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LIFE HISTORIES AND DEMOGRAPHY OF SHADE-TOLERANT TEMPERATE FOREST HERBS: A REVIEW

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SUMMARY

Information is reviewed on the life histories and demographic patterns of shade-tolerant herbs of temperate deciduous forest. Most of the species that have been studied are deciduous perennials. These species generally have a juvenile (non-flowering) period of several years followed by an extended period of flower and seed production. About half the species reviewed are self-incompatible, the others are at least partially self-compatible. Although vegetative reproduction is common, replacement does not always occur by vegetative spread; many species appear to be able to replace themselves by seed. Sexual reproductive effort ranges from 1.5 to 50% among the species reviewed; seed weight averages 2.6 mg. Short dormancy periods (one season) are most common, with germination rates generally below 50%.

Mortality rates of small plants are high, but decline as plant size increases. 'Ageing' does not appear to occur. No information exists on population growth rates of temperate deciduous forest herbs, or on the temporal stability of their population sizes or structures. The transition matrix model is suggested as a promising approach to future studies in plant demography.

INTRODUCTION

The decade between the publication of John Harper's (1967) paper, 'A Darwinian Approach to Plant Ecology', and his (1977) book, *Population Biology of Plants*, has seen a tremendous increase in the number of studies being conducted on the life histories and demography of plants. Largely through Harper's influence, the attention of plant ecologists has finally focused on processes occurring at the population level. Yet for the vast majority of plant species, we have only extremely limited information about their life histories and population dynamics. To draw attention to this lack of information for one group of species with similar ecological requirements, I have reviewed what is known about shade-tolerant herbs of temperate deciduous forests, and tried to identify areas in particular need of investigation.

I have chosen to exclude from this review a large group of herbs that regularly occupy grassland and hedgerow as well as forest situations. Some of these more light-demanding herbs are a frequent component of deciduous forest ecosystems, especially in light gaps created by tree falls (probably their primordial habitat). But because of the difficulty involved in distinguishing among those species in fact native to light gaps, and those that occasionally invade disturbed deciduous forest, but whose natural habitat is elsewhere (e.g. dunes, rocky ledges or floodplains), I have decided to ignore all species demanding high light levels.

A review of this nature is forced, for reasons of brevity, to give little attention

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to the amount of variability that is inevitably present in all of the characteristics under discussion. I wish to emphasize, therefore, that most of the figures included here were generated by a single study, sometimes of a single population and often during only 1 year, and therefore represent only part of the range of possible values. Factors such as whether a population is growing in full or partial shade, its size or age structure, its past history, various environmental characteristics, the degree of disturbance to which it has been subjected, and the successional status of its particular plot, can influence both mean values and the amount of variation observed in many demographic parameters.

PHENOLOGY

Although most deciduous forest herbs lose their leaves, a considerable number have leaves that are winter-green, including: *Carex plantaginea* Lam., *Chamaelirium luteum* (L.) Gray, *Claytonia virginica* L., *Epigaea repens* L., *Goodyera pubescens* (Willd.) R.Br., *Hepatica acutiloba* DC. and *H. americana* (DC.) Ker. (Beatley, 1956); *Hexastylis arifolia* (Michx.) Small (Gonzalez, 1972); *Hydrophyllum appendiculatum* Michx., *Isopyrum biternatum* (Raf.) T. & G., *Maianthemum canadense* Desf., *Mitchella repens* L., *Pyrola elliptica* Nutt. and *P. rotundifolia* L., *Tiarella cordifolia* L., *Trientalis borealis* Raf., and *Viola blanda* Willd., *V. papilionacea* Pursh and *V. rostrata* Pursh (Beatley, 1956).

Leaves of the deciduous species usually emerge in early spring, as soon as the ground thaws or somewhat later, but well before the forest canopy closes. New leaves of the winter-green species usually appear just after flowering. In many species, flower initials are formed the preceding autumn and only unfold in the spring. *Arisaema triphyllum* (L.) Schott (Pickett, 1915), *Geranium maculatum* L. (Martin, 1965), *Hexastylis arifolia* (Gonzales, 1972), *Narcissus pseudonarcissus* L. (Caldwell and Wallace, 1955) and *Uvularia perfoliata* L. (Whigham, 1974) behave this way, and Foerste (1891) lists numerous others. Depending on the species, flowering may occur before, during or after canopy closure. When a species produces both chasmogamous flowers (which expand normally) and cleistogamous flowers (which are self-fertilized within the closed bud), e.g. *Oxalis acetosella* L. (Packham, 1978) and *Viola* spp., the chasmogamous flowers are generally present in the spring, the cleistogamous flowers being produced later in the summer. Although many deciduous forest herbs flower in late summer (Newell and Tramer, 1978), none of these species has been the subject of a life history study.

Seeds of spring-flowering herbs usually mature and are dispersed by mid- to late summer, and senescence of above-ground tissue takes place at about the same time. In some areas with dry summers and mild winters (e.g. parts of Japan), there is a late summer and autumn dormancy period, with growth resumed in the winter. Seed germination begins in the autumn of the same year in *Allium victorialis* Hulten (Kawano and Nagai, 1975), *Endymion non-scriptus* (L.) Garcke (Knight, 1964), *Erythronium americanum* Ker. (Muller, 1978) and *Hydrophyllum appendiculatum* (Morgan, 1971), but occurs more commonly the following spring. Seeds of some species, like *Trientalis borealis* (Anderson and Loucks, 1973), do not germinate until the autumn of their second year.

LONGEVITY

Annuals are relatively rare in forest herb communities. Struik (1965), studying records from Wisconsin forests, found that only 5.6% of forest species were annuals. Most of the annuals that do occur in deciduous forests are light-demanding species of gaps and edges; this review includes no annuals and only one biennial, *Hydrophyllum appendiculatum*. Reliable estimates of the life spans of deciduous forest perennials are not available, because long-term studies of individuals are so rarely conducted, but Table 1 presents estimated average life spans for a number of species. Although few studies make this explicit, it is probably wise to assume that these averages apply to plants that have already survived the dangerous juvenile mortality period (see 'Patterns of Mortality', p. 769). The life expectancy of a seed is probably considerably shorter. Table 1 also presents the estimated age of first flowering when such information is available. It usually takes at least several years for deciduous forest herbs to reach sexual maturity; just how long depends greatly on local conditions, especially light availability and amount of competition.

