LIFE-CYCLE VARIATION IN GEOPHYTES

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Abstract

Storage patterns in geophytes are integrated into one general scheme. Two patterns are recognized: geophytes in which flowers and leaves appear simultaneously (synanthous) and geophytes in which flowers and leaves appear in different seasons (hysteranthous). Within each pattern two variants can be recognized, those with annual and those with perennial storage organs. The annual developmental cycle of storage organs, of leaves, and of flowers and seeds characteristic of each type is related to ecological conditions and possible selection pressure. Large perennial storage organs are expected and found in plants of arid unpredictable areas. Hysteranthous leaves are expected to be more frequent in arid unpredictable climates.

A geophyte is a plant with a life-form in which the perennating bud is borne on a subterranean storage organ. In most geophytes the life cycle includes a dormant period that can extend from a few weeks to most of the year (Raunkiaer, 1934). Relatively few geophytes are active throughout the whole year and these are typical of the tropics (Holttum, 1955; Holdsworth, 1961).

In such a life cycle two patterns can be distinguished and in each type, annual and perennial storage organs are found: (1) Geophytes with synanthous leaves, in which leaves and flowers are simultaneous and the course of events is growth, storage, flowering and dormancy. (2) Geophytes with hysteranthous leaves, in which flowers and leaves appear in separate seasons and the course of events is growth, storage, dormancy, and flowering (Dafni et al., 1981).

Most geophytes live in and are adapted to a seasonal climate (Raunkiaer, 1934; Burns, 1946; Svoskin, 1960; Rees, 1972). A seasonal climate may also be characterized by its unpredictability. A storage organ may enable a plant to perennate in a seasonal climate, and to persist through large fluctuations in climate from year to year.

The storage organs of geophytes are able to supply food reserves for rapid leaf growth at the beginning of the season. This is typical of regions having a short photosynthetic period (Mooney & Billings, 1960, 1961; Russel, 1940, 1948; Fonda and Bliss, 1966). Storage organs may also provide reserves for growth in periods when net production is reduced. For example, food storage in bulb plants enables them to make rapid leaf growth after cold winters and/or dry summers (Rees, 1972).

In geophytes with hysteranthous leaves an accumulation of storage materials is a prerequisite for flowering (Burt, 1970).

In the literature there are few works devoted to carbohydrate concentration in geophytes throughout the year, either as the main (Mooney & Billings, 1960; Fonda & Bliss, 1966; Risser & Cottam, 1968; Ogden, 1974) or even as a minor subject (Rees, 1966, 1969, 1972; Ho & Rees, 1975; Frontanier, 1973).

The present study is an attempt to develop a single systematic treatment of the various consumption rhythms of geophytes.

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Observations and Generalizations

ANNUAL STORAGE ORGANS

Geophytes with Synanthous Leaves.—In this group the storage organ is completely renewed every year. The storage materials provide for the early growth of the photosynthetic organs. The allocation of resources for next year storage, for flowering, and for seed production may be at the expense of the storage organ or from current production.

In some Mediterranean orchids (*Ophrys, Orchis, Serapias*), the root-tuber is replaced every year, gradually increasing in size, and first flowering occurs only after five to eight years, after accumulating a minimal "critical mass," as it is well known from cultivated bulbs (see discussion). Most of the species in this group flower two to three months after the first rain. This is interpreted as a "lag period" for production and allocation of the reserve materials for the next year. A shortage of rain in this period injures mainly the current flowering and to a lesser extent the allocation for the next year. It seems that, for the survival of the genotype in unpredictable environments, the risk of injuring storage organs is more harmful than the risk of not producing flowers and seeds for one year. We assume that allocating reserves for the coming year with first priority may be considered a mechanism for achieving minimal risk. Figure 1 represents the hypothetical reserve course during the season in this group. A similar type of reserve course was found in the cultivated tulip (Rees, 1966).

