1979) is that by the action of this mechanism, one should find *prominent patchiness* in organisms with both a *high r* and *moderate dispersal.* Furthermore, the pattern of the population is inevitably *more patchy* than the resource distribution.

Genetic structure

The *genotypic spatial structure* of a plant population may be defined, I propose, in

terms of the number, size and form, density and spatial distribution (or degree of intermixing) of the clones. In addition, one might characterize the genotypes and devise measures of their relatedness. Such a definition, however, would only consider a transect in time. In order to extrapolate into the past or the future one also needs information on the breeding system and its local and temporal variations in the population. To acquire all this information for a natural population would be a heavy task. So far, we have fallen short of these ambitions.

Nevertheless, we already know that *most populations* of plants have a genetic (sub)-*structure:* alleles and genotypes are spatially aggregated (HAMRICK and SCHNABEL 1984). How persistent these spatial aggregates usually are is a question still open to debate.
HEDRICK (1983, p. 278) considers a population *'structured'* if it has localized subpopulations in which there is genetic drift, if mating is not random throughout the population, or if migration does not have equal probabilities throughout the population.

The general conclusion of LEVIN and KERSTER (1974) was that in plants most *gene flow* is *restricted* in space. This idea stood out in contrast to the evolutionary and ecological theories prevailing at that time. One of the consequences of this restriction should be *genetically non-random pollination.*
HAMRICK and SCHNABEL (1984), however, call into question the general conclusion that in plant populations neighbourhood sizes should be small. They consider that this generalization is based on vague information; data on gene flow are few and largely indirect, usually resting upon *unrealistic assumptions.*

While populations often *deviate* from the ideal assumptions (eg. of panmixis), there have been efforts to define various *'effective'* measures. An effective measure relates the characteristic of a real population to that of an ideal one. The most widely applicable and serviceable concepts have proved to be the effective size of a population and the size of a neighbourhood.

Effective size of a population

The *effective size of a population* applies to discontinuous populations, such as eg. those in the island (WRIGHT 1943), stepping stone (KIMURA and WEISS 1964) and continent-island (HEDRICK 1983) models.

The effective size (ramet or genet number) of a population should be defined *in relation to* the behaviour or quantitative degree of a chosen *characteristic.* Its effective size will then be the size of an ideal (reference) population giving rise to an equivalent degree of behaviour regarding the characteristic in question. To give an example, from the standpoint of a change in heterozygosity, the effective size of a population *('effective inbreeding size* of a population') is the size of an ideal population that would result in the same rate of inbreeding as the rate recorded in the real population.

Other features may be used in defining effective sizes, too. Gene frequency variance gives rise to an *'effective size* with respect to *variance'* of a population. This is the size of an ideal population that yields the same amount of gene frequency variance between generations as that prevailing in the real population under consideration. Since the random drift in gene frequencies is affected by just this sampling variance, a synonym used for the effective size in question is the *'effective drift size'* of a population.

Effective 'inbreeding' and 'variance' numbers of population size should coincide in many circumstances but may *differ* enormously in populations that are *rapidly changing* in size. (WRIGHT 1969, CROW and KIMURA 1970, ROUGHGARDEN 1979).

Local measures

In large, continuous populations, and also in smaller though still structured populations, local measures (indices) will be needed. This will become apparent during the following considerations.

Around any ramet, let us construct a circle

A_r with a radius r. Then, on average, either of the parents of the central ramet will be included within the surrounding circle with a probability p_r. Let us choose the radius r appropriately large, so that any parent of the ramets near the centre of the circle will only rarely fall outside the encompassed area.

Then the genetic constitution of next generation's ramets near the centre of the circle A_r should be largely determined by the subpopulation of the present generation's ramets inside the circle. Therefore it proves useful to introduce 'local' indices pertinent to parts of populations, eg. the number of ramets or genets inhabiting the defined circle, the area of the circle, 'local F' (TIGERSTEDT et al. 1982) etc.

Effective size of a neighbourhood

In a continuous population, a measure analogous to the effective size (number) of a population is the *effective size of a neighbourhood*.

WRIGHT (1946) defines a *'neighborhood'* as that part of a continuous population within which the parents of individuals born near the center may be treated as if drawn at random.

For a two-dimensional population WRIGHT (1969), in effect, equates 'neighbourhood area' to a circle of radius 2σ, where σ = (axial) standard deviation of the distance between a parent and its offspring. Then the 'effective size of a neighbourhood' will be the otherwise effective number of individuals in the respective neighbourhood area (WRIGHT 1969, p. 303).

Provided the distribution of the axial dispersion distances is a normal one, it will be totally determined by the first two moments, ie. the mean and variance. The axial distribution will always have a mean of zero. Hence, all we need in order to describe the areal extent of the neighbourhood is the variance, σ^2_{axial}, of the axial dispersal distances.

Utilizing this parameter we are now able to define the radius of a circle encompassing a pre-determined proportion of the parents of

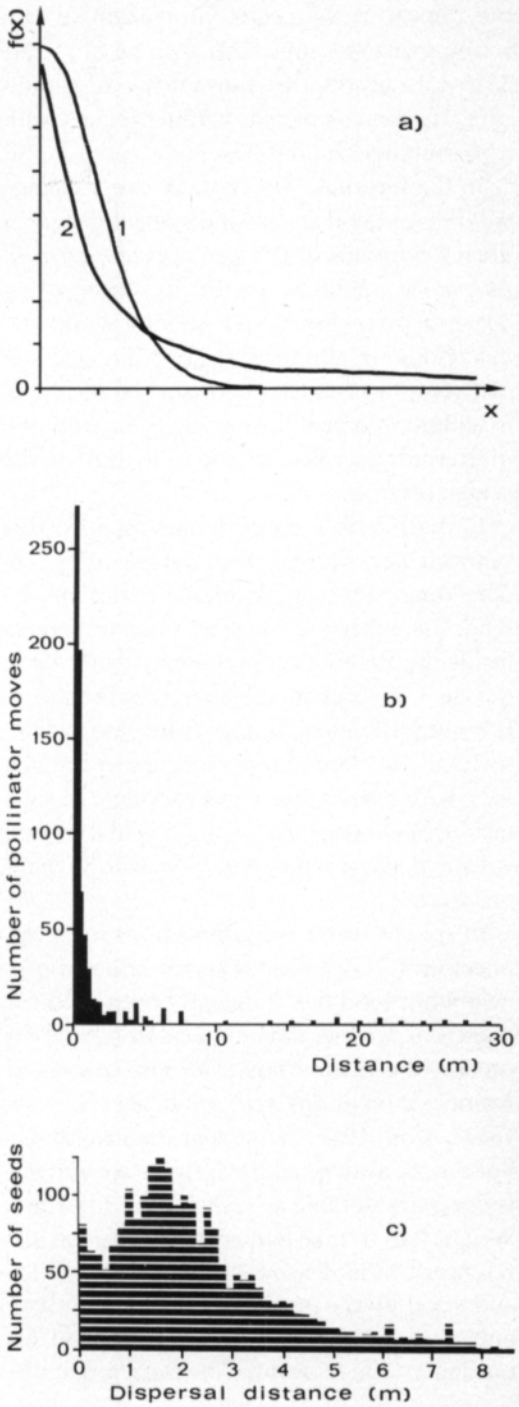

Fig. 4. Deviations from normality in dispersal distributions: a) the leptocurtic curve (2) characteristically has a narrower peak and a broader tail than the normal curve (1), b) leptocurtic distribution of pollinator flight distances in populations of *Phlox pilosa* (After KERSTER and LEVIN 1968), c) axial seed dispersal distances of *Liatris aspera* (After LEVIN and KERSTER 1969 b).

the ramets in the centre. For example, describing around any ramet a circle of radius 2σ (while postulating normality) we should catch the ramet's parents within the circle with a probability of 86.5 %.

In the rationale presented above a change will be needed if the axial dispersal distances are not normally distributed. *Deviations from normality* might be expected, since pollen dispersal often displays a markedly leptocurtic behaviour. In addition, the two-dimensional distribution of axial seed dispersal distances is seldom maximal at the origin; instead one often finds a »hole» instead of a »hill» in the centre (Fig. 4).

If the distribution of axial dispersal distances is non-normal, then the use of σ_{axial} in determining the neighbourhood radius may be inadequate. That is, the proportion of parents inside the circle of radius 2σ may differ from the 86.5 % presented above. Furthermore, this proportion may change from case to case, with the distribution remaining undetermined even with a fixed mean and variance. In such instances *comparison* of the neighbourhood values of *different populations* will be *inappropriate.*

In spite of certain complications in its application (Crawford 1984), the concept of a neighbourhood has frequently been used for plants, as well as for animals. In plants, estimates of neighbourhood size need to account for migration at *different life stages* (Hedrick 1983). Dijk (1987) states that the neighbourhood size, as defined by Wright (see above), is *not* quite suitable as such for use in plants. Wright fails to take into account the great differences in the dispersal of eg. seeds, pollen and vegetatively produced ramets, and uses only one (overall) dispersal variance in his rationale, which results in conceptual difficulties.

In plants, the probability of finding a parent within a circle will be *different for male and female* parents. Hence, concepts such as the size of a neighbourhood and isolation by distance should be kept strictly apart. The size of a neighbourhood (or *'local effective population size',* as renamed by Dijk 1987) will be largely determined by the smallest dispersal parameter (ie. the dispersal component with the smallest range of dispersion). Isolation by distance, on the contrary, will be governed by the largest parameter (ie. the dispersal component with the longest range).

Thus, Dijk (1987) proposes a more straightforward measure for *isolation by distance,* ie. the *'mean gene transport per generation* (M)'. This measure will give the mean distance of a parent from its offspring. For wind-pollinated plants,

$$(1) \quad M = \sqrt{\tfrac{1}{2}\pi\,(\sigma^2_s + \tfrac{1}{2}t\sigma^2_p)}\ ,$$

where t = proportion of cross-pollination.