Table 1. *Estimated average life spans and age of first sexual reproduction. Figures are for ramets unless otherwise indicated*

| Species | Life span (years) | Age of first reproduction (years) | Reference |
|--|------------------------------|-----------------------------------|------------------------------|
| <i>Allium ursinum</i> L. | 8-10 | 4-5 | Ernst (1979) |
| <i>A. victorialis</i> | 10-15 | 8-9 | Kawano & Nagai (1975) |
| <i>Anemone hepatica</i> L. | at least 6-30 | — | Persson (1975) |
| <i>A. nemorosa</i> L. | at least 9-13 | — | Persson (1975) |
| <i>Anemone</i> sp. | 25-30 | — | Ernst (1979) |
| <i>Arisaema triphyllum</i> | 15-25 | 5 | Bierzchudek (unpub. data) |
| <i>Arnica cordifolia</i> Hook. | 12 | — | Treshow & Harper (1974) |
| <i>Arum maculatum</i> L. | — | 7 | Sowter (1949) |
| <i>Chamaelirium luteum</i> | — | — | Meagher (1978) |
| <i>Desmodium nudiflorum</i> (L.) DC. | 10 or more | — | Schaal & Smith (1980) |
| <i>Hexastylis arifolia</i> | 15 | 7-10 | Gonzalez (1972) |
| <i>Lilium cordatum</i> (Thunb.) Koidz. | — | 10 | Kawano (1975) |
| <i>Maianthemum bifolium</i> (L.) F. W. Schmidt | — | 'a number' | Kawano <i>et al.</i> (1968) |
| <i>M. dilatatum</i> (Wood) A. Nels. & Macbr. | — | 'a number' | Kawano <i>et al.</i> (1968) |
| <i>Mitchella repens</i> | at least 15 for large clones | — | Hicks (pers. comm.) |
| <i>Narcissus pseudonarcissus</i> | 12 (shade)-18 (sun) | — | Barkham (1980a) |
| <i>Oxalis acetosella</i> | 'several' | 1 | Packham (1978) |
| <i>Polygonatum multiflorum</i> (L.) All. | 35 | — | Ernst (1979) |
| <i>Primula veris</i> L. | 5-6 | — | Tamm (1948) |
| <i>Teucrium scorodonia</i> L. | 50-100 for large clones | 7-10 | Hutchinson (1968) |
| <i>Thalictrum fendleri</i> Engelm. | 12 | — | Treshow & Harper (1974) |
| <i>Uvularia perfoliata</i> | — | 3 | Whigham (1974) |
| <i>Viola</i> spp. | 10 | 4 | Cook (1979) |
| <i>Viola sororia</i> Willd. | 10-14 | — | Solbrig <i>et al.</i> (1980) |

MODES OF REPRODUCTION

Typically, deciduous forest herbs can reproduce by vegetative spread as well as by seed. It is commonly believed that replacement through seed production is rare in these species (e.g. Abrahamson, 1980). However, this belief is not supported by the published trends. Table 2 lists the predominant means of replacement, and the frequency with which seedlings have been observed, for some species of forest herbs. Only half the species studied rely on vegetative reproduction as a primary means of population growth; in the others, authors have felt that seed production, germination and establishment are at least frequent enough to replace those individuals that die.

Even for those species that replace themselves primarily vegetatively, seeds are necessary for the establishment of new populations, and nearly all species flower and produce seeds regularly. Table 3 provides information on the breeding systems of many deciduous forest herbs. It is necessary to interpret this information cautiously, however, because breeding systems, especially degrees of compatibility, can vary widely among different populations of the same species. In general, though, most species possess hermaphroditic flowers; partial or complete self-incompatibility is exhibited by about half of the species, self-compatibility by the others.

The pollination syndromes of deciduous forest herbs vary widely. The most commonly-observed pollinators are the honeybee, *Apis mellifera*, many species of bumble bees, andrenid and halictid bees and bombyliid and syrphid flies; many plants are visited by more than one species of potential pollinator. A few species are pollinated by fungus gnats and/or thrips (e.g. *Arisaema triphyllum*: Bierzychudek, 1981a; Rust, 1980), and a few species are wind-pollinated (e.g. *Thalictrum dioicum*: Melampy and Hayworth, 1980). Because almost nothing is known about pollen dispersal distances, we know very little about the genetic structure of any of these species.

REPRODUCTIVE EFFORT

In addition to the existence of intrinsic species-specific differences, measures of reproductive effort can vary for a number of other reasons. Methodology is not standardized; some investigators include below-ground parts, while others do not; some measure the energy of flowers and seeds, others simply that of seeds; some sample periodically over a season, others once a year. Underlying this source of variability is that caused by the various factors referred to in the Introduction. The only generalization one can make with assurance is that the amount of energy devoted to sexual reproduction (i.e. flower and seed production) is usually less for forest herbs than for herbs of grasslands or early-successional habitats (Newell and Tramer, 1978; Abrahamson, 1979). It is impossible to judge whether species relying primarily on seeds for replacement devote more effort to sexual reproduction than do species that commonly reproduce vegetatively, because this information is not available. Table 4 lists sexual reproductive effort for many forest herbs.

The way energy is distributed among propagules represents another important difference between shade-tolerant and light-demanding herbs. Seeds of shade-tolerant species tend to be heavier (Salisbury, 1942), presumably because, when competition for light is intense, embryos require a greater supply of food to assure successful establishment. The mean dry wt per seed of the species listed in Table 5

Table 2. *The predominant (as determined by the investigator) reproductive mode, and the frequency of seedlings*

