The Concept of r- and K-Selection: Evidence from Wild Flowers and Some Theoretical Considerations

Madhav Gadgil; Otto T. Solbrig

THE CONCEPT OF r- AND K-SELECTION: EVIDENCE FROM WILD FLOWERS AND SOME THEORETICAL CONSIDERATIONS

MADHAV GADGIL[1] AND OTTO T. SOLBRIG

Biological Laboratories and Gray Herbarium, Harvard University,
Cambridge, Massachusetts 02138

The relationship of the demographic parameters of a population to its ecological niche constitutes one of the central problems of population biology. A most interesting theoretical notion pertinent to this problem is r- and K-selection (MacArthur 1962; Cody 1966; MacArthur and Wilson 1967; Hairston, Tinkle, and Wilbur 1970; Roughgarden 1971). The central idea of r- and K-selection is that populations living in environments imposing high density-independent (D.I.) mortality (r-strategists) will be selectively favored to allocate a greater proportion of resources to reproductive activities at the cost of their capabilities to propagate under crowded conditions, and conversely, populations living in environments imposing high density-dependent (D.D.) regulation (K-strategists) will be selectively favored to allocate a greater proportion of resources to non-reproductive activities, at the cost of their capabilities to propagate under conditions of high D.I. mortality.

From the argument just stated, it may be deduced that the birth rate of an r-strategist will be greater than that of a related K-strategist. However, increased birth rate under conditions of high D.I. mortality is not sufficient evidence for an r-strategy, because, as demonstrated later in this paper, any increase in D.I. mortality must by itself produce a new equilibrium of birth and death rates at higher values of both. The crucial evidence needed for r- and K-selection is whether an organism is allocating a greater proportion of its resources to reproductive activities (r-strategists) than another related one (K-strategist) under any and all D.D. and D.I. mortality conditions.

Here we provide evidence for r- and K-selection by comparing different species, as well as different genotypes within a species (all of the same basic life form). The concepts of r- and K-selection are not absolute, but are meaningful only by comparison. A given organism is more or less of an r-strategist only in comparison with another organism. Thus, herbaceous plants tend to be r-strategists more than trees, dandelions more than skunk cabbage, and one biotype of dandelion more of an r-strategist than another. Data presented here are exclusively from herbaceous plants, mostly peren-

nials. Empirical data are presented for r- and K-selection within these life forms (which are r-strategists when compared with trees and shrubs), derived from a comparison of genotypes within and between three adjacent populations of dandelions (*Taraxacum officinale sensu latu*) and from a comparison of all herbaceous species in three plant communities.

In addition to presenting new empirical data, we review the theoretical background. This is necessary to remove the confounding of population dynamic effects from those of r- and K-selection, and to show that the magnitude of D.I. mortality is the crucial factor in the r- and K-selection argument. As a corollary of this latter point, we shall show that an r-strategist need not necessarily be a colonizing species.

THEORY

Population Dynamic Effect

Higher D.I. mortality results in a higher birth rate without any change in the proportion of resources allocated to reproduction. By definition $m = b - d$, where m is the Malthusian parameter, b the birth rate, and d the death rate. An increase in D.I. mortality by definition increases the death rate at all densities but need not affect the birth rate. The population thereby comes to equilibrium at a lower density K_2 from its original density K_1 (fig. 1). However, at equilibrium both the birth and death rates will be greater than before. This increased birth rate is made possible by a decrease in the equilibrial population density which implies a less severe D.D. limitation of resources in the population.

The reproductive effort of an individual is a product of the total re-
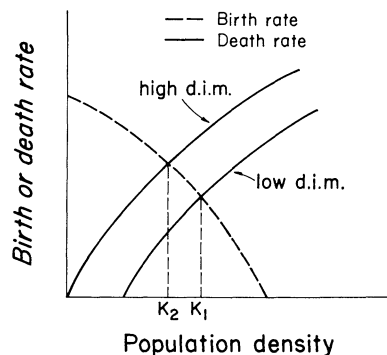
FIG. 1.—Birth and death rates as a function of population density at two levels of density-independent mortality. The birth rate is assumed to decrease and the death rate to increase with an increase in population density. The death rate is assumed to increase at all levels of population density with an increase in density-independent mortality. There is no particular significance to other features of the figure such as the parallel nature of death curves or points of intersection of the curves with the axes; $d.i.m. = $ density-independent mortality; $K = $ carrying capacity.

sources obtained by the organism and the fraction devoted to reproduction. An increased D.I. mortality leading to a lower D.D. limitation implies that a higher quantity of resources is obtained by an individual. Even if the individual devotes the same fraction of these to reproduction, the birth rate must rise.