Effects of clonality

In the populations of clonal plants, each mature ramet can often produce new ramets asexually as well as sexually. Furthermore, there is usually an overlapping of generations. Both of these circumstances lead to a *gradual* rather than to a sudden attainment of Hardy—Weinberg proportions (Crow and Kimura 1970). Hence, the persistence of old clones constitutes a(n extra) *memory* not only of gene, but also of genotype frequencies over generations.

Clonality results in *genotypic redundancy* (at the level of ramets). Thus it reduces the effective population size (Wright 1969) and accordingly, also the genetic variance. This reduction should *diminish* the *response to selection.* In part, though, this consequence will be counterbalanced by the fact that mass selection should be more effective in a population consisting of a mixture of clones, in the sense that it will there act on the entire genetic variance instead of only on its additive component (Wright 1977).

Furthermore, clonality effectively *extends* the age of genets and thus their *generation time.* The »effective» generation span is inversely proportional to the percentage of sexual progeny.

Hence, the populations of (facultatively)

clonal plants should as a rule respond more slowly to selection than purely sexual populations (LEVIN and KERSTER 1971, LEVIN and WILSON 1978).

In facultative apomicts and in most plants with clonal growth, there is usually some gene flow via pollen, while in the so called (almost) obligate apomicts there should, of course, be practically no gene flow via the pollen.

Paradoxically, instead of decreasing the size of the breeding unit, clonality should increase it (LEVIN and KERSTER 1971). This results from the fact that, due to self-incompatibility or dioecy, strict cross-fertilization prevails among the clonal plants.

As the degree of clonality (ie. proportion of ramets asexual in origin) increases, relatively less compatible pollen is found near a flower. Simultaneously, the origin of the effective pollen will, on average, be more distant. Thus, clone formation will usually *expand* both *neighbourhood size* and area. Underlying this deduction, however, is the implicit assumption that the clones are not intermixed.

Potential for differentiation

Regarding selection and migration effects, LEVIN and KERSTER (1971) conclude that, due to increased neighbourhood size, the potential for selective differentiation among local populations is *retarded* by clonality, in spite of the fact that clonality provides the best means of perpetuating superior genotypes.

Nevertheless they generalize that whatever the actual movement of pollen and seeds in natural and artificial plant populations, it will be sufficiently restricted for *natural selection* to override it. Accordingly they regard it as likely that most species of seed plants are composed of multiple isolated or semi-isolated breeding units of various sizes and areas, each of which may adapt to local environmental conditions (LEVIN and KERSTER 1974).

Random differentiation of populations may also occur, provided the effective population size or the effective size of a neighbourhood is small enough. The effect of finite population size is to cause allelic frequencies in the subpopulations to drift apart, whereas migration between the subpopulations serves to counteract this effect and to keep their frequencies similar (HEDRICK 1983).

WRIGHT (1943, 1946) summarizes that if the *effective breeding population* of a neighbourhood were only 20, there would be great differentiation among neighbourhoods. When the effective size of a neighbourhood is 200, there should be still a moderate amount of differentiation among the neighbourhoods, while with an effective size of 1000 there would, in effect, be universal panmixis.

The effective size over a period of time is the *harmonic mean* of the values of succeeding generations. This holds both for 'inbreeding' and for 'variance' effective size (WRIGHT 1969, CROW and KIMURA 1970).

As can be seen from the formula (ROUGHGARDEN 1979, p. 68; his script carries a mistake corrected here):

$$(2) \quad N_e = \frac{k}{1/N_{e1} + 1/N_{e2} + \ldots + 1/N_{ek}},$$

the effective size over generations is very sensitive to the exceptionally small values which may sometimes occur. Thus, when the population size *fluctuates,* its long-term effective size will be largely determined by the *smallest sizes* (bottlenecks) occurring in the sequence.

In *short-lived plants,* considerable fluctuations in population size often occur. Examples might be found among the most intensively r-selected species, many of which are apomictic. On the other hand, the seeds of weedy species are often very long-lived. An accumulated *seed bank* would reduce the probability of genetic drift, keeping the actual size of the population much greater and less variable over time than is the apparent one (ie. that based on only the numbers of grown-up ramets present).

In addition, a seed bank constitutes a migration from the past and thus tends to maintain genetic polymorphism in the population. Hence it will retard the response to selection,

too (LEVIN and WILSON 1978, LEVIN and KERSTER 1971).

In *long-lived plants* with *clonal growth,* the population size is usually much more stable over time, resulting in a relatively higher effective population size. A further, however small, gain in effective population size is caused by the *overlapping of generations* commonly met in such populations.

Furthermore, as well as the relatively short-lived plants mentioned in Chapter 6 above, some long-lived plants have long-term seed banks, too (RABOTNOV 1978). In rhizomatous plants, banks of dormant rhizome buds should also buffer the population against occasional drops in size.

Hence, in spite of the genotypic redundancy, expressed as a small effective population size with a large number of ramets, the role of random drift may be of secondary importance in the clonal plants. This is due to the several mechanisms, presented above, which keep the gene frequency variance with time moderate in clonal plants. Thus, while the *gene flow in plants* might be overridden by natural selection (LEVIN and KERSTER 1974), it still may be strong enough to counteract the effect of random genetic drift.

The generalizations presented above are open to criticism, since information on the real situation prevailing in the populations of clonal plants is still scattered and incomplete. Furthermore, many potentially important factors, eg. mutation and somaclonal variation (see Chapter 9) have been left without concern here.

Parent-offspring dispersal variance σ^2

According to CRAWFORD (1984), estimates of neighbourhood size up until that time had been incorrect, due to the use of an incorrect method of obtaining the parent-offspring dispersal variance. None of the three methods commonly in use for combining the two components, dispersal via pollen and via seed, to yield the parent-offspring dispersal variance, are correct. The published estimates for neighbourhood areas (ie. circles of radius 2σ) may vary from half to twice the correct values which, according to CRAWFORD (1984), should be based on the value of σ in the expression

$$(3) \quad \sigma^2 = \tfrac{1}{2}\sigma^2_p + \sigma^2_s,$$

where p refers to 'pollen' and s to 'seed'. The value of the parent-offspring dispersal variance σ^2 can be *estimated* by substituting into (3) estimates of variances for the respective population parameters:

$$(3') \quad \hat{\sigma}^2 = \tfrac{1}{2}\hat{\sigma}^2_p + \hat{\sigma}^2_s.$$

One should notice that in these formulas, all the dispersal distances are expressed as *axial* ones, ie. carrying negative as well as positive values (CRAWFORD 1984).

Regarding clonal plants it is, however, insufficient to consider only their sexual dispersion, ie. the dispersion via pollen and seed. Wandering via ramets, ie. *clonal migration,* should also be taken into consideration.

For this purpose, I shall consider a randomly chosen ramet in the population. Next I shall construct (see Appendix) a random variable, X(g) to represent the 'dispersal distance'. This is the distance between the ramet under consideration (generation t) and the ramet it originated from (generation t—1). In an asexual case, we must take as the originating ramet the youngest one in the vegetative sequence which was mature at the time of the previous *sexual* generation, t—1. Thus, the time scale will be pertinent to sexual generations.

Hence, D^2 [X(g)], the variance of X(g) (worked out in Appendix) will give the variance of offspring-parent axial dispersal distances, denoted by σ^2:

$$(4) \quad \sigma^2 = (1—a) \cdot (\tfrac{1}{2}\sigma^2_p + \sigma^2_s) + a \cdot \sigma^2_c.$$

Here σ^2_p, σ^2_s and σ^2_c, respectively, are the axial dispersal variances for pollen, seed and for clonal dispersal (on a sexual time scale), while a is the proportion of asexually produced ramets in the ramet population.

The consideration above may be *generalized*

further by supposing that there exist *n* different kinds of asexual dispersion in the population. For example, a plant may spread simultaneously via *sexual seed,* via *apomictic seed* and via *rhizomes.*

Though somewhat more complicated than those used in deriving expression (4), the considerations required to cope with the more general assumptions will still be fairly straightforward. They are, however, by-passed here and only the final result is presented:

$$(5)\quad \sigma^2 = (1-\sum_{i=1}^{n} a_i)\cdot(\tfrac{1}{2}\sigma^2_p + \sigma^2_s) + \sum_{i=1}^{n} a_i \cdot \sigma^2_{ci}.$$

In applications, one should notice that the expression refers to ramets, not genets. Therefore, densities etc. should also be expressed on the appropriate basis.

CRAWFORD's (1984) result (3) may be derived from this formula as a *special case* with no clonal dispersion ($a_i = 0$ for all $i = 1, \ldots, n$).

This general expression (5) may be applied eg. to a plant population with both *facultatively apomictic* seeds and *clonal growth;* examples might be found eg. in blackberries *(Rubus,* subgenus *Eubatus):*

$$(6)\quad \sigma^2 = (1-a_{cs}-a_{cg})\cdot(\tfrac{1}{2}\sigma^2_p + \sigma^2_s) + a_{cs}\cdot\sigma^2_{cs} + a_{cg}\cdot\sigma^2_{cg}.$$

Supposing that the dispersion of apomictic seeds does not differ from the dispersion of sexual seeds, ie. $\sigma^2_{cs} = \sigma^2_s$, this expression will reduce to

$$(6')\quad \sigma^2 = \tfrac{1}{2}(1-a_{cs}-a_{cg})\cdot\sigma^2_p + (1-a_{cg})\cdot\sigma^2_s + a_{cg}\cdot\sigma^2_{cg},$$

where the index c_s refers to apomictic seed and the index c_g to clonal growth.

By substituting zero for a_{cg} in expression (6'), we arrive at

$$(4')\quad \sigma^2 = \tfrac{1}{2}(1-a_{cs})\cdot\sigma^2_p + \sigma^2_s,$$

which is valid for a population having both *sexual* and clonal *(apomictic) seeds.*

Similarly, by substituting zero for a_{cs} in (6') we can arrive at the expression

$$(4'')\quad \sigma^2 = (1-a_{cg})\cdot(\tfrac{1}{2}\sigma^2_p + \sigma^2_s) + a_{cg}\cdot\sigma^2_{cg},$$

pertinent for a population equipped only with *sexual seeds* and *clonal growth.*

Dispersal variance and the degree of clonality

Let us examine the effect of the degree of clonality, a, upon the axial dispersal variance, σ^2.