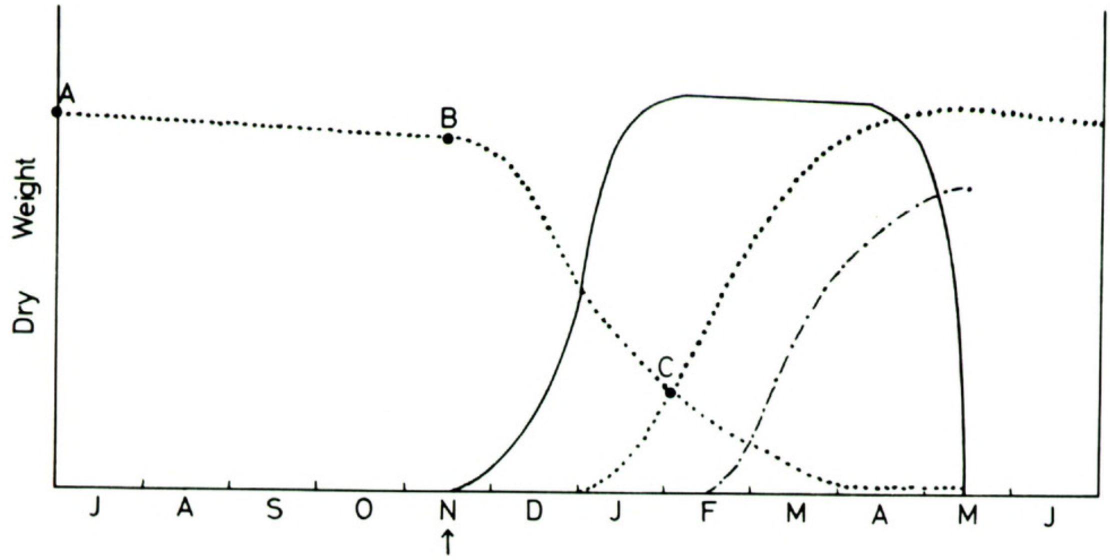
Phenological differences are summarized in two subgroups based on the speed of leaf development and the duration of the photosynthetic period.

The rapid route: Rapid leaf development may be advantangeous when the photosynthetic period is very short (Burt, 1974). The most common limiting factor is available moisture. This occurs mainly in steppes, deserts, soil pockets in rock fissures, light soils, sand dunes, etc. It may be also advantageous under conditions of high competition (Harper, 1967), when the first plant to be established is the first to succeed. The risk is that any damage to the leaves by grazing, sea spray, frost, etc. is irreparable owing to restricted reserves.

Since the productive season is very short, it is advantageous to first ensure the reserve for the coming year, and only after this to provide for the current reproductive cycle. Such a shorted and rapid development is found in *Gagea dayana* and *G. chlorantha* growing in fissures of calcarous rocks, in dry dunes and steppes in which the photosynthetic period is 2–3 months (Heyn & Dafni, 1971).

The slow route: Slow leaf production is suitable for a long photosynthetic period when the moisture, light, or temperature are not limiting factors. Typical habitats of this kind are open Mediterranean dwarf shrubs communities ("batha") with quite deep soils or field fringes. The longer exposure means greater hazards of competition.

When the leaves are active for a long period simultaneously with flowering, it is possible to allocate reserves for the coming year and for flowering at the same time, without risking survival for the next year. Because of the extended favorable conditions, current production contributes to flowering and flowering is possible even if the allocation for reserves for the coming year is incomplete,



FIGURES 1–4. Development of vegetative, reproductive, and storage organs during the year from July to June. Leaves ———. Storage organs . . . . Flowers and seeds –·–·–·–. The arrow indicates the first rain.

FIGURE 1.—An annual plant with synanthous leaves; based on data from *Serapias vomeraceae*.

because there is a reasonable chance to support seed setting from current production. Thus, we expect that the critical mass would be smaller than in the rapid route.

Slow extended flowering may be advantageous when there is a shortage of pollinators, or when a long flowering period compensates for a low number of individuals, as it is in rare species with specific pollinators (Drury, 1974) provided that there is no risk in long flowering exposures. An example is *Gagea villosa*, which grows in damp fields in the Mediterranean region in which the photosynthetic period lasts 4–6 months (Heyn & Dafni, 1977).

Geophytes with Hysteranthous Leaves.—Owing to the complete separation between the productive and consuming phases, the reserves necessary for flowering are accumulated in the previous year. If the reserves are insufficient, flowering does not occur in the following year and all the reserves are utilized to establish the photosynthetic organs. The critical mass for flowering in geophytes with an annual storage organ and hysteranthous leaves has to include the exact amount of reserves required for flowering and *seed production*, which is independent of environmental variation. This is in contrast to annuals with synanthous leaves, which risk the chance of failure in seed setting if poor conditions follow flowering.