| Species | Predominant means of replacement | Seedlings observed in field? | Reference |
|------------------------------------|----------------------------------|------------------------------|-----------------------------|
| <i>Allium ursinum</i> | Seed | Often | Tutin (1957) |
| <i>A. monanthum</i> Maxim. | Vegetative | No | Kawano & Nagai (1975) |
| <i>A. victorialis</i> | Seed | 'Regularly' | Kawano & Nagai (1975) |
| <i>Anemone hepatica</i> | — | 'Large numbers' | Persson (1975) |
| <i>A. nemorosa</i> | — | 'Large numbers' | Persson (1975) |
| <i>Arisaema triphyllum</i> | Vegetative | Yes, some | Bierzchudek (1981a) |
| <i>Arnica cordifolia</i> | Seed | — | Treshow & Harper (1974) |
| <i>Arum maculatum</i> | Vegetative | — | Sowter (1949) |
| <i>Chamaelirium luteum</i> | Seed; no vegetative reproduction | Yes | Meagher (1978) |
| <i>Desmodium nudiflorum</i> | Seed; no vegetative reproduction | Yes | Schaal & Smith (1980) |
| <i>Endymion non-scriptus</i> | Seed | 'Constantly' | Knight (1964) |
| <i>Erythronium americanum</i> | Vegetative | Rarely | Holland (1974) |
| <i>Fragaria vesca</i> L. | Vegetative | — | Tamm (1948) |
| <i>Hexastylis arifolia</i> | Seed | Yes | Gonzalez (1972) |
| <i>Hydrophyllum appendiculatum</i> | Seed | — | Morgan (1971) |
| <i>Maianthemum bifolium</i> | Vegetative | Only 1 in 4 years | Kawano <i>et al.</i> (1968) |
| <i>Maianthemum dilatatum</i> | Vegetative | Only 1 in 4 years | Kawano <i>et al.</i> (1968) |
| <i>Mercurialis perennis</i> L. | Vegetative | Yes, some | Hutchings & Barkham (1976) |
| <i>Mitchella repens</i> | Vegetative | No | Hicks (pers. comm.) |
| <i>Narcissus pseudonarcissus</i> | Vegetative | Yes | Barkham (1980a) |
| <i>Oxalis acetosella</i> | — | Regularly | Packham (1978) |
| <i>Sanicula europaea</i> L. | — | Common | Tamm (1948) |
| <i>Teucrium scorodonia</i> | Vegetative | Yes | Hutchinson (1968) |
| <i>Thalictrum fendleri</i> | Seed | — | Treshow & Harper (1974) |
| <i>Trientalis borealis</i> | Vegetative | None | Anderson & Loucks (1973) |
| <i>Uvularia perfoliata</i> | Vegetative | 11 m ⁻² | Whigham (1974) |

Table 3. *Breeding systems*

| Species | Breeding system | Compatibility | Reference |
|---|--|------------------------------------|-------------------------------|
| <i>Allium monanthum</i> | Populations vary from dioecious to hermaphrodite to (mostly) unisexual | Varies; no apogamy | Kawano & Nagai (1975) |
| <i>A. victorialis</i> | Hermaphrodite | Autogamous | Kawano & Nagai (1975) |
| <i>Arisaema dracontium</i> (L.) Schott | Monoeocious | Self-incompatible | Cole (1962) |
| <i>A. triphyllum</i> | Sequentially hermaphrodite, functionally dioecious | — | Bierzychudek (in press) |
| <i>Arum maculatum</i> | Monoeocious | ? | Sowter (1949) |
| <i>Asarum canadense</i> L. | Hermaphrodite | Autogamous | Wildman (1950) |
| <i>Carex pedunculata</i> Muhl. | Monoeocious | Self-compatible | Handel (1976) |
| <i>C. plantaginea</i> | Monoeocious | ? | Handel (1976) |
| <i>C. platyphylla</i> Carey | Monoeocious | ? | Handel (1976) |
| <i>Chamaelirium luteum</i> | Dioecious | — | Meagher (1978) |
| <i>Claytonia virginica</i> | Hermaphrodite | Self-incompatible | Schemske <i>et al.</i> (1978) |
| <i>Dentaria laciniata</i> Muhl. | Hermaphrodite | Self-compatible | Schemske <i>et al.</i> (1978) |
| <i>Desmodium nudiflorum</i> | Hermaphrodite | Partially self-compatible | Schaal & Smith (1980) |
| <i>Dicentra canadensis</i> (Goldie) Walp. | Hermaphrodite | Self-incompatible | Schemske <i>et al.</i> (1978) |
| <i>D. cucullaria</i> (L.) Bernh. | Hermaphrodite | Self-incompatible | East (1940) |
| <i>Endymion non-scriptus</i> | Hermaphrodite | Self-incompatible | Knight (1964) |
| <i>Erythronium albidum</i> L. | Hermaphrodite | Self-compatible | Schemske <i>et al.</i> (1978) |
| <i>Geranium maculatum</i> | Hermaphrodite | Partially self-compatible | Martin (1965) |
| <i>Goodyera repens</i> (L.) R.Br. | Hermaphrodite | Partially self-compatible | Hagerup (1952) |
| <i>Isopyrum biternatum</i> | Hermaphrodite | Self-compatible but not autogamous | Melampy & Hayworth (1980) |
| <i>Maianthemum bifolium</i> | Hermaphrodite | Self-incompatible | Kawano <i>et al.</i> (1968) |
| <i>M. dilatatum</i> | Hermaphrodite | Self-incompatible | Kawano <i>et al.</i> (1968) |
| <i>Mercurialis perennis</i> | Dioecious | — | Hutchings & Barkham (1976) |
| <i>Mitchella repens</i> | Hermaphrodite, heterostylous | Self-incompatible | Hicks (pers. comm.) |

Table 3 (cont.)

| Species | Breeding system | Compatibility | Reference |
|---|--|---|---------------------------|
| <i>Narcissus pseudonarcissus</i> | Hermaphrodite | 'Probably self-incompatible' | Caldwell & Wallace (1955) |
| <i>Oxalis acetosella</i> | Hermaphrodite, both cleistogamous and chasmogamous flowers | Partially self-compatible | Packham (1978) |
| <i>Panax quinquefolius</i> L. | Polygamodioecious | ? | Fryxell (1957) |
| <i>Pyrola minor</i> L. | Hermaphrodite | Partially or completely self-compatible | Hagerup (1954) |
| <i>Sanguinaria canadensis</i> L. | Hermaphrodite | Facultatively autogamous | Schemske (1978) |
| <i>Smilacina racemosa</i> (L.) Desf. | Hermaphrodite | Obligately apomictic | Gorham (1953) |
| <i>Teucrium scorodonia</i> | Hermaphrodite | Partially self-compatible | Hutchinson (1968) |
| <i>Thalictrum clavatum</i> L. | Hermaphrodite | Self-compatible | Melampy & Hayworth (1980) |
| <i>T. dioicum</i> L. | Dioecious | — | Melampy & Hayworth (1980) |
| <i>T. polygamum</i> L. | Androdioecious, functionally dioecious | — | Melampy & Hayworth (1980) |
| <i>Trillium erectum</i> L. | Hermaphrodite | Obligately apomictic | Jeffrey & Haertl (1939) |
| <i>T. grandiflorum</i> (Michx.) Salisb. | Hermaphrodite | Obligately apomictic | Jeffrey & Haertl (1939) |
| <i>T. sessile</i> L. | Hermaphrodite | Obligately apomictic | Jeffrey & Haertl (1939) |
| <i>T. undulatum</i> Willd. | Hermaphrodite | Obligately apomictic | Jeffrey & Haertl (1939) |
| <i>Uvularia perfoliata</i> | Hermaphrodite | Mostly self-incompatible | Whigham (1974) |
| <i>Viola blanda</i> | Hermaphrodite, both cleistogamous and chasmogamous flowers | Partially self-compatible | Cook (1979) |
| <i>V. fimbriatula</i> Sm. | Hermaphrodite, both cleistogamous and chasmogamous flowers | Partially self-compatible | Cook (1979) |
| <i>V. rostrata</i> | Hermaphrodite, both cleistogamous and chasmogamous flowers | Partially self-compatible | Thompson & Beattie (1981) |
| <i>V. sororia</i> | Hermaphrodite, both cleistogamous and chasmogamous flowers | Partially self-compatible | Cook (1979) |