First, it seems reasonable to postulate that the level of a (ie. the proportion of ramets asexual in origin) has no influence on the variance of axial *clonal dispersal distances,* σ^2_c.

Regarding σ^2_s, the distribution of *dispersal distances of sexual seeds* is perhaps not essentially affected by the degree of clonality in the population.

Secondary effects are not difficult to imagine, however. For instance, animals foraging for berries will usually be only marginally interested in populations with few berries, and accordingly fewer seeds will be transported by animals in such populations. This in turn may affect the distribution of dispersal distances of seeds.

Nonetheless, a high degree of clonality is not necessarily associated with a low seed set.

In self-compatible plants, seeds will arise in purely uniclonal patches as well, though self-compatibility is not common among clonal species (see above). In the populations of self-incompatible plants, a high degree of clonality (ie. high proportion of clonal ramets) may not be the final result of a low seed set, in fact seeds may be produced in abundance.

Instead, the level of clonality may be determined principally by the relative abilities of the sexually and the clonally emerging ramets to establish themselves. This should hold especially in certain late successional species, in which migration via seed may remain only a potential means of dispersal for decades, since the seeds accumulate into a bank of dormant seed. A high level of competition prevails in ecosystems dominated by K-strategists, and the seeds are prevented from germinating successfully. Viable seedlings appear only as a consequence of an occasional disturbance yielding free ground available for establishment. This slows down the effective migration rate via seed, so that the overwhelmingly predominant mode of migration of zygotes in such populations will occur via clonal growth.

In the following, I shall *ignore* secondary effects and postulate that the level of clonality does *not* have any effect on σ^2_s.

In *self-compatible* plants, a, the degree of clonality, should exert no influence on σ^2_p, the variance of the axial dispersal distances of successful pollen. In *self-incompatible* plants, on the contrary, the *dispersal distance of successful pollen* should on average *increase* with increasing degree of clonality (LEVIN and KERSTER 1971, see above); ie. $d(\sigma^2_p)/d(a) > 0$.

We are now in a position to study the *behaviour of* σ^2 as a function of the degree of clonality, a. Postulating that $d(\sigma^2_s)/d(a) = 0 = d(\sigma^2_c)/d(a)$, and taking derivatives in (4) we shall obtain for *self-incompatible* plants:

$$(7) \quad \frac{d(\sigma^2)}{d(a)} = \sigma^2_c - (\tfrac{1}{2}\sigma^2_p + \sigma^2_s) + \tfrac{1}{2}(1-a)\frac{d(\sigma^2_p)}{d(a)} .$$

This expression holds for populations with sexual seeds and with only one means of clonal dispersal.

Respectively, (4') yields

$$(7') \quad \frac{d(\sigma^2)}{d(a_{cs})} = \tfrac{1}{2} \cdot [(1-a_{cs}) \cdot \frac{d(\sigma^2_p)}{d(a_{cs})} - \sigma^2_p],$$

which will be valid for populations with both sexual and clonal (apomictic) seeds.

Furthermore, (4'') yields

$$(7'') \quad \frac{d(\sigma^2)}{d(a_{cg})} = \sigma^2_{cg} - (\tfrac{1}{2}\sigma^2_p + \sigma^2_s) + \tfrac{1}{2}(1-a_{cg}) \cdot \frac{d(\sigma^2_p)}{d(a_{cg})} ,$$

which holds for populations with sexual seeds and clonal growth.

Regarding *self-compatible* plants, we also supposed above that $d(\sigma^2_p)/d(a) = 0$. Hence (cf. 7'), for a population of facultatively apomictic self-compatible plants, ie. for a population of self-compatible plants with both sexual and clonal (apomictic) seeds, it should follow that

$$(8) \quad \frac{d(\sigma^2)}{d(a_{cs})} = -\tfrac{1}{2}\sigma^2_p < 0.$$

Respectively, for self-compatible plants with sexual seeds and clonal growth:

$$(8') \quad \frac{d(\sigma^2)}{d(a_{cg})} = \sigma^2_{cg} - (\tfrac{1}{2}\sigma^2_p + \sigma^2_s) < 0 \quad \text{if, and only if } \sigma^2_c < \tfrac{1}{2}\sigma^2_p + \sigma^2_s.$$

Clonality and patchiness

As pointed out previously, the shorter the (axial) dispersal σ^2, the less gene flow will there be between patches, the smaller will be the neighbourhoods and the more possibilities will be found for genetic differentiation among neighbourhoods. In short: smaller σ^2 values mean more genetic patchiness.

Considering (8), in *self-compatible apomicts* the axial dispersal variance, σ^2, should decrease whenever the degree of clonality, a_{cs}, increases. In other words, a *rise in clonality* will mean *more* genetic patchiness.

The situation is not so straightforward in *self-compatible* plants with *clonal growth*. From formula (8') we can see that the total parent-offspring dispersal (measured via σ^2, the axial variance of a gamete-equivalent) will be a decreasing function of the degree of clonality (a_{cg}) only in populations where the clonal dispersal (given by the axial variance σ^2_c) is shorter than the sexual dispersal (given by $\tfrac{1}{2}\sigma^2_p + \sigma^2_s$). That is, a rise in clonality will result in an increase in genetic patchiness only if clonal dispersal is *shorter-ranged* than sexual dispersal.

In practice, such a situation might occur rather often. Depending on the foraging habits of pollinating insects, or on plant height and wind velocities, and on the dispersal mechanisms of seeds, gene flow per generation via the wandering of genets by eg. runners or rhizomes is often likely to be more tightly restricted in space than the flow mediated by pollen and seeds.

If, on the contrary, clonal dispersal were usually further ranging than sexual dispersal,

increasing clonality would increase the parent-offspring dispersal distances and the outcome would be less genetic patchiness.

Considering *self-incompatible* plants with both sexual and clonal seeds, expression (7') reveals that eg.

$d(\sigma^2)/d(a_{cs}) < 0$ if, and only if
$d(\sigma^2_p)/d(a_{cs}) < \sigma^2_p/(1—a_{cs})$.

As a rule, though, differential inequalities such as the one above do not, unfortunately, have any general solution. Referring directly to (4'), we can still see that σ^2 will behave as a function of clonality exactly as $(1—a_{cs}) \cdot \sigma^2_p$ does; thus $d(\sigma^2)/d(a_{cs}) < 0$ for all a_{cs} values if, and only if $(1—a_{cs}) \cdot \sigma^2_p$ is a monotonously decreasing function of a_{cs}. Therefore, only if the rate of increase of σ^2_p with clonality is sufficiently slow may an increase in clonality cause an increase in the degree of genetic patchiness as well. At least if the clones are well intermingled, such a slow growth of σ^2_p with clonality may occur.

In the case of self-incompatible apomicts, without more detailed information about the rate of increase of σ^2_p as a function of clonality, we can, however, draw *no general conclusions* about how the degree of clonality affects the amount of genetic patchiness in the population.

If we consider *self-incompatible* plants with *clonal growth,* the situation is still more complicated. Compared to (4'), formula (4'') incorporates an extra term of interest $a_{cg} \cdot (\sigma^2_{cg} — \sigma^2_s)$. If $\sigma^2_{cg} < \sigma^2_s$, this extra term will decrease monotonously with clonality. Hence, σ^2 too will now have a greater tendency to decrease than in (4'). Therefore, in self-incompatible plants with clonal growth, an increase in the degree of clonality should have a *greater tendency* than in self-incompatible apomicts to cause an *increase in genetic patchiness,* rather than a decrease.

This does not perhaps always accord with a statement by LEVIN and KERSTER (1971), presented above, that the potential for selective differentiation among local populations is likely to be retarded by clonality.

Taken altogether, the arguments above predict that the populations of ramets in *self-compatible clonal* plant species may display even *more patchiness* in genotype and allele frequencies than is usually met in plants. That is to say, genetic substructuring, peculiar to plant populations, may be still further accentuated in some clonal plant species. In *self-incompatible clonal* plants, however, which apparently comprise the clear majority of clonal plants, the *opposite* may (or may not) tend to be true.

Some measures of diversity

PEET (1974) complains that, despite considerable interest in the subject, no generally accepted *definition* of diversity has emerged. HURLBERT (1971) even suggested abandoning the term because of the multiplicity of meanings and interpretations attached to it.

Diversity, as with so many other ecological concepts, has actually been well defined only *by virtue of the indices* used to measure it. Hence there have been almost as many definitions in vogue as there are different indices. This lack of uniformity makes for difficulties in the clear exposition of ideas and hypotheses, as PEET (1974) points out.

A. Richness

Species *richness* (MCINTOSH 1967) is a frequently used, fundamental concept. In essence it indicates the number of species in a community.

In our context, since we are comparing populations within a single plant species, the units in question will not be species but some substructures below the population level, say genets or ramets. Thus, instead of 'species richness' we should use terms such as eg. *'genet richness'*.

Unfortunately, the various indices of species richness are highly dependent on *sample size* (PEET 1974). When we do not know how the number of species in the sample will rise as a function of sample size, then the number of species in the sampling universe (community) is *impossible to estimate.* Different

models concerning the form of this relationship will yield different indices (eg. FISHER et al. 1943, PRESTON 1948, 1960, 1962). We may test the relevance of the model, and accordingly of the index, in the community by repeating the samplings with varying sample sizes.

One way of trying to circumvent the problem has been to use direct *species counts* in samples. Comparison of two communities will require equal sample sizes in each. *Constant sample size* (eg. 1000) is used in the 'rarefaction method' of SANDERS (1968), corrected by HURLBERT (1971).

Unfortunately, however, as PEET (1974) demonstrates, there exists no proper basis for comparing the richness of a series of communities by means of a single index if the communities under consideration differ too widely in their species-individual relationship. If the numbers or relative abundance of species differ too much between communities, a comparison of communities based on direct counts may give entirely contradictory results depending on the sample size being chosen.