The yearly course of accumulation and consumption of reserves is shown in Figure 2. A to B represents the preparation period in the storage organ for flowering (August–September). *B* to *C* represents expenditure on flowering and seed production. *C* to *D* represents the time interval between the end of seed production and the appearance of leaves. *D* to *E* represents expenses for leaf establishment.

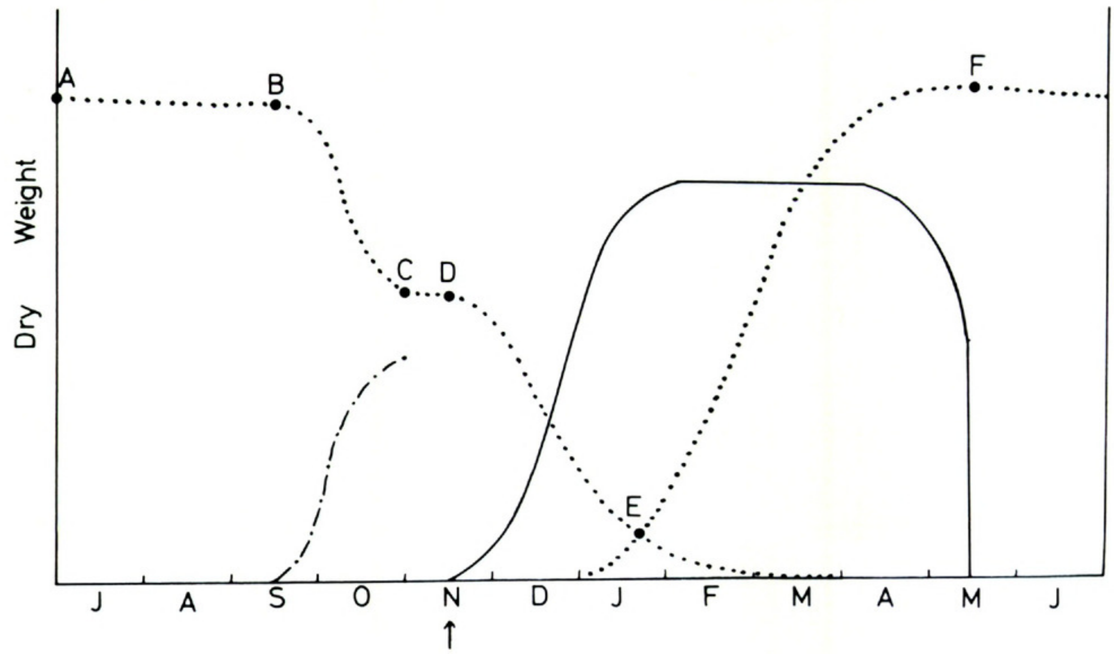


FIGURE 2.—A model of an annual plant with hysteranthous leaves.

E is the point of minimal reserve. *E* to *F* represents productive phase and allocation of reserves for the coming year (November–April).

The same routes and combinations described under the former group are also expected in this group. Flowering is completely dependent on the level of storage reached by the end of the previous year and not on current ecological conditions. Local conditions could dictate the time course of flowering. After the rains (October) one expects to find either a rapid route with a rapid production and storage, as in steppe or desert plants like *Colchicum tunicatum* and *Crocus damascenus*, or a slow route in moderate Mediterranean conditions in plants like *Colchicum hierosolymitanum* and *Crocus ochroleucus*.

PERENNIAL STORAGE ORGANS

Geophytes with Synanthous Leaves.—In perennials, the critical mass has a different significance, since the first flowering occurs only after accumulation of surplus reserves (Rees, 1972; Frontanier, 1973) so that flowering may be completed even if there is a shortage of reserves in the current year. We can suppose that in moderate and predictable habitats the "shortage fund" (the reserves above the consumption of one year) may be quite small since there are fewer chances for successive bad years. In extreme and unpredictable habitats, there is a greater chance for successive dry years, and it is expected that the first flowering would occur only after the allocation of a large "shortage fund." This "fund" has to be sufficient to support several successive years of shortage, so that flowering may be expected to occur every year. Our field observations support the suggestion that if the storage organ is large enough, indicating a large "shortage fund," flowering will occur almost every year. It should be borne in mind that the re-