Table 4. Mean percentage of biomass devoted to sexual reproduction. When a range is indicated, values are for different sites or different studies

| Species | Reproductive effort (%) | Reference |
|--|-------------------------|--|
| <i>Allium victorialis</i> | 2·6* | Kawano & Nagai (1975) |
| <i>Anemone virginiana</i> L. | 21·0 | Abrahamson (1979) |
| <i>Anemonella thalictroides</i> (L.) Spach. | 7·0 | Abrahamson (1979) |
| <i>Arisaema triphyllum</i> | 6·7–10·9 | Bierzzychudek (1981a) |
| <i>Cardamine bulbosa</i> (Schreb.) BSP. | 7 | Newell & Tramer (1978) |
| <i>Cimicifuga racemosa</i> (L.) Nutt. | 5·0 | Abrahamson (1979) |
| <i>Circaea quadrisulcata</i> (Maxim.) Franch & Sav. | 3·0–6·0 | Struik (1965) |
| <i>Claytonia virginica</i> | 49·0–51·0 | Schemske <i>et al.</i> (1978), Abrahamson (1979) |
| <i>Clintonia udensis</i> Traut. & C. A. Mey | 5·9* | Kawano (1975) |
| <i>Dentaria laciniata</i> | 1–27·0 | Newell & Tramer (1978), Schemske <i>et al.</i> (1978) |
| <i>Desmodium glutinosum</i> (Muhl.) Wood | 17·0 | Abrahamson (1979) |
| <i>Dicentra canadensis</i> | 14·0 | Schemske <i>et al.</i> (1978) |
| <i>D. cucullaria</i> | 8·0–19·0 | Schemske <i>et al.</i> (1978), Abrahamson (1979) |
| <i>Disporum sessile</i> Don. | 1·5 | Kawano (1975) |
| <i>D. smilacinum</i> A. Gray | 3·2 | Kawano (1975) |
| <i>Erythronium albidum</i> | 14·0–16·0 | Schemske <i>et al.</i> (1978), Muller (1979) |
| <i>E. americanum</i> | 20·0 | Abrahamson (1979) |
| <i>E. japonicum</i> Decne. | 17·5 | Kawano (1975) |
| <i>Fragaria virginiana</i> Duchesne. | 5 | Holler & Abrahamson (1977) |
| <i>Fritillaria japonica</i> Miq. | 4·5 | Kawano (1975) |
| <i>Geranium maculatum</i> | 14·0 | Abrahamson (1979) |
| <i>Geum canadense</i> Jacq. | 17·0 | Abrahamson (1979) |
| <i>Hieracium venosum</i> L. | 43·0 | Abrahamson (1979) |
| <i>Isopyrum biternatum</i> | 3·4–5·0 | Schemske <i>et al.</i> (1978), Melampy & Hayworth (1980) |
| <i>Lilium cordatum</i> | 13·0 | Kawano (1975) |
| <i>Lysimachia quadrifolia</i> L. | 2·0 | Abrahamson (1979) |
| <i>Mertensia virginica</i> L. | 7·0 | Abrahamson (1979) |
| <i>Podophyllum peltatum</i> L. | 2·0–10·0 | Sohn & Policansky (1977), Newell & Tramer (1978) |
| <i>Polygonum virginianum</i> L. | 2 | Newell & Tramer (1978) |
| <i>Prenanthes alba</i> L. | 11 | Newell & Tramer (1978) |

Table 4. (cont.)

| Species | Reproductive effort (%) | Reference |
|--|---------------------------|-------------------------------|
| <i>Sanguinaria canadensis</i> | 15.0 | Schemske <i>et al.</i> (1978) |
| <i>Sanicula gregaria</i> Bickn. | 5 | Newell & Tramer (1978) |
| <i>Saxifraga virginensis</i> Michx. | 10.0 | Abrahamson (1979) |
| <i>Smilacina japonica</i> A. Gray | 6.7* | Kawano (1975) |
| <i>S. robusta</i> Makino & Honda | 14.1* | Kawano (1975) |
| <i>Streptopus streptopoides</i> (Ledeb.) Frye & Rigg. | 2.5* | Kawano (1975) |
| <i>Thalictrum clavatum</i> | 5* | Melampy & Hayworth (1980) |
| <i>T. dioicum</i> | 5* (for female plants) | Melampy & Hayworth (1980) |
| <i>T. polygamum</i> | 4* (for female plants) | Melampy & Hayworth (1980) |
| <i>Trientalis borealis</i> | 2.0 | Anderson & Loucks (1973) |
| <i>Trillium grandiflorum</i> | 10 | Newell & Tramer (1978) |
| <i>Viola blanda</i> | 4.9 | Thompson & Beattie (1981) |
| <i>V. papilionacea</i> | 4.0 | Abrahamson (1979) |
| <i>V. rostrata</i> | 9.3 | Thompson & Beattie (1981) |

* Figure represents investment in seeds only, not flowers.

is 4.98 ± 8.18 mg, but if the two species with extremely heavy seeds, *Arisaema triphyllum* and *Hydrophyllum appendiculatum*, are excluded this figure drops to 2.59 ± 2.45 mg.

Because reproductive effort is lower, and individual seeds heavier, the total number of seeds produced per plant per year must be much lower for forest herbs than for light-demanding ones. And for species with any degree of self-incompatibility, if there is competition for pollinators, not all ovules may be fertilized; this also contributes to low seed numbers. Pollination success for *Maianthemum bifolium* and *M. dilatatum*, an extreme case, is less than 5% (Kawano, Ihara and Suzuki, 1968). Levels of mean seed production per plant per year are listed in Table 6. Because several studies suggest that levels of seed production may be limited by the activity of pollinators (Schemske *et al.*, 1978; Bierzychudek, 1981b), the values of reproductive effort in Table 4 should not be considered to represent physiologically maximum levels; they may be much lower than what a fully-pollinated individual is able to achieve.