B. Equitability or evenness

While richness measures the number of species present in the community, it tells us nothing about how equally individual species are represented in terms of numerical abundance, ie. how similar are their so called importances in the community. There exist indices, however, which measure the *evenness among species* of the numbers of individuals in the community. Some of the indices relate the evenness to a specific standard such as the broken-stick model of MACARTHUR (1957); such indices are called *equitability* indices by PEET (1974). These indices of evenness or equitability may be utilized at any level of community hierarchy, eg. to quantify the evenness of ramet numbers of different clones in a population.

Various indices of evenness are frequently used in the literature (eg. LYMAN and ELLSTRAND 1984, KORPELAINEN 1986), without too much concern for the weaknesses in their statistical bases. As PEET (1974) and PIELOU (1977) show, evenness values will be *impossible to estimate* unless the *total number of species* in the community is known.

Many researchers have tried to circumvent the difficulty by substituting the number of species *in the sample* for the number in the community. This will, however, cause severe difficulties. Firstly, since the number of species is always underestimated, equitability will always be overestimated. Secondly, equitability indices are *extremely sensitive* to a change in the *number of species* in the community. In an example, PEET (1974) shows that a minor change from a community with three species (numbering 500, 300 and 200 individuals) to one with four species (with 500, 299, 200 and 1 individuals) will radically (by anything from 10 % to 300 %) alter the values of the different equitability indices.

Since observations on *rare species* are highly susceptible to error, such small, and indeed considerably larger differences in species numbers between samples will occur frequently. Such variation in the number of species between different samples could be avoided only if the underlying community were very even with respect to the numbers of individuals in different species and their spatial distribution in the community. Such »super-even» communities are, however, very rare, and can be identified as such only after we have censused the whole community.

If the community is small enough to be *censused in its entirety,* then there exist relevant indices of equitability (evenness). Their value is *exactly determinable* from the censused records, and values for different communities will then be comparable (PIELOU 1977).

One should also note, as PIELOU (1977) points out, that it is rarely legitimate to treat a censused collection as a *sample* from a larger (conceptually infinite) parent community. Such an approach is permissible only if the *boundaries* of the postulated parent community can be precisely specified and if the collection at hand is a truly random sample from it. This is seldom the case. The separate

sampling units (quadrats, say) are not, as a rule, *randomly* or *independently* drawn from the parent community. On the contrary, due to the universal *patchiness* of ecological communities, the sampling units are usually closely interdependent. Thus the diversity of the contents of a single small sampling unit is nearly always much *less* than that of the community from which it is taken.

Hence, only trial and error can show *how many sampling units* must be drawn from the community to represent it adequately. Therefore PIELOU (1977) suggests that usually a *censused collection* is best treated as an *entity in its own right*. If we follow her suggestion, we should determine evenness values for such collections, instead of estimating evenness values for their respective reference populations. Although different large populations are still excluded from the comparisons, these various *collections can than be compared* with regard to evenness.

For *fully censused collections,* a convenient measure of evenness will be (HURLBERT 1971, PIELOU 1977)

$$(9) \quad V = \frac{H - H_{min}}{H_{max} - H_{min}} .$$

In this formula, BRILLOUIN's (1962) function $H = (1/N) \log (N!/(N_1!N_2! \ldots N_s!))$ has been scaled with respect to the maximum and minimum possible values it could attain for a collection of the specified total number of individuals (N) and of species (s) in the collection.

Since V pertains to a fully censused collection, it is exact, ie. free of sampling error.

The values for H_{min} and H_{max} are

$$(10) \quad H_{max} = \frac{1}{N} \cdot \log \frac{N!}{X!^{s-r} \cdot Y!^{r}}, \text{ and}$$

$$H_{min} = \frac{1}{N} \cdot \log \frac{N!}{1!^{s-1} \cdot (N - s + 1)!} ,$$

where $X = [N/s]$ is the integer part of N/s, $Y = X + 1$, and $N = sX + r$.

C. Heterogeneity or diversity indices

There is a third category of indices, which measure *simultaneously* the confounded level of richness and evenness in the community. These indices are called by PEET (1974) *heterogeneity* indices and by PIELOU (1977) *diversity* indices. The diversity measure depends on two independent properties of a collection; thus a collection with few species but high evenness could display the same amount of diversity as another collection with many species but low evenness.

According to PEET (1974), an infinite array of such heterogeneity indices could be constructed. Among them, PIELOU (1977) prefers two *information indices* of diversity, due to their property of additivity. Accordingly, if the community under study is subdivisible in any way, the diversity index can be subdivided into appropriate *additive components.* Due to their versatility, these additive indices are ecologically much more useful than the others which do not share this property. They can be utilized eg. to study at what level in the taxonomic hierarchy diversity is most strongly manifested.

Shannon's H'

The first of the indices suggested by PIELOU (1977), applicable to large, sampled (not totally censused) populations, is the information function *H' of Shannon* (SHANNON and WEAVER 1949)

$$(11) \quad H' = -\sum_j p_j \cdot \log p_j .$$

Its maximum likelihood estimator will be

$$(11') \quad \hat{H}' = -\sum_j \frac{N_j}{N} \cdot \log \left(\frac{N_j}{N}\right) .$$

This estimator is, however, *biased.* If natural logarithms are used, it underestimates the true community value of H' by an amount approximately equal to $s^*/(2N)$, where s^* is the number of species in the community. Thus no correction can be made for the bias unless s^* is known, which it rarely is.

The information function of Shannon, H', was originally designed to *measure uncertainty.* If someone picks at random a ramet from a

community with many species present, he will *a priori* be uncertain which species it will belong to. On the other hand, dealing with the meaning of the term 'diversity' PIELOU (1977) regards it as intuitively acceptable to think that the greater the community's diversity, the greater should be our uncertainty in the game of »guess the ramet». Thus she considers it reasonable to *equate diversity with uncertainty* and use the same measure for both.

Brillouin's H

The other of the indices preferred by PIELOU (1977) is *Brillouin's function H* (BRILLOUIN 1962, see above), applicable to small, *totally censused* communities:

$$(12) \quad H = \frac{1}{N} \cdot \log \frac{N!}{N_1!N_2!\ldots N_s!} \ .$$

One should notice that this measure will be *determined,* not estimated, ie. it is free of sampling error. Secondly, H depends on *community size.* Thus if A and B are two communities with identical numbers and relative abundances of species, then the one with more individuals, say A, will have the higher value of H, ie. $H_A > H_B$. However, except for very small communities, the discrepancy is negligible.

Brilloun's index is analogous to Shannon's H'. These two indices are *closely related* to each other, since if we allow the size of the community to tend towards infinity, in such a way that the minimum number of individuals in a species increases without limit, then the two indices will converge (PIELOU 1977).

Estimating H'

PIELOU (1977) utilizes a sequence of Brillouin's H values to construct an *estimator of H',* superior to the biased one presented above. In addition to bias, another difficulty in estimation is that because of the universal patchiness of ecological communities, the individuals in separate sampling units (quadrats) are usually not independent but closely dependent.

The essence of the method of estimation will be briefly described here. Suppose a sample of n quadrats has been examined and their contents listed. These quadrats are now to be taken one by one, in a randomized order, and added to an accumulating pool of quadrats. The purpose of this procedure is to obtain a sequence of subcollections, each containing one quadrat more than the previous one. The Brillouin index H of these subcollections is monitored graphically until there is no further obvious tendency for H values to increase as a function of the number of quadrats, k (see Fig. 5).

Suppose we have reached this critical value of k and denote it by t. For $k = t + 1, t + 2, \ldots, n$ we shall calculate the values of

$h_k = (M_kH_k - M_{k-1}H_{k-1})/(M_k - M_{k-1})$,

where $H_k = (1/M_k) \log (M_k!/(M_{k1}!\ldots M_{ks}!))$ is the Brillouin index of the subcollection of k quadrats, s is the number of species and M_k the total number of individuals in the respective subcollection.

It can be shown that an *estimate of H'* is given by

$$(11'') \quad \tilde{H}' = \frac{1}{n-t} \cdot \Sigma\, h_k = \bar{h} \ ,$$

and the sampling variance of this estimate is estimated by

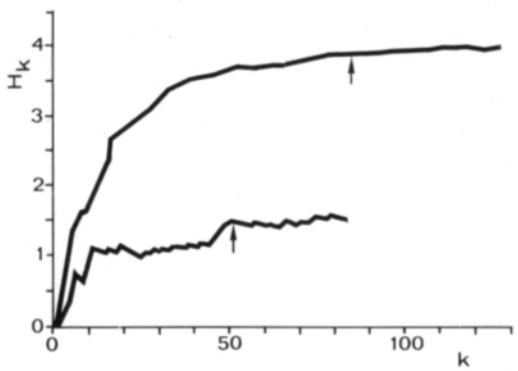

Fig. 5. Plots of Brillouin's index (H_k) versus sample size (k) for communities of amphibians and reptiles in moist tropical forest in Equador (upper curve) and dry evergreen forest in Thailand (lower curve). The arrows show the chosen positions of k = t to represent where steady values of H_k start. (Redrawn from PIELOU 1977).

$$(11''') \quad \text{var}(\tilde{H}') = \frac{1}{n(n-1)} \cdot [\Sigma h^2_k - n(\bar{h})^2] \,,$$

where the summations are to be taken over $k = t + 1$ to n.

Derivations from Simpson's C

One of the most commonly used indices utilized in the construction of various diversity indices is that of SIMPSON (1949). His *index of concentration* or, as it is now more commonly called, of *dominance,* measures the probability that two individuals selected at random from a sample will belong to the same species.

If the *probability* that both of the individuals belong to the *same species* is high, then it is reasonable to say that the community exhibits a high degree of concentration (PIELOU 1977). The probability itself may be used as an index of concentration, usually denoted by C.

For a community of *finite size,*

$$(13) \quad C = \sum_j \frac{N_j(N_j-1)}{N(N-1)} \,,$$

where the summation is made over all species ($j = 1,\ldots,s$) represented in the community and N_j denotes the number of individuals in species j; $\Sigma N_i = N$ (PIELOU 1977).