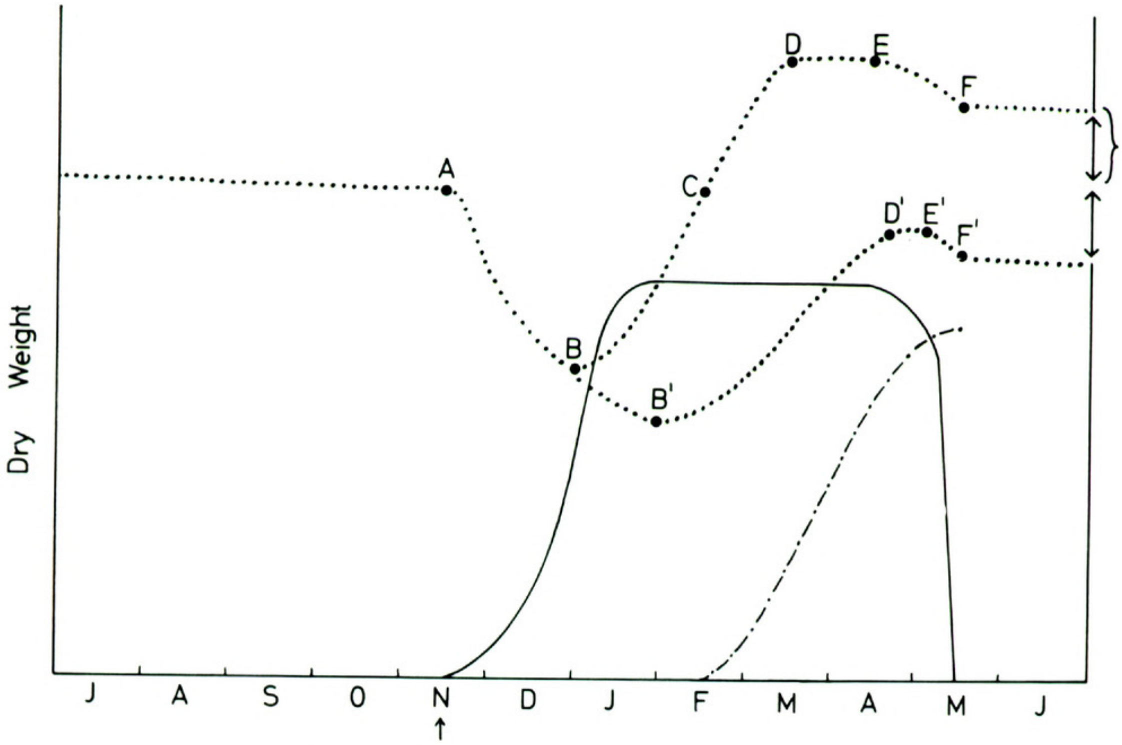


FIGURE 3.—A model of a perennial plant with synanthous leaves.

serves are not the only conditions for flowering and that other triggers like the temperature regime can be very important (Hartsema, 1961; Rees, 1966). Species with large reserves which flower almost every year are: e.g., *Scilla hyanthoides, Cyclamen persicum, Lilium candidum,* and many others.

The yearly course of accumulation and consumption of reserves is shown in Fig. 3. In a good year (*A–F*), the following phases could be distinguished: *A* to *B*, expenses for leaf establishment until net production occurs; *B* to *C*, the "store walls" plus the "shortage fund"; *C* to *D* the beginning of flowering and continuation of net production; *D* to *E* the balance period between the expenditure and production; *E* to *F* the expenditure for flowering plus seed production is greater than the production; *A* to *F* is the profit of the current season added to the "shortage fund." In a "bad year" (*A–F′*): *A* to *B′*, the expenditure period for leaf establishment, is longer than *A–B* and the rate of net production accumulation is slower. *A* minus *F′* is the shortage of the current year.

A similar type of reserve course was found in cultivated *Narcissus* (Grainger, 1941), *Polygonum bistortoides,* and *Geum turbinatum* (Mooney & Billings, 1960) and in two species of *Erythronium* and of *Dicentra* (Risser & Cottam, 1968).

The rapid and slow secondary routes are also expected in this group.