Year-to-year and site-to-site variability in seed production is typical, since this process depends heavily on levels of light and competition.

Table 5. Mean dry weight (mg per seed)

| Species | Mean dry wt (mg) | Reference |
|------------------------------------|------------------|---|
| <i>Allium ursinum</i> | 5.4 | Ernst (1979) |
| <i>A. victorialis</i> | 6.0 | Kawano <i>et al.</i> (1968) |
| <i>Anemone virginiana</i> | 0.7 | Abrahamson (1979) |
| <i>Arisaema triphyllum</i> | 34.4 | Bierzychudek (1981a) |
| <i>Cimicifuga racemosa</i> | 2.9 | Abrahamson (1979) |
| <i>Claytonia virginica</i> | 1.2-1.3 | Schemske <i>et al.</i> (1978), Abrahamson (1979) |
| <i>Dentaria laciniata</i> | 1.8 | Schemske <i>et al.</i> (1978) |
| <i>Desmodium glutinosum</i> | 0.03 | Abrahamson (1979) |
| <i>Dicentra canadensis</i> | 1.0 | Schemske <i>et al.</i> (1978) |
| <i>D. cucullaria</i> | 1.2-2.0 | Schemske <i>et al.</i> (1978), Abrahamson (1979) |
| <i>Erythronium albidum</i> | 6-9.7 | Muller (1979), Schemske <i>et al.</i> (1978) |
| <i>Geranium maculatum</i> | 5.6 | Abrahamson (1979) |
| <i>Geum canadense</i> | 0.8 | Abrahamson (1979) |
| <i>Hieracium venosum</i> | 0.3 | Abrahamson (1979) |
| <i>Hydrophyllum appendiculatum</i> | 21.0 | Morgan (1971) |
| <i>Isopyrum biternatum</i> | 2.2 | Schemske <i>et al.</i> (1978) |
| <i>Lysimachia quadrifolia</i> | 0.8 | Abrahamson (1979) |
| <i>Mitchella repens</i> | 2.3 | D. Hicks (pers. comm.) |
| <i>Sanguinaria canadensis</i> | 7.1 | Schemske <i>et al.</i> (1978) |
| <i>Thalictrum clavatum</i> | 0.7 | Melampy & Hayworth (1980) |
| <i>T. dioicum</i> | 1.7 | Melampy & Hayworth (1980) |
| <i>T. polygamum</i> | 1.6 | Melampy & Hayworth (1980) |

SEED DISPERSAL AND GERMINATION

Many deciduous forest herbs lack any special seed dispersal mechanisms; the diaspores simply fall off their stems when mature. Since by this time senescence of above-ground parts is well under way, stems are usually prostrate at the time

Table 6. Yearly mean seed production. When a range is indicated, values are from different sites or different years

| Species | Seeds per plant per year | Reference |
|---|--------------------------|---|
| <i>Allium monanthum</i> | 0 | Kawano & Nagai (1975) |
| <i>A. tricoccum</i> Ait. | 15 | Curtis (1959) |
| <i>A. ursinum</i> | 20 | Ernst (1979) |
| <i>A. victorialis</i> | 34·8 | Kawano & Nagai (1975) |
| <i>Arisaema triphyllum</i> | 5·2 | Bierzchudek (in press) |
| <i>Arum maculatum</i> | 38 | Sowter (1949) |
| <i>Cardamine bulbosa</i> | 33 | Newell & Tramer (1978) |
| <i>Caulophyllum thalictroides</i> (L.) Michx. | 7 | Curtis (1959) |
| <i>Claytonia virginica</i> | 29–47 | Schemske <i>et al.</i> (1978) |
| <i>Clintonia udensis</i> | 31 | Kawano (1975) |
| <i>Dentaria laciniata</i> | 24–66 | Newell & Tramer (1978), Schemske <i>et al.</i> (1978) |
| <i>Desmodium nudiflorum</i> | 31 | Schaal & Smith (1980) |
| <i>Dicentra canadensis</i> | 2–7 | Schemske <i>et al.</i> (1978) |
| <i>D. cucullaria</i> | 14–57 | Curtis (1959), Schemske <i>et al.</i> (1978) |
| <i>Disporum sessile</i> | 4·7 | Kawano (1975) |
| <i>D. smilacinum</i> | 1·5 | Kawano (1975) |
| <i>Endymion non-scriptus</i> | 2–13·1 | Knight (1964) |
| <i>Erythronium albidum</i> | 0·5–5·8 | Schemske <i>et al.</i> (1978), Muller (1979) |
| <i>E. americanum</i> | 4–7 | Muller (1978) |
| <i>E. japonicum</i> | 16·6–27·1 | Kawano (1975) |
| <i>Fritillaria japonica</i> | 37 | Kawano (1975) |
| <i>Geranium maculatum</i> | 25 | Martin (1965) |
| <i>Hepatica acutiloba</i> | 90 | Curtis (1959) |
| <i>Hexastylis arifolia</i> | 22 | Gonzalez (1972) |
| <i>Hydrophyllum appendiculatum</i> | 36–41 | Morgan (1971) |
| <i>Isopyrum biternatum</i> | 4–9 | Schemske <i>et al.</i> (1978) |
| <i>Lilium cordatum</i> | 452 | Kawano (1975) |
| <i>Maianthemum bifolium</i> | 0·6–4·3 | Kawano <i>et al.</i> (1978) |
| <i>M. dilatatum</i> | 0–4·8 | Kawano <i>et al.</i> (1978) |
| <i>Mitchella repens</i> | 1000/large clone | Hicks (pers. comm.) |
| <i>Narcissus pseudonarcissus</i> | 34–42 | Caldwell & Wallace (1955) |
| <i>Podophyllum peltatum</i> | 33 | Curtis (1959) |
| <i>Prenanthes alba</i> | 118 | Newell & Tramer (1978) |
| <i>Ranunculus ficaria</i> L. | 73 | Taylor & Markham (1978) |
| <i>Sanguinaria canadensis</i> | 24–35 | Schemske (1977), Schemske <i>et al.</i> (1978) |
| <i>Sanicula gregaria</i> | 26 | Newell & Tramer (1978) |
| <i>Smilacina japonica</i> | 24·9 | Kawano (1975) |
| <i>S. racemosa</i> | 11 | Curtis (1959) |
| <i>S. robusta</i> | 139 | Kawano (1975) |
| <i>Streptopus streptopoides</i> | 28 | Kawano (1975) |
| <i>Trientalis borealis</i> | 9·4 | Anderson & Loucks (1973) |
| <i>Trillium recurvatum</i> Beck | 29 | Curtis (1959) |
| <i>Uvularia grandiflora</i> Sm. | 10 | Curtis (1959) |
| <i>U. perfoliata</i> | 4·1 | Whigham (1974) |
| <i>Viola pubescens</i> Ait. | 20 | Curtis (1959) |

of seed dispersal. Therefore, the distance seeds are dispersed from the parent is often not more than the height of the stem. Species that simply drop their seeds to the ground include *Allium ursinum* (Ernst, 1979), *Carex plantaginea* and *C. platyphylla* (Handel, 1976), *Endymion non-scriptus* (Knight, 1964), *Hydrophyllum appendiculatum* (Morgan, 1971), *Isopyrum biternatum* (Schemske *et al.*, 1978),