For fully censused communities, the index of concentration, C, is *determinable exactly,* without sampling error.

In *infinitely large* communities, the true value of C will be

$$(14) \quad C = \sum_j p^2_j \,.$$

On the basis of sampling we may estimate C; and unbiased estimator is given by

$$(14') \quad \tilde{C} = \sum_j \frac{N_j(N_j-1)}{N(N-1)} \,.$$

This expression is, however, applicable only if the sample is a truly *random* sample of the community's individuals (see above). Furthermore, an essential prerequisite is that *all* the community's *species* are represented in the sample. This condition is very hard to fulfill, as already stated above. The community must consist of only a few species, each with similar frequencies, and the sample size must be very large.

These stringent conditions greatly reduce the applicability of Simpson's index in large populations. It should perhaps be used preferably for the collections taken in the populations (instead of using it for the populations themselves), in agreement with PIELOU (1977) (see above).

Since Simpson's index C measures the *opposite of diversity,* ie. dominance, some kind of mathematical inversion is needed for C to provide a measure of diversity. Of the various possible ways of doing this, only two will be presented here.

HURLBERT (1971) simply considers the *reciprocal* of C. It can be interpreted as the number of equally abundant species required in the community to produce the same heterogeneity as observed in the sample, ie. it can be regarded as an 'effective number of species' in the community.

PIELOU (1977), however, prefers the *negative logarithmic* modification for providing a diversity index D, ie.

$$(15) \quad D = -\log C.$$

Her first premise is that D defined in this way and Shannon's H' are closely related, both being special cases of a more general function, called entropy of order α (RENYI 1961), used in the theory of communication.

Unfortunately, however, Pielou's D does *not* share with Shannon's H' and Brillouin's H the merit (see above) of being amenable to breakdown into additive components (PIELOU 1977). Hence H and H' promise to be far more useful in ecological studies than D.

8.2. Examples

If one has collected enough *(a priori)* information on the genets and of the variation in their characteristics, it may be possible to *discriminate* between them in the population.

This usually presupposes careful *measurements* of the quantitative or qualitative characteristics of the ramets (eg. OINONEN 1967 a, b, c, ENGELS 1983 a, b). However, even after having observed the plants in an experimental garden throughout the growing season, a worker may succeed quite reliably in *subjectively assessing* the isoclonality of a pair of plants, at least in a grass species like *Festuca rubra* (HARBERD and OWEN 1969). The subjective approach can work especially well if the characters utilized show non-continuous variation (HARBERD 1962).

In the main, though, it is clear that morphological homogeneity as such does not completely rule out the possibility that a cluster of ramets consists of several clones (OINONEN 1967 c). Furthermore, extensive morphological variation may exist among the ramets of a clone, due to environmental, especially pathological variation eg. virus infections (HARBERD 1962). In addition, somaclonal variation (see Chapter 9) may occur. Hence, *morphological similarity* does *not prove,* and dissimilarity does not disprove, the *isoclonality* of ramets.

Thus, however easy it may be in practice to apply to natural populations, unless we have conclusive evidence regarding its discriminatory power in the populations considered, the *intuitive* approach based on a subjective assessment of morphological characteristics is to be regarded with grave suspicion. That is, we ought to have resort to identifying the clones of some representative populations *a priori,* on the basis of a relatively *independent* source of information (say, based on isozymes or DNA techniques or by founding experimental populations), in order to be able to test how often the intuitive method will yield a *wrong classification* of a ramet into a clone.

A good array of registered *isoenzyme loci* polymorphic in the populations will render possible a rather reliable discrimination of genets in certain plant species (HARPER 1978). New *DNA techniques* (eg. JEFFREYS et al. 1985 a, b), though so far too expensive for large scale studies, promise to yield still more stable and reliable arrays of marker loci, suitable in plants, too, for *identifying individual clones.*

All the same, however easy and reliable the method for discriminating between genets, *mapping of the genets* (ie. delineating their borders, at least) in a population of a clonal plant species still remains a formidable task. It corresponds to studying separately the genotype of every branch in a population of large non-clonal plants. Depending on the method, the *amount of labour* required to discriminate among the genets may be proportional even to the square of the number of ramets.

Thus it is not surprising that relatively *few studies* have been devoted to the examination of clonal diversity in predominantly asexual plant species (LYMAN and ELLSTRAND 1984). Much more work has been done to examine the population structure in *clonal animal species,* even though these are much less common in the animal kingdom than are the respective cases in the plant kingdom.

Clonal plant species should have low levels of within-population polymorphism but a high degree of interpopulational differentiation (LEVIN and KERSTER 1971). One should bear in mind, however, that in unisexual animals, studies have revealed *unexpected amounts of clonal diversity* within and among populations. In animals, most parthenogenetic species studied appear to consist of multiple clones (Eg. SAURA et al. 1977, PARKER 1979, LYMAN and ELLSTRAND 1984, KORPELAINEN 1986).

I have already alluded to the results of certain case studies on plant species with a high degree of clonality in their populations. These and some extra cases will be briefly reviewed in the following.

Bracken

In studies on Finnish bracken populations (*Pteridium aquilinum* (L.) Kuhn.), OINONEN (1967 a, b) established that most stands consist of separate and often *very large clones.*

Bracken regeneration via spores appears to have been very rare in Finland. Such regeneration may have occurred only following a fire. The radial growth of bracken clones seems to have averaged no more than 20 cm a year.

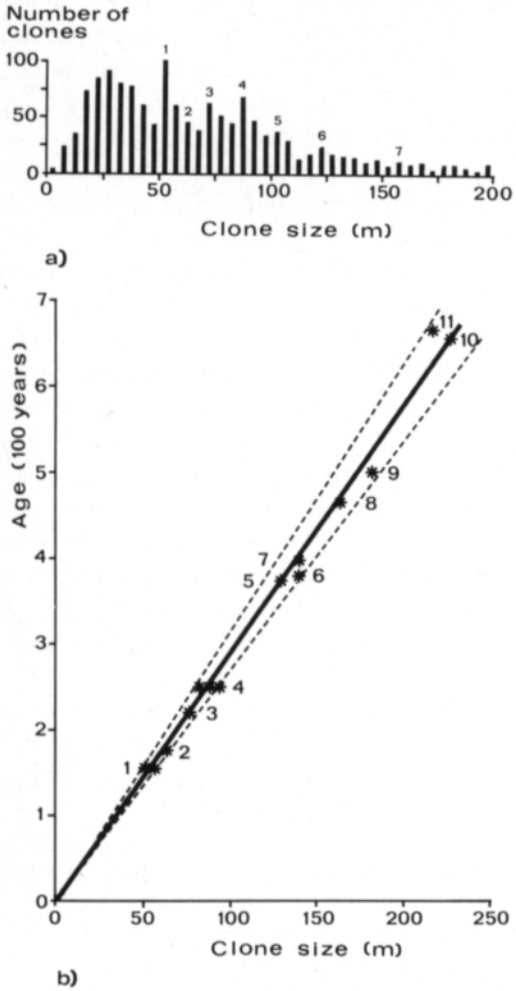

Fig. 6. a) Size distribution of bracken clones up to a diameter of 200 m. The tallest columns concide with war periods: 1 = The 1808—1809 War for Finland, 2 = The 1788—1790 War of Gustafus III, 3 = The 1741—1743 War of the Hats, 4 = The 1700—1721 Great Northern War, 5 = The 1656—1658 War with Russia, 6 = The 1570—1595 Long War, 7 = The 1489—1497 Big Russian War.
b) Spread of some representative bracken clones. The broken lines are the 95 % confidence limits. 1 = Sauvo, Ruissalo, Porkkala in 1808, 2 = Laitaatsilta in 1789, 3 = Huruksela, Anjala, in 1741, 4 = Tvärminne in 1714, 5 = Virolahti raided in 1590, 6 = Battle in Ilomantsi in 1587, 7 = Raids in Virolahti and Lappee in 1571, 8 = Sappu, Heinävesi, settled in ca. 1500, 9 = Putkilahti, Rantasalmi in 1468, 10 = Turku raided in 1318, 11 = Old fortress at Sulkava in ca. 1300.
(After Oinonen 1967 b).

About 1400 clones were studied. The frequency histogram of clone sizes correlates rather well with periods of war in Finland (Fig. 6). Furthermore, if one examines the historical records locality by locality, the size of a clone often coincides very closely with the occurrence of an ancient battle in the location.

While most of the clones were, say, between 15 and 150 metres in diameter (corresponding to about 40—430 years of age), some of the »distinctly identifiable» clones were almost 500 m in diameter and hence about *1400 years old.*

A weak point in Oinonen's study is that the ramets were identified as belonging to a certain clone solely on the basis of certain *»distinct» morphological characteristics,* eg. the colour of a petiole, and the size, colour and shape of nectaries, etc. Thus, the amount of clonal mixtures will be underestimated to an unknown degree, since all but the most clear-cut mixtures have been left unanalyzed.

Lycopodium complanatum L.

Oinonen (1967 c) also made a corresponding study in ground pine (*Lycopodium complanatum* L.). Its results were in good agreement with those of bracken, since its stands were of roughly the same age and size as those of bracken. Oinonen was now, however, more careful than before in equating these stands or clusters with clones. He now acknowledges that visually determined identity alone provides far from conclusive evidence.

Although the good agreement between the bracken and ground pine studies supports Oinonen's morphological diagnoses of clones, there still remains the possibility that the huge clone sizes he reported may be *overestimates* of the real situation.

Cardamine spp.

Studying *Cardamine* species in Central Switzerland, Urbanska-Worytkiewicz (1980)

found great differences in the reproductive strategies between species and also between populations, resulting in different compositions and patterns of genets in them.

In an autoallohexaploid species, *C. Schulzii,* sexual reproduction is well balanced by clonal growth. The respective triploid hybrid species, *C. insueta,* allocates its resources strongly to vegetative propagation, accompanied by early fragmentation of the clones.

A diploid species, *C. rivularis,* produces no stolons but is dispersed almost exclusively by seeds. Young seedlings are, however, very rare; hence, only a very limited proportion of the population will be recruited in a year.