The rapid route can be a possible adaptation to extreme habitats in which annual geophytes cannot exist and which can only be occupied for a short time. For example, in *Polygonum bistortoides,* which grows in the extreme tundra, 50% of its total reserves were utilized in one week (Mooney & Billings, 1960). A rapid growth cycle also exists in *Erythronium* and *Dicentra* species which grow in a forest of sugar maple and basewood beech (Risser & Cottam, 1968) during

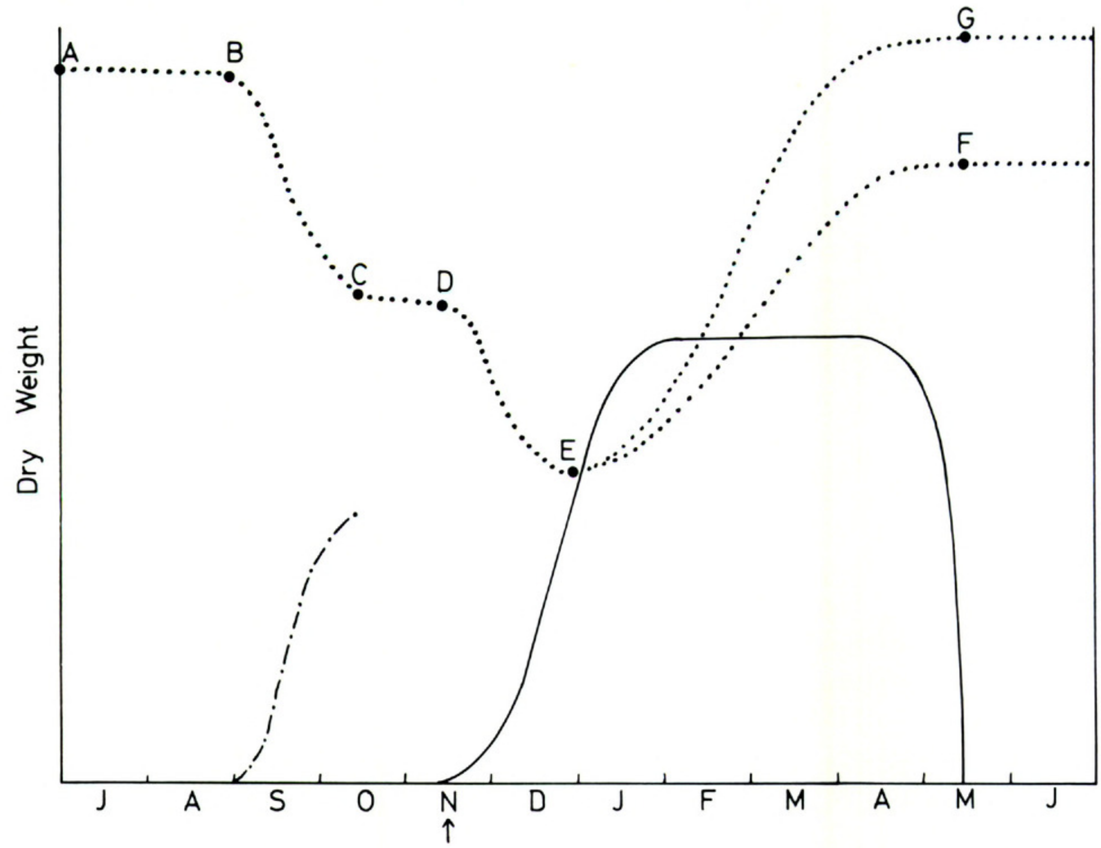


FIGURE 4.—A model of a perennial plant with hysteranthous leaves.

a short period of photosynthesis in the spring, before the tree leaves develop, and also in *Carex bigelowii* from alpine regions with short growth season (Fonda & Bliss, 1966).

The slow route is found in habitats which permit a long season of growth. In typical Mediterranean conditions five to six months of continuous growth are possible. Many geophytes expand their leaves after the first rains but flower only in late winter or in the spring, e.g., *Lilium candidum, Scilla hyanthoides, Ranunculus asiaticus, Asphodellus microcarpus,* and many others.

Perennial Geophytes with Hysteranthous Leaves.—In this group flowering and storage of new reserves occur in different seasons. The abundance of flowering can only be influenced to a limited extent by the current climatic conditions. After the accumulation of the initial critical mass, flowering can occur almost every year. It is expected that only slight differences will be found in the abundance of flowering from year to year.

The hypothetical reserve course during the season (Fig. 4) is similar, in principle, to that of annuals with hysteranthous leaves (Fig. 2), with one major difference—the existence of a "shortage fund" plus the "store walls." In a good year, a surplus (Fig. 4, *A–G*) is added to the "shortage fund" and, in a bad year, the deficit is taken from the shortage fund (Fig. 4, *A–F*). The course of development up to the next leaf production can be the same in good or bad years, since flowering is independent of concurrent climatic conditions.