Table 7. *Germination rates*

| Species | Germination (%) | Conditions | Reference |
|----------------------------------|-----------------|---|--|
| <i>Allium ursinum</i> | 56-63 | In laboratory, on moist filter paper, after 4 months at 15 to 20 °C and 4 months at 5 to 10 °C | Ernst (1979) |
| <i>Arisaema triphyllum</i> | 20 | In field, protected from seed predators | Bierzychudek (in press) |
| <i>Carex plantaginea</i> | 21.8 | In laboratory, in soil in growth chamber simulating natural conditions; 13 months after sowing | Handel (1978) |
| <i>C. platyphylla</i> | 4.3 | | |
| <i>Endymion non-scriptus</i> | 80 | In field Sown in clay pots in humus or sand in March, left outside; cotyledons counted 4 mo. later | Knight (1964) Kawano <i>et al.</i> (1968) |
| <i>Maianthemum bifolium</i> | 38-43 | | |
| <i>M. dilatatum</i> | 54-60 | In field, untreated With long stratification and chemical or physical scarification | D. Hicks (pers. comm.) |
| <i>Mitchella repens</i> | 0 10-20 | | |
| <i>Narcissus pseudonarcissus</i> | up to 50 | Details not given (presumably in lab.) | Caldwell & Wallace (1955) |
| <i>Teucrium scorodonia</i> | 60-80 | If collected in October (in lab.) | Hutchinson (1968) |
| | 80-100 | If collected in January (in lab.) | |

Narcissus pseudonarcissus (Barkham, 1980a) and perhaps *Arum maculatum* (Sowter, 1949). Ants disperse the seeds of *Hexastylis arifolia* (Gonzalez, 1972), and Handel (1976) provides a long list of other forest herbs, including *Carex pedunculata*, that are thought to be ant-dispersed. *Geranium maculatum* (Martin, 1965) releases seeds explosively (usually 1 to 2 m, but sometimes up to 9 m), as do *Claytonia virginica* (Schemske, 1978) and *Dentaria laciniata* (Schemske *et al.*, 1978). Many of the species in the Araceae and Liliaceae have seeds surrounded by fleshy berries; birds and probably mammals eat and disperse berries of *Arum maculatum* (Sowter, 1949) and *Arisaema triphyllum* (Bierzychudek, 1981a). Animals brushing against capsules of *Endymion non-scriptus* throw seeds 1 to 2 m (Knight, 1964). Fruits of *Desmodium nudiflorum* (beggar's ticks) are covered by hooked hairs that adhere to the fur of mammals and thus may be carried long distances (Schaal and Smith, 1980).

Seeds of most species will not germinate without undergoing a cold treatment, but only a few have dormancy periods of longer than 6 months. These include *Carex plantaginea* and *C. platyphylla* (Handel, 1978) and *Trientalis borealis* (Anderson and Loucks, 1973), which germinate during the autumn of their second year. Some seeds of *Arisaema triphyllum* appear to do likewise (Bierzychudek, personal observation). Seeds of *Viola* spp. are dormant for at least 1 to 2 years (Cook, 1979). The dormancy period of some species is shorter than it appears, because during their first season they produce only roots, and no above-ground parts. Species exhibiting this 'cryptic' germination include *Allium victorialis* (Kawano and Nagai, 1975), *Hydrophyllum appendiculatum* (Morgan, 1971), *Uvularia perfoliata* (Whigham, 1974), and some individuals of *Arisaema triphyllum* (Pickett, 1913).

Most germination tests are performed in the laboratory, where germination success is usually better than what can be expected in the field, because seeds are provided with 'ideal' conditions. Rates for some species are listed in Table 7; they range from 4.3% for *Carex platyphylla* (Handel, 1978) to 80% for *Endymion non-scriptus* (Knight, 1964). Germination rates under several different kinds of laboratory conditions for an additional 35 species are given by Struik (1965); only eight of these had rates exceeding 50%.

PATTERNS OF MORTALITY

Almost universally, small or young plants are reported to have higher mortality rates than larger or adult (sexually reproductive) plants. This pattern appears to hold not simply for deciduous forest herbs, but for plants in general (Harper, 1977). However, the actual number of studies that have attempted to measure the mortality rates of forest herbs is rather limited.

Mortality during the first 2 years of life for *Allium ursinum* is reported at 21.2%, a rather low figure by comparison with most others. But Ernst (1979) says this rate increases during a plant's third year, when its bulb develops contractile roots that pull it deeper into the ground, where (he says) it is subjected to attack by insects and nematodes. The presence of contractile roots is common among forest monocotyledons: at least, *Arisaema triphyllum* (Pickett, 1915), *Arum maculatum* (Sowter, 1949), *Endymion non-scriptus* (Knight, 1964) and *Narcissus pseudonarcissus* (Barkham, 1980b) have them as well. Mortality during the third or fourth year of seedlings of *Allium ursinum* is high enough that only about 1 to 10% of seedlings reach reproductive age (4 to 5 years).

Cook (1979) has measured mortality rates of *Viola* seedlings. *V. sororia* has a mortality rate of 79% during its first year; mortalities for *V. blanda* and *V.*

fimbriatula are smaller, but are still high. Most mortality occurs during the winter; summer mortality is usually a result of grazing or drought. The probability of death depends on the size of the individual and declines with growth (Cook, 1980). Mortality rates of *V. blanda* seedlings are much lower (less than 50% per year) in plots from which adult plants have been removed than in undisturbed plots (about 90% per year) (Solbrig, 1980).

Seedling *Chamaelirium luteum* have annual mortality rates ranging from 20.1 to 27.3% in their first year, 10 to 15.1% in their second and 12.6% in their third. Larger, but subadult plants have annual mortality rates of 8.4 to 10.8% (Meagher and Antonovics, in press). Within particular size classes, mortality of these subadults declines with increasing size.