The other diploid species, *C. amara,* is well equipped for sexual reproduction as well as clonal propagation via runners. In the study area, it frequently formed elongated populations (along the narrow banks of brooks), in which sexual reproduction was as a rule totally suppressed. In these populations, the *clones* were *single* (well separated) and remarkably dense, providing possibilities neither for seed production (due to self-incompatibility) nor for successful germination of seedlings.

Populus tremuloides

The Rocky Mountain aspen (*Populus tremuloides* Michx., *var. aurea* Tidestrom) dominates much of the mountainous terrain in Utah at elevations between 2000 and 3000 m. The aspen often occurs in *almost pure stands,* which may vary in size from a few square rods to several square miles of solid forest. The stands are sharply discontinuous, even-aged and usually dense.

Surrounded by the main form of aspen, there are *colonies of prevernal aspen* which attain full leaf two of three weeks earlier than the major stand. The line that separates the colonies of these two forms is sharp — only rarely do the two forms intermingle. COTTAM's (1954) transplanting experiments give support to the proposition that these two forms are genetically controlled.

Cottam made attempts, using radioactive phosphorus, to prove that the trees of these two forms never belong to a common clone. These attempts failed, however, since the radioactive phosphorus did not pass into any of the neighbouring trees. Hence, his results suggest *complete (physiological) separation* of the aspen sprouts from the parent clone before or soon after maturity.

Considering local prehistory, Cottam draws the conclusion that the distribution of aspen clones in Utah traces back approximately 8000 years. Sexual reproduction of aspen should have been common in the climate prevailing there during the pluvials associated with the extensive Pleistocene glaciations. As from about *8000 years* ago, after the onset of the Postpluvial climate with scant and irregular precipitation during the summer months, aspen appears virtually to have ceased reproducing by seed. Since then migration should have been through *clonal growth only,* resulting over the centuries in the merging of many previously separated colonies into forest stands.

These conclusions of COTTAM's (1954) rest, however, solely on ecological grounds, without any conclusive, direct evidence of the size or age of the aspen clones.

Taraxacum officinale (Web.) Marss.

In a study of clonal diversity in USA populations of dandelion (*Taraxacum officinale,* a triploid and an obligate gametophytic apomict there), *more genotypic diversity* was revealed than in other clonal plants previously studied.

The clones numbered from one to thirteen, on average five clones per population. In two-thirds of the cases, a clone was restricted to a single population. But, remarkably enough, there were also clones whose distribution area covered the entire continent, and which were found in almost every population studied (LYMAN and ELLSTRAND 1984).

Rorippa sylvestris (L.) Bess.

In a plant species with propagules apparent-

ly less well equipped for distant colonization than the dandelion seed, one would expect to find far fewer clones common to many populations.

In *Rorippa sylvestris* (a self-incompatible plant with vegetative reproduction from fragments of creeping roots), there were *no instances* of a common clone being shared among any of the 14 tetraploid populations studied (MULLIGAN and MUNRO 1984). The discrimination into clones was made on the basis of a series of incomplete diallel crosses between populations. In contrast to the tetraploids, *13 out of the 47* hexaploid populations studied turned out to have *identical* incompatibility relations in crosses, suggesting that they may have originated from a single clone.

There are other possible explanations, I suspect. If the hexaploid gene pool in North America only holds a *few incompatibility alleles,* (occasional bursts of) sexual propagation, too, should result in widespread identity of incompatibility genotypes in spite of otherwise genetically diverse backgrounds. Another possibility is that agamospermy may have occurred, facilitating distant colonization.

In the 73 populations studied, only a single population (a hexaploid) was able to produce seed. In all the others, the siliquas were aborting; this appeared to be the case, too, in most specimens of *R. sylvestris* collected in herbaria in North America. Hence Mulligan and Munro state that most populations of this species in North America should be *uniclonal.*

The genetic constitution of ramet populations of this species might be worth investigating in Finland, since this noxious weed is a newcomer and will likely pose severe problems of control in practical horticulture.

Oenothera laciniata Hill

This species is a permanent translocation heterozygote, thereby possessing an *'effectively asexual'* mode of reproduction via seed. It has been studied throughout its entire distribution range in USA (ELLSTRAND and LEVIN 1982).

In the 60 populations sampled the number

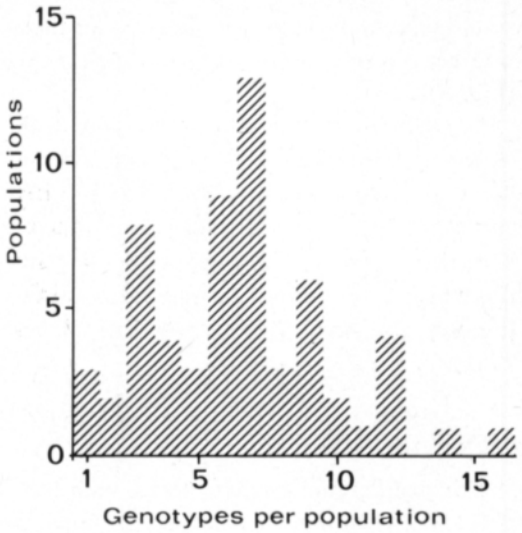

Fig. 7. Distribution of the number of genotypes in populations of *Oenothera laciniata* (After ELLSTRAND and LEVIN 1982).

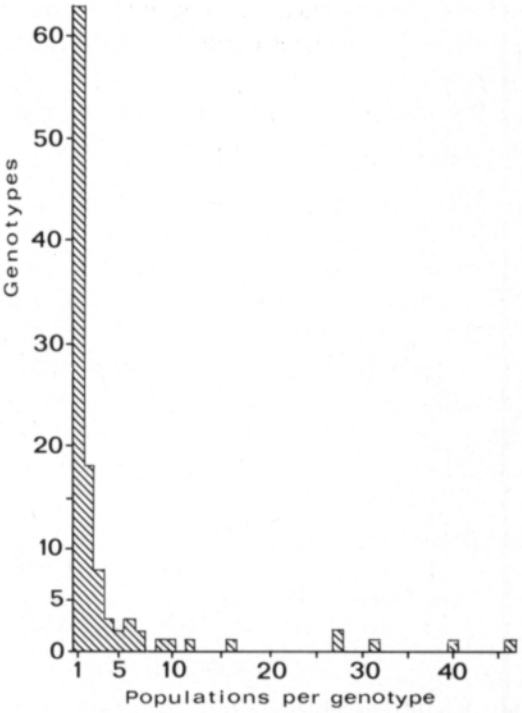

Fig. 8. Distribution of the number of populations in which a genotype occurs in *Oenothera laciniata* (After ELLSTRAND and LEVIN 1982).

of genotypes (classified on the basis of 18 enzyme loci, of which 5 were polymorphic), ranged from 1 to 16, averaging 6.5 per population (Fig. 7). Most genotypes (63) were unique to a single population, while one was found in as many as 46 populations; the mean number of populations per genotype was 5.2 (Fig. 8).

O. laciniata displays about the same order of *genotypic diversity* (0.045 genotypes per individual studied) as *clonal animals* (for difficulties in measuring diversity, see above). There were no trends in genotypic diversity detectable along either latitudinal or longitudinal gradients (ELLSTRAND and LEVIN 1982).

Festuca rubra L.

This is a perennial grass species with *well-developed rhizomes;* it is largely self-incompatible. In a natural population, HARBERD and OWEN (1969) recorded a *very large number of clones.* Several of them were extensively reduplicated but none of them so extensively as to numerically dominate the entire population.

The clonal constitution was *not uniform* over the site. The red fescue tended to be more abundant in those parts of the site where the local population was dominated numerically by a *single clone.*

The average probability of two ramets belonging to the same genotype decreases rather rapidly with distance (Fig. 9).

The identification of clones was made by a *subjective assessment* of identity of a pair of isolates in the experimental field, after the workers had observed them for a season. The reliability of the identification was controlled later in a limited number of apparently difficult cases, using cross-fertility tests. Some doubt may remain, however, as to the validity of the results.

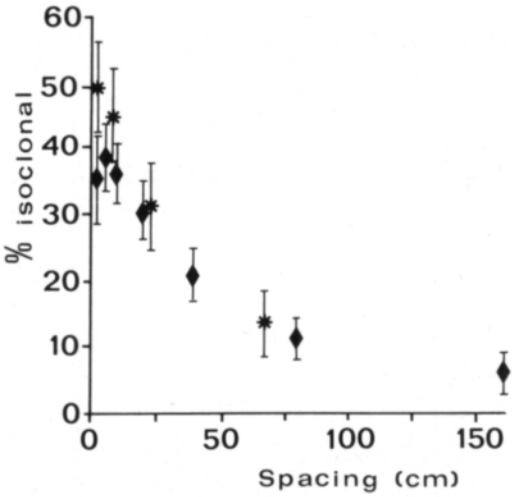

Fig. 9. The relationship between the percentage of isoclonal samples and the distance between a pair of isolates in *Festuca rubra* L. Different symbols refer to different sampling designs. (After HARBERD and OWEN 1969).

Festuca ovina L.

This is a perennial grass species rather similar to red fescue. It is, however, *non-creeping* since the daughter tillers are born intravaginally. Hence the clones grow in size very slowly, taking more than 150 years to attain a diametric spread of 1 m.

Ramets belonging to a common clone (ortet) were found from points up to 9 metres apart. Hence the age of the clones is to be measured in centuries; some clones may be more than *1000 years old.*

Several putative clones were found in a 9 m × 9 m square quadrat. Four of them were rather common. The classification of the ramets into clones was made principally by an examination of *morphological characters,* confirmed later on in a »cloned clone» trial. Only *discontinuously distributed* characters were utilized, since a virus infection affected the morphology of the plants considerably, obscuring the genetic differences. The classification was in some cases verified with a cross-incompatibility test as well.

Some doubts still remain about the classification into clones. One should remember that even a cross-incompatibility test will not conclusively reveal clonal identity; at its best it will yield only a division into *equivalence classes of incompatibility.*

Spartina patens (Aiton) Muhl.