Fast and slow secondary routes are similar to those in the other groups. In *Scilla hunburyi*, which grows in steppes, the leaves are active for about two months; in *Scilla autumnalis*, which grows in the Mediterranean area, the photosynthetic season lasts 3 to 4 months, in *Urginea maritima* for about 8 months and in *Pancratium maritimum* about 9 months. The growth season seems to correspond to the availability of moisture. Vegetative growth varies widely between years, but flowering occurs every year.

Discussion and Conclusions

It is well known from horticultural practice that bulbs and corms below a certain size do not flower. There appears to be a minimum size of storage organ in each species and variety for flowering to occur (Rees, 1969, 1972). Frontanier (1973) notes that the juvenile period in bulbs and corms varies from one to seven years and that this variation can be related to the minimum bulb weight. Considering that all this evidence was collected under predictable agricultural conditions, it is quite reasonable to assume that the size of the reserve is the major regulating factor and that after the first flowering, flowering is expected to occur every year. In a natural unpredictable environment, plants must be more flexible in order to prevent flowering in a bad year as a means of escaping starvation at the end of the season and primarily to ensure the next vegetative phase.

Geophytes growing in a seasonal climate with a restricted growth period, must have a more complicated use of reserves in order to reduce risks. Frontanier (1973) stresses that when the time between initiation and flowering in cultivated bulbs is long, one must distinguish between a minimal reserve for the initiation of flowering and a second amount of reserves for flower development. According to his data, it can be concluded that the bulb size is more important in geophytes in which the initiation of flowering occurs during the storage period (e.g., *Tulipa, Crocus*), than in those in which the initiation of flowering occurs after planting (e.g., *Lilium, Allium*).

Since an annual pattern is more opportunistic than a perennial pattern due to the lack of a "shortage fund," one expects to find fewer annual geophytes than perennial geophytes in deserts and steppes. Since the life cycle of annual geophytes with hysteranthous leaves is less risky than the life cycle of those with synanthous leaves, due to the separation of phases, it is reasonable to find relatively more representatives of the first group in arid environments. Thus, it is expected to find relatively larger storage organs under arid conditions, compared with those from mesophytic environments, and that the storage organs of geophytes with hysteranthous leaves would be larger than those with synanthous leaves, because of the need for keeping a larger "shortage fund." The first prediction was confirmed by Shimshi (1972) in the genera *Crocus, Colchicum,* and *Tulipa,* and there are more examples in *Scilla* and *Pancratium*; so far there is no information about the second prediction.

It is expected that the fraction of the whole perennial reserve devoted to flowering will be smaller in unpredictable regions.

In all cases, a strategy that requires a larger amount of storage material will be favored by a high conversion efficiency of the reserves and a low maintenance cost of the storage organs (Cohen, unpublished).

Perennial geophytes with hysteranthous leaves require larger reserves, and it is expected that the efficiency of utilization of reserve materials will be greater than in those with synanthous leaves and that the maintenance costs are lower in the former.

If the storage costs are high, it is expected that at least some of the leaves would be produced at the expense of current production and not out of reserves. Such a situation can be revealed by comparing the allocation of reserves for leaf production with the decline of the reserve in the storage organ (Rees, 1972:47; Grainger, 1941).

To summarize, the following conclusions can be drawn:

1. Two main patterns can be defined in geophytes: those with a perennial storage organ; and those with an annual storage organ which is completely renewed every year. In each group there are two main routes: a rapid route and a slow route with short and long periods of vegetative growth.

2. In annual geophytes with synanthous leaves, flowering will take place only after the accumulation of a minimal reserve during the photosynthetic period. This mass is termed "the critical mass." The most environmentally dependent phase would be seed production, since it seems that this phase needs additional reserves from current production. In a poor year, flowering and, especially seed production, would be very poor, if it occurred at all, due to failure to reach the "critical mass." In perennials the accumulated reserve is greater than the requirement for one year, and it is termed the "shortage fund." This reserve enables completion of flowering and seed production even if the net production that year is insufficient to complete it. Therefore relatively slight differences are expected from year to year in the abundance of flowering.

3. In annual geophytes with hysteranthous leaves, the reserve accumulated in one year must provide for flowering, seed production and leaf establishment of the next year. Annuals depend on environmental fluctuations, and if the "critical mass" is not accumulated, then flowering cannot occur. However, if it does occur, full seed production is expected, because the critical mass includes almost all the requirements for seed production also.

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