Winter mortality is also high for young *Hydrophyllum appendiculatum* (Morgan, 1971). While the summer mortality of first-year plants (from seeds that germinated the preceding fall) was measured at only 0.5%, mortality during the following winter varied from 17 to 91% for different cohorts. Tamm (1948) describes mortality for seedlings of *Primula veris* and *Anemone hepatica* as 'very high'. In his observations, *Sanicula europaea* seedlings suffered 60% mortality, while that of older, but still small plants was 30%. He measured the mortality rate for new vegetatively-produced plants of *Fragaria vesca* at only 18.1%, but these plants were nearly as large as the parents that produced them, though with smaller root systems. Gonzalez (1972) reports mortality rates of 96.5% for clumped seedlings of *Hexastylis arifolia*, 86.5% for dispersed seedlings. Finally, none of 160 seeds of *Teucrium scorodonia* sown in the field survived to the age of 18 months (Hutchinson, 1968).

'Juveniles' of *Narcissus pseudonarcissus* possess yearly mortality rates ranging from 20.2% (in the shade) to 43.1% (in a more open site). These figures represent means of at least 3 years of data (Barkham, 1980a). Plants characterized by Barkham as 'subadult' had lower mortality rates, 7.9% (shade) to 9.6% (sun) per year.

The mortality rate of *Arisaema triphyllum* plants having leaf areas of less than 50 cm² (these included seedlings of 1 year and older as well as vegetatively-produced plants) ranged from 21 to 38%, and varied with the site of the population (Bierzychudek, in press). Levels of adult mortality on the other hand, were much lower. Usually fewer than 10% of the sexually reproductive *A. triphyllum* died per year; this rate did not depend on the size of the plant or its sex, but was constant once reproductive maturity had been reached. Kawano (1975) reported similar results for Japanese forest herbs. He measured Deevy type II survivorship curves (i.e. constant risk of death for all size or age classes), once plants reached maturity, for *Erythronium japonicum*, *Fritillaria japonica*, *Lilium cordatum* and *Trillium tschnoskii*. Tamm (1948) measured yearly risk of death for *Anemone hepatica* (0.6%), *Fragaria vesca* (6.3%), and *Sanicula europaea* (0.4%); he did not distinguish between plants of different sizes once adulthood had been reached. Barkham (1980a) reports mortality rates for adult *Narcissus pseudonarcissus* growing in the shade and in the open of 5.6 and 3.8% per year respectively. The annual mortality rates of male and female *Chamaelirium luteum* are 1.3 to 3.0% and 2.6 to 5.1% respectively (Meagher and Antonovics, in press). In a somewhat different habitat (dry, open, aspen forests in western North America), Treshow and Harper (1974) measured mortality rates for adult *Arnica cordifolia* and *Thalictrum fendleri* at 7.5% per year. These low rates of adult mortality are the basis for the long life spans estimated for all these plants (Table 1). *Erythronium americanum* may be an exception to the pattern; Muller (1978) estimates 59%

annual mortality, but does not say whether juvenile plants are included in this figure.

There seems to be no increase in mortality rates for very old or very large individuals. For most of these species, tissue is continually renewed. Old tissue is sloughed from the bottoms of *Arisaema* corms as new tissue is added to the top, so that no part of any plant, even one 20 years old, is ever really over 4 years old (Pickett, 1912). In rhizomatous species, old rhizomes decay as new ones are produced. If no tissue ever really achieves 'old age', then there is no reason to expect senescence, or increasing mortality with age.

POPULATION STRUCTURE AND STABILITY

There is information on the densities of some species of forest herbs, but these figures should be viewed with caution. Generally, the species chosen for study are those that are most common, and the sites chosen for study are the places these common species are most abundant. Therefore, most of the information in Table 7 should be considered the maximum density likely to be encountered rather than the average density.

To analyze population structure, individuals are usually classified by size rather

Table 8. *Population densities of ramets. When a range is indicated, values are for different years or different sites. (R) indicates that quadrats were randomly placed*

| Species | Mean population density m ⁻² | Reference |
|---|---|---|
| <i>Allium ursinum</i> | 320-3350 | Ernst (1979) |
| <i>Arisaema triphyllum</i> | 2-5.6 | Bierzuchudek (in press) |
| <i>Cardamine douglasii</i> (Torr.) Britt. | 0.7 (R) | Brewer (1980) |
| <i>Carex pennsylvanica</i> Lam. | 0.5 (R) | Brewer (1980) |
| <i>Claytonia virginica</i> | 28-122.8 (R) | Schemske <i>et al.</i> (1978), Brewer (1980) |
| <i>Dentaria laciniata</i> | 2.6-7 (R) | Schemske <i>et al.</i> (1978), Brewer (1980) |
| <i>Desmodium nudiflorum</i> | 1-2 | Schaal & Smith (1980) |
| <i>Dicentra canadensis</i> | 0.3-35.1 (R) | Schemske <i>et al.</i> (1978), Brewer (1980) |
| <i>D. cucullaria</i> | 1.3-1.9 (R) | Schemske <i>et al.</i> (1978) |
| <i>Epifagus virginiana</i> (L.) Bart. | 0.7 (R) | Brewer (1980) |
| <i>Erigenia bulbosa</i> (Michx.) Nutt. | 5.8 (R) | Brewer (1980) |
| <i>Erythronium albidum</i> | 1-330 (R) | Schemske <i>et al.</i> (1978), Muller (1979) |
| <i>E. americanum</i> | 107.1 (R) | Brewer (1980) |
| <i>Hepatica acutiloba</i> | 0.28 (R) | Brewer (1980) |
| <i>Hexastylis arifolia</i> | 3 | Gonzalez (1972) |
| <i>Isopyrum biternatum</i> | 1 (R) | Schemske <i>et al.</i> (1978) |
| <i>Laportea canadensis</i> (L.) Wedd. | 0.28 (R) | Brewer (1980) |
| <i>Maianthemum bifolium</i> | 70 | Kawano <i>et al.</i> (1968) |
| <i>M. dilatatum</i> | 202 flowering scapes | Kawano <i>et al.</i> (1968) |
| <i>Mercurialis perennis</i> | 219 | Hutchings & Barkham (1976) |
| <i>Mitchella repens</i> | up to 800 | D. Hicks (pers. comm.) |
| <i>Phlox divaricata</i> | 0.07 (R) | Brewer (1980) |
| <i>Sanguinaria canadensis</i> | 0.1-0.3 (R) | Schemske <i>et al.</i> (1978) |
| <i>Uvularia perfoliata</i> | 241 | Whigham (1974) |
| <i>Viola blanda</i> | 8.6-18.4 (R) | Thompson & Beattie (1981) |
| <i>V. rostrata</i> | 6.3-13.8 (R) | Thompson & Beattie (1981) |
| <i>V. sororia</i> | 23-59 | Solbrig <i>et al.</i> (1980) |

than by age. Few forest herbs can be aged by the examination of annual growth increments analogous to tree rings, and when this is possible, it usually necessitates the destruction of the plant. Moreover, for organisms with indeterminate growth, like most plants, parameters such as mortality and fecundity are more dependent on the size of the individual than on its age (Werner and Caswell, 1977; Solbrig, Newell and Kincaid, 1980).