In the salt marsh cord grass (a predominantly outcrossing, *rhizomatous* perennial species) SILANDER (1984) recorded considerable heterogeneity in the distribution of clones among subpopulations. The dune subpopulation was dominated by a *small number* of *large clones,* while the marsh subpopulation carried a *large number* of *small clones,* with little overlap in genotype composition. Clinal trends were apparent for two loci. Larger clones tended to be less heterozygous than smaller ones.

In this list of examples one may notice that a *considerable degree of genetic variation* is found also in the populations of species with a strong allocation of resources to clonal growth or apomictic seed production.

The question of *how polymorphism is maintained* within clonal populations is a knotty problem. Clones may coexist because of adaptive differentiation, or simply because the population is not at equilibrium. Long-term seed banks (and maybe banks of resting rhizome buds as well, I propose) and long-distance though infrequent gene flow could also contribute to intra-populational heterogeneity (ELLSTRAND and LEVIN 1982).

In clonal plant populations, there is usually a certain degree of *sexual reproduction* as well. Hence, in such populations *new genotypes* are continuously being added to the pool of ramets, and therefore the maintenance of genotypic variation should be far more prevalent in them than it is in »strictly clonal» populations.

9. Some aspects of germplasm conservation and plant breeding

The breeding of plant species which are *easily reproduced by asexual means* offers us the possibility of utilizing *all the genetic variation* in the character under consideration (WRIGHT 1977). The dominance and interaction components of the genetic variance are fully available in these species. The superiority of an individual genotype may be totally transferred to its descendants (the cultivar), without the necessity for undergoing and resisting the dilution effect of meiosis and fertilization.

In highly clonal plant species, spreading chiefly by asexual means, the problem is how to *find or generate* enough *genetic variation* in the breeding population. The case studies presented indicate that there exists a good deal of genetic variation in their populations, and we can in particular expect to find a high degree of *interpopulational differentiation* between their populations (LEVIN and KERSTER 1971).

Characteristically, these populations consist of a *few genotypes,* not usually identifiable by visual means, each present in unpredictable numbers of replicates (ramets) and more or less intermingled. Hence, in order to be sure of securing all the genotypes in a population, one would have to take a disproportionately large sample.

A *more effective* way of allocating collection resources might be to screen as *many populations* as possible, taking only a *restricted sample* from each (TAMMISOLA 1981). This procedure should yield more genotypes, since most clones are restricted to one or relatively few populations.

In the almost total absence of sexual reproduction, the small amount of genetic variation may be rather soon used up. A case in point might be *Bougainvillea,* a self-incompatible ornamental species. Since very many of the cultivars share the same incompatibility alleles, crossings between them do not succeed. Hence, cultivated *Bougainvillea* has, in effect, become transformed into an *asexually reproducing* species. Accordingly, mutation breeding has been predominant, *Bougainvillea* growers having selected for cultivars which display a very high rate of *somatic mutations* (KHOSHOO 1981).

Another possibility for creating new variation in a clonal plant is by tissue culture. Single cultured cells are not usually genetically stable, and therefore among the plants regenerated from such cultured cells, genetic variation

(termed *'somaclonal variation'* by LARKIN and SCOWCROFT 1981) will often be found (REISCH 1983).

As regards the breeding of an apomictic species, KHOSHOO (1981) suggests that in order to increase the genetic variation, one should utilize the sexually reproducing *elemental species* (often diploid) and *facultative apomicts.*

In facultative apomicts, the recombination needed for further breeding work may be achieved through *environmental manipulation,* while in the (almost) obligate apomicts one should apply new *somatic crossing* methods (e.g. protoplast fusion), possibly combined with *haploidization.* Thus, a breeder might imitate the *diploid-tetraploid-dihaploid cycles* described for the natural evolution of the *Panicum maximum* agamic complex (SAVIDAN and PERNES 1982).

In some crop species, eg. fodder grasses in which the farmer aims for the vegetative yield, apomixis can serve to *fix* a desirable *heterozygous cultivar.* The genotype will remain intact even when the cultivar is *propagated by seed,* as is usual in northern Europe.

Attempts are being made to *introduce apomixis* into cultivated crops from their wild relatives via eg. back-crosses. Projects reported include at least wheat, sugar-beet, maize, potato and forage grasses (ASKER 1979, NOGLER 1984). According to NOGLER (1984), the great efforts undertaken in this direction have so far led to only a rather modest success, because a thorough understanding of the *genetic* and *physiological background* of gametophytic apomixis is still lacking.

MARSHALL and BROWN (1981) suggest that mutagen-treated populations of plants which are *male fertile* but *female sterile* would provide ideal starting material to search for apomictic mutants in crop plants.

In natural stands, there may in many instances have been a selective tendency for longer internodes and rather sparse, even sprawling growth habits. This »guerilla»-type of clonal growth, as defined by Clegg (HARPER 1978), should have promoted a good seed set by promoting interpollination between clones.

In the *cultivated field,* however, the nutritional status is even and very high, and the species is usually grown in monoculture (or in a mixture of a couple of clones, as in self-incompatible plant species). In addition, the field may be saturated with nursed populations of suitable pollinator insects. In these circumstances, productivity for the purposes of man might be increased through selection for a *tighter, more erect and more condensed* (short internode) *growth habit.* This compact type of clonal growth should also confer on the cultivar a better competitive ability against other species (weeds) in the field.

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11. Selostus: Klooneja muodostavien kasvien populaatioista

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Tutkimus on mesimarjan marjontaa luonnonkasvustoissa käsittelevän väitöskirjatyön johdanto-osa. Se on *kriittinen yleiskatsaus*, jossa ensisijaisesti kirjallisuuden perusteella tarkastellaan *putkilokasvien populaatioissa*

esiintyviä ilmiöitä ja populaatioiden rakennetta.

Kasvipopulaatiot poikkeavat monella tavoin eläinpopulaatioista, joten eläinpopulaatioita koskevia teorioita ja tuloksia ei välttämättä voida aina yleistää koskemaan myös kasveja. Teorian kannalta vaikea ryhmä ovat ne kasvit, joilla on kyky muodostaa klooneja. Katsauksessa onkin erityistä huomiota kiinnitetty *klonaalisuuden* mukanaan tuomiin *erikoispiirteisiin* populaatioiden rakenteessa ja varsinkin pölytystapahtumissa.

Kasviekologian alalla *käsitteistö* on monenkirjavaa ja hyvin usein puutteellisesti määriteltyä. Eri kirjoittajat käyttävät saman nimisiäkin käsitteitä usein jopa päinvastaisissa merkityksissä. Vain harvoin on jokin termi lukuisista tarjolla olevista saavuttanut yleisesti hyväksytyn standardin aseman. Tämä käsitteistön selkiintymättömyys on aiheuttanut vaikeuksia alan tutkimusten suunnittelulle sekä luotettavien johtopäätösten ja yleistysten rakentamiselle julkaistujen tulosten perusteella.

Senvuoksi tässä kirjoituksessa on käytetty melko runsaasti palstatilaa käsitteistön tarkasteluun. Mm. tutkitaan käsitettä 'klooni' (jolle tässä ehdotan suomennosta *'monieliö'*; kasveilla klooni olisi siis *'monikasvi'* ja kloonien muodostamiseen kykenevä kasvi olisi *'monistuva kasvi'*; kloonaaminen olisi vastaavasti *'monistamista'*).

Katsauksessa esitetään muutamia esimerkkejä tutkituista klooneja muodostavien kasvien populaatioista. Lopuksi tarkastellaan lyhyesti klonaalisuuden eräitä vaikutuksia *kasvinjalostuksessa* ja jalostusaineiston *keruussa* luonnonpopulaatioista geenipankkeja varten.

12. Appendix: Parent-offspring dispersal variance σ^2

Let us construct a »facultative» random variable

$$(1) \quad X(g) = \alpha_1(g) \cdot r_{pr} + \alpha_2(g) \cdot r_{sr} + \alpha_3(g) \cdot r_c$$

to represent the 'dispersal distance'. This is the distance (to be denoted by r) between the ramet under consideration (generation t) and the ramet it originated from (generation t—1). In an asexual case, we must take as the originating ramet the youngest one in the vegetative sequence which was mature at the time of the previous *sexual* generation, t—1. Thus, the time scale will pertain to sexual generations. Hence, r_{pr} will denote the ramet's distance from its pollen parent, and r_{sr} the distance from its seed parent. Respectively, r_c will denote the dispersal distance pertinent to an asexual ramet.

Let all the distances be defined as axial ones (Crawford 1984), ie. carrying negative as well as positive values.

The coefficients α_i (i = 1, 2, 3) are defined as being functions of a random variable g such that, for any value of g, one and only one of the coefficients has a value of 1 while all the others have a value of O. Hence, let the variable g take on one of the values 1, 2 or 3 with probabilities of ½ (1—a), ½ (1—a) and a, respectively. Furthermore, let $\alpha_1(g) = 1$ when g = 1 but let $\alpha_1(g) = 0$ for the two other possible values of g (g = 2 or g = 3); similarly, $\alpha_2(g) = 1$ if and only if g = 2, and $\alpha_3(g) = 1$ if and only if g = 3, random variables α_i (i = 2, 3) having a value of zero for the other values of g. Let the parameter a above denote the probability that (mature) ramet taken at random from the population will be asexual in origin.

The idea of such a construction is that so defined, X(g) will represent a *'random gamete-equivalent'* from the population. With a probability a (ie. the probability of obtaining an asexual ramet) it will carry the value of the random variable r_c, ie. the dispersal distance pertinent to an asexually produced ramet. With half of the remaining probability, ie. (1—a)/2, it will carry a dispersal distance value r_{pr}, pertinent to the originating pollen, and with the same probability the value r_{sr}, pertinent to the originating seed parent of a sexually produced ramet.