The theory of r- and K-selection postulates the allocation of an increased fraction of resources to reproduction (i.e., higher birth rate) under conditions of higher D.I. mortality. This postulated effect is in the same direction as the simpler population dynamic effect, and hence, changes in birth rate as such cannot provide definitive evidence for the subtler r-selection. Consequently, Cody's (1966) evidence for higher clutch size in bird species from harsher environments is not sufficient evidence that they have been r-selected. Such evidence, though at a very gross level, is provided by Harper, Lovell, and Moore (1970) when they point out that annual herbs, perennial herbs, and trees allocate a progressively smaller fraction of their resources to reproduction and consequently constitute progressively more and more K-selected life forms.

Independence of r and K

The instantaneous rate of natural increase, r, denotes the maximal growth rate a population can attain, while the carrying capacity of the environment K is the highest density at which a population can be maintained in a constant idealized environment. That these two parameters are not necessarily positively correlated has been realized for at least a century. Thus, Darwin (1859) already noted that "one fly deposits hundreds of eggs, and another, like the hippobosca a single one; but this difference does not determine how many individuals of the two species can be supported in a

Fig. 2.—Malthusian parameter or the population growth rate as a function of population density for two biotypes; $r =$ growth rate of the population unlimited by density; $K =$ carrying capacity; $d =$ population density at which the Malthusian parameters of the two biotypes are equal in their value.

district.'' This notion is expressed in figure 2, where we imagine the two parameters to be negatively correlated for the two biotypes under consideration. The figure shows the Malthusian parameter of a biotype as a function of population density. The biotype with higher values of m under conditions of low population density is the r-strategist; the biotype with higher values of m under conditions of *high* population density is the K-strategist. In population maintained consistently below d, the r-strategist replaces the K-strategist; conversely, the advantage is with the K-strategist in populations maintained consistently above d. As noted above, an increase in D.I. mortality depresses the equilibrial levels at which a population is maintained. Therefore, any increase in D.I. mortality should favor the r-strategist.

Changes in Allocation

Under conditions of high D.I. mortality, an organism is under positive selection to allocate a greater proportion of its resources to reproductive activities than an organism in similar environmental circumstances under D.D. regulation. This assertion follows from the argument below.

A consequence of selection is that nonreproductive activities are favored at the expense of reproductive activities only when they enhance reproduction at later stages in the life history and thereby maximize overall fitness. The more regular in its occurrence and the more predictable in its effects that a given unfavorable environmental or biological phenomenon is, the more likely an organism will be able to increase its fitness by diverting some of its resources to combating or altering it, provided this is within the range of possibilities of the organism. For example, it will pay for a squirrel to reduce winter mortality by diverting its energy to combat the rigors of cold winters with the growth of a layer of fat; or for a turtle to grow a carapace to reduce predation; or for a redwood tree to grow a large stem to compete more effectively for light. But the fitness of these organisms will not be enhanced by growing more layers of fat to survive extreme winter conditions occurring only rarely, such as once in a century; or to grow carapaces any stronger than needed to combat the common predators; or to grow much beyond the tallest tree in the forest. Any organism expending energy in nonreproductive activities beyond what is needed to combat usual causes of mortality lowers rather than increases its fitness by diverting resources from reproduction to activities that normally do not increase survival. Thus, the amount of resources allocated to nonreproductive activities will depend on the relation between the cost of such diversion versus the benefit derived from it; the less frequent a source of mortality is, the less benefit will be gained from the diversion of energy to combat it.

We contend that organisms under D.D. regulation (through either resources or predation) can enhance their future reproduction by diverting

some of their resources to nonreproductive activities, while such diversion is of less value for organisms subjected to a great deal of D.I. mortality. This is so because many more causes of D.I. mortality are unpredictable—such as mud slides, floods, extreme droughts, rains, cold, etc., than resources and predation that cause D.D. regulation. Therefore, in a statistical sense, the causes of D.I. mortality are less predictable and, consequently, organisms divert less energy to reduce their detrimental effects than under D.D. regulation (all other factors being equal). However, for some causes of D.I. mortality, it is profitable for an organism to divert resources to combat them, for example, cold winter temperatures for many vertebrates or extreme dry conditions for many plants.

But even when the predictability of two D.I. and D.D. causes of mortality is the same and originally it is equally costly to combat them, there is good reason to expect an organism eventually to devote more resources to combat the D.D. source. Agents of D.I. mortality differ from those of D.D. mortality. The former are almost always physical factors which do not change as a result of the organism's response to them. For example, winter temperatures are unaffected by layers of fat on the back of a wolf. Density-dependent regulation involves competition for resources or prey-predator interactions. In such cases, if avoidance (through character displacement) is not possible, as the organism expands energy to reduce the harmful effects of competitors or predators, these will respond in a like manner. So, as one plant commits resources to producing a tall stem to gain more light (and by such action shades other species) competing plants respond evolutionarily by growing taller and reducing the benefits of the first plant, which now has to commit even more resources to stem growth in order to secure its former share of sunlight. Therefore, the relation between benefit and cost for this latter case changes so that nonreproductive activities consume more and more energy in an effort to maximize the difference between benefit and cost. Therefore, normally nonreproductive activities have a high value when D.D. regulation is significant but a low value under conditions of high D.I. mortality