A few studies have plotted the size class structure of populations of deciduous forest herbs. The most typically encountered pattern is the presence of abundant seeds, considerably fewer seedlings, and then each succeeding class containing even fewer individuals. This approximate pattern was exhibited by the species studied by Kawano (1975), who interpreted it and a similar pattern in *Allium victorialis* (Kawano and Nagai, 1975) as evidence of regular yearly recruitment and constant mortality rates. *Arisaema triphyllum* has a similar size structure, but careful scrutiny of its population dynamics indicates that a different explanation is in order, and that the population behaves quite differently from one year to the next (Bierzychudek, in press). Conclusions about population behaviour drawn from static size structures are not particularly reliable, because individuals do not inevitably grow from one year to the next; some may get smaller over time.

The size class structures of *Disporum sessile* and *D. smilacinum* are quite irregular by comparison with that described above; Kawano (1975) interpreted these as being due to the existence of both sexual and vegetative reproduction in these species.

Because several years are often required to reach reproductive maturity, usually only a small fraction of the individuals in a population are sexually reproductive. This fraction ranges from a maximum of 12 to 24% in two populations of *Erythronium japonicum* (Kawano, 1975) to less than 1% for *Lilium cordatum* and *Trillium tschnoskii*. Corresponding values for *Arisaema triphyllum* are 3.5 to 6.5% (Bierzychudek, 1981a).

Populations of *Arisaema triphyllum* are not in equilibrium; populations are declining or expanding, and population sizes fluctuate from year to year through the effects of environmental variability on rates of growth, mortality and fecundity (Bierzychudek, in press). Is *Arisaema* typical in this respect? No other studies have yet been published that allow the estimation of population growth rate, or that have attempted to measure temporal stability, but what little data exist suggest that population fluctuations are more the rule than the exception. Tamm (1956) reported that the number of adults of *Anemone hepatica* remained stable over a period of 12 years, but that levels of recruitment differed from one year to the next. The population sizes of young plants of *Hydrophyllum appendiculatum* changed by as much as 50% from year to year (Morgan, 1971). Tamm (1956) took two censuses, 12 years apart, of 17 species of herbs in a Swedish forest. He did not keep track of individuals, but recorded degree of cover on a five-point scale. Only about half of the species had the same density at the end of the interval as at the beginning; the other half had either increased or decreased substantially. These changes can be attributed, at least in part, to changing levels of canopy cover.

Barkham (1980a) describes significant year-to-year differences for *Narcissus pseudonarcissus* in the mean number of capsules containing seeds. Over the course of a 10-year study, he examined whether year-to-year changes in numbers of shoots and flowers might be correlated with variations in weather and canopy conditions. Marked temporal changes were found to be related in complex ways to environmental variation (Barkham, 1980b).

Brewer (1980) compares the current abundance of over 40 species of forest herbs in a climax forest in Michigan with their abundance 50 years ago in that same forest. At least 16 species declined considerably in abundance (some of these disappeared completely); three increased substantially. Brewer attributes these changes mostly to an increase in the degree of shading of the forest floor, as the forest has matured.

On the other hand, Solbrig *et al.* (1980) report year-to-year changes in net population size of *Viola sororia*, over an 8-year period, as 'remarkably small', and Holland (1974) interpreted the small change in numbers of sterile bulbs of *Erythronium americanum* as evidence that *Erythronium*'s demographic structure was 'fairly stable'.

DISCUSSION

There is adequate information to permit generalizations about deciduous forest herb life histories. Most have a long juvenile period and an extended reproductive life, vegetative as well as sexual reproduction, and produce a few relatively heavy seeds each season that are dormant for a few months or not at all. Mortality of seedlings and young plants is high, but decreases once plants reach adulthood and remains low and more or less constant for large plants. Forest herb species can be divided into two groups on the basis of whether their main means of replacement is through vegetative reproduction or seed. The types of selective pressures that would favour one method over another have not been identified.

It is more difficult to generalize about the population dynamics of these species. Some of the questions that remain unanswered are:

- (1) what factors regulate population sizes of forest herbs?
- (2) how stable are population sizes of forest herbs?
- (3) how much site-to-site variation occurs in population behaviour?

Answering any of these questions requires a different approach from the methods of most of the studies reviewed here. Instead, the types of studies that promise to yield new information are, first, those that use experimental manipulations in field situations to assess the influence of different factors. Only Handel's (1978) study of the population biology of three *Carex* species has attempted to identify the factors limiting their distribution; he did this by a series of transplant experiments in the field, and competition experiments in the greenhouse.

A second approach, which is becoming more common, is that of following individually-marked plants over long periods of time to learn their fates. This technique was pioneered by Tamm (1948), but has not come into common practice until recent years. Using the information so collected in a mathematical demographic model, such as the Leslie matrix model, allows the calculation of population growth rate and the identification of stages particularly vulnerable to selection, and puts the information in a standard framework that permits comparison with other species.

The fact that forest herbs should usually be classified by size rather than by age may have hindered the use of mathematical approaches in the past; straightforward Leslie matrix models are not strictly applicable. For whatever reason, rates of increase have not been calculated for any forest herbs except *Arisaema triphyllum* (Bierzychudek, in press) and *Chamaelirium luteum* (Meagher, 1978). But models are available that can accommodate not only size-structured populations (Hartshorn, 1975; Werner and Caswell, 1977; Caswell and Werner, 1978), but also vegetative reproduction (Sarukhan and Gadgil, 1974; Enright and Ogden, 1979).

More extensive use of these models, which really require very little mathematical expertise, is the only route likely to lead to answers to questions 2 and 3 above. With these models, we can examine the effect of small year-to-year changes over much longer periods of time, and we can determine the probable outcome of changes in a population's life history parameters.

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