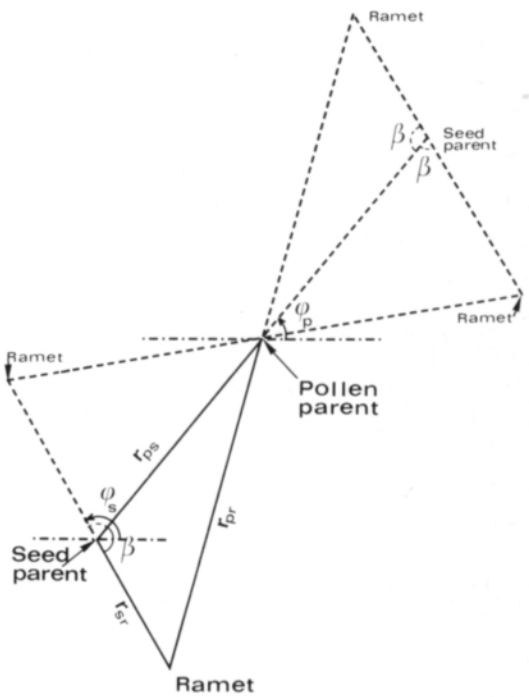

Fig. 1. Axial dispersal distances of successful gametes in seed plants. For explanations see text. $\varphi_s > \varphi_p$. One case (Case 1) out of the four possible ones is presented in detail (solid lines): $r_{ps} < 0$, $r_{sr} < 0$, $r_{pr} < 0$, $\beta = \pi - (\varphi_s - \varphi_p)$.

Therefore, the desired parent-offspring dispersal variance, σ^2, will be secured by determining the *variance of X(g),* ie. $D^2\{X(g)\}$. It would be easy to arrive at this variance, if all random variables in (1) were independent of each other. Unfortunately this is not the case, since r_{pr} and r_{sr} are interdependent. The latter part of the journey of the gamete-equivalent arriving from the pollen parent, is undergone together with the gamete-equivalent arriving from the seed parent, ie. they are travelling in the same seed.

Hence, we must introduce a notation r_{ps} for the interval from the pollen parent to the seed parent of the ramet under consideration (Fig. 1). That is, r_{ps} is the (axial) »flight» distance of effective pollen. In the model, windspeed as well as the foraging trips of pollinators are assumed to be evenly distributed in all directions. Then the random variables r_{ps} and r_{sr} will be *independent* of each other. Furthermore, r_{ps} will be identically distributed in any direction. Since it is an axial variable, we can regard it as being identically distributed in any direction (to be denoted by φ_p) between 0 and π in relation to a reference vector. Similar reasoning holds for r_{sr}.

Our purpose is to express r_{pr} in terms of r_{ps} and r_{sr}. This, we hope, will transform expression (1) for X(g) into the desired form, where it will contain only independent components. First we shall consider case 1. in the figure (Fig. 1). From ordinary trigonometry, we arrive at an expression

$r^2_{pr} = r^2_{ps} + r^2_{sr} - 2 \cdot r_{ps} \cdot r_{sr} \cdot \cos\beta$, where

in this case the angle $\beta = \pi - (\varphi_s - \varphi_p)$. Now, however, there is the difficulty that being axial variables, values of r may also be negative (as they actually are in case 1). This may affect the sign of the third term in the sum. In order to be able to fix the sign under consideration, we shall therefore make an inquiry letting the angle β tend to the value π. At this limit, the expression must reduce to

$r^2_{pr} = r^2_{ps} + r^2_{sr} + 2 \cdot |r_{ps}| \cdot |r_{sr}|$,

since then $|r_{pr}| = |r_{ps}| + |r_{sr}|$. The sign must be chosen so that this reduced form is achieved. Making such an inquiry in all possible cases (the four cases presented in Fig. 1, and the four respective ones pertinent to the situation where $\varphi_s < \varphi_p$), we can see that the expression

$$(2)\quad r^2_{pr} = r^2_{ps} + r^2_{sr} + 2 \cdot r_{ps} \cdot r_{sr} \cdot \cos(\varphi_s - \varphi_p)$$

will apply in each case.

The last term in the sum in expression (1) is seen to be independent of the others. Hence,

$$(3)\quad D^2\{X(g)\} = D^2\{\alpha_1 \cdot r_{pr} + \alpha_2 \cdot r_{sr}\} + D^2\{\alpha_3 \cdot r_c\}.$$

Next we shall evaluate the latter, 'clonal' variance in (3).

$$(4)\quad D^2\{\alpha_3 \cdot r_c\} = E\{(\alpha_3 \cdot r_c)^2\} - (E\{\alpha_3 \cdot r_c\})^2,$$

where the notation E signifies the expectation (ie. average value). Since α_3 and r_c are independent random variables, and $E\{r_c\} = 0$ (since r_c is an axial variable), the latter term will disappear and the former term will be divided into two parts in expression (4), yielding

$$(4')\quad D^2\{\alpha_3 \cdot r_c\} = E\{\alpha_3^2\} \cdot E\{r_c^2\}.$$

Since $E\{r_c\} = 0$, the variance $D^2\{r_c\} = E\{r_c^2\}$, and expression (4') can be put in the form:

$$(4'')\quad D^2\{\alpha_3 \cdot r_c\} = E\{\alpha_3^2\} \cdot D^2\{r_c\}.$$

Now, the expectation for α_3^2 (g) can be obtained from the formula

$$\begin{aligned}(5)\quad E(\alpha_3^2(g)) &= \tfrac{1}{2}(1-a) \cdot \alpha_3^2(1) \\ &+ \tfrac{1}{2}(1-a) \cdot \alpha_3^2(2) + a \cdot \alpha_3^2(3) \\ &= \tfrac{1}{2}(1-a) \cdot 0^2 + \tfrac{1}{2}(1-a) \cdot 0^2 \\ &+ a \cdot 1^2 \\ &= a.\end{aligned}$$

Hence, for the asexual component we shall arrive at

$$(4''')\quad D^2\{\alpha_3 \cdot r_c\} = a \cdot D^2\{r_c\} = a \cdot \sigma^2_c\ ,$$

where σ^2_c is the variance of the distance the species is able to invade in one direction by clonal means during a time interval of one sexual generation.

Now let us return to consider the 'sexual' part of expression (3). Applying (4) and noticing the zero expectations as above, we can conclude that

$$\begin{aligned}(6)\quad D^2\{\alpha_1 \cdot r_{pr} + \alpha_2 \cdot r_{sr}\} &= E\{(\alpha_1 \cdot r_{pr} + \alpha_2 \cdot r_{sr})^2\} \\ &= E\{(\alpha_1 \cdot r_{pr})^2\} + E\{(\alpha_2 \cdot r_{sr})^2\} \\ &+ 2 \cdot E\{\alpha_1 \cdot \alpha_2\} \cdot E\{r_{pr} \cdot r_{sr}\}.\end{aligned}$$

However, the last term in the expression will disappear: since the product $\alpha_1(g) \cdot \alpha_2(g)$ will be zero for any value of g (g = 1, 2 or 3), its expectation will be zero as well. Therefore

$$\begin{aligned}(6')\quad D^2\{\alpha_1 \cdot r_{pr} + \alpha_2 \cdot r_{sr}\} &= E\{(\alpha_1 \cdot r_{pr})^2\} \\ &+ E\{(\alpha_2 \cdot r_{sr})^2\}.\end{aligned}$$

To start with, let us consider the first part of this expression. Since random variables α and r are independent from each other, we can arrive at

$$(7)\quad E\{(\alpha_1 \cdot r_{pr})^2\} = E\{\alpha_1^2\} \cdot E\{r_{pr}^2\}.$$

The value of $E\{\alpha_1^2\}$ will be $\tfrac{1}{2}(1-a) \cdot 1^2 + \tfrac{1}{2}(1-a) \cdot 0^2 + a \cdot 0^2 = \tfrac{1}{2}(1-a)$ (cf. expression 5). The value from formula (2),

$r^2_{pr} = r^2_{ps} + r^2_{sr} + 2 \cdot r_{ps} \cdot r_{sr} \cdot \cos(\varphi_s - \varphi_p)$

will be substituted for r^2_{pr} in expression (7), yielding

$$\begin{aligned}(7')\quad E\{(\alpha_1 \cdot r_{pr})^2\} &= \tfrac{1}{2}(1-a) \cdot [E\{r^2_{ps}\} + E\{r^2_{sr}\} \\ &+ 2 \cdot E\{r_{ps}\} \cdot E\{r_{sr}\} \cdot E\{\cos(\varphi_s - \varphi_p)\}].\end{aligned}$$

Since the expextancies of r_{ps} and r_{sr} will have values of zero, the last term in the sum will disappear. For the same reason, the first two terms in the sum will represent their respective variances. Hence we shall arrive at the expression

(7'') $E\{(\alpha_1 \cdot r_{pr})^2\} = \frac{1}{2}(1-a) \cdot [D^2\{r_{ps}\} + D^2\{r_{sr}\}]$
$= \frac{1}{2}(1-a) \cdot (\sigma^2_p + \sigma^2_s).$

Here σ^2_p denotes the variance of the distance (along the shortest possible route) taken by a successful pollen grain from its pollen parent to the receptive seed parent. Respectively, σ^2_s denotes the variance of the distance (along the shortest route) taken by a successful seed from its seed parent to the position of its emergence as a grown-up ramet.

Lastly, we shall evaluate the latter part of expression (6'). Making manipulations similar to those above,

(8) $E\{(\alpha_2 \cdot r_{sr})^2\} = E\{\alpha^2_2\} \cdot E\{r^2_{sr}\}$
$= \frac{1}{2}(1-a) \cdot \sigma^2_s.$

Combining (7'') and (8) yields

(6'') $D^2\{\alpha_1 \cdot r_{pr} + \alpha_2 \cdot r_{sr}\} = (1-a) \cdot (\frac{1}{2}\sigma^2_p + \sigma^2_s).$

Substituting the formulas in (4''') and (6'') into their respective expressions in (3), we shall finally obtain the parent-offspring dispersal variance reduced to the desired form

(3') $\sigma^2 = D^2\{X(g)\} = (1-a) \cdot (\frac{1}{2}\sigma^2_p + \sigma^2_s) + a \cdot \sigma^2_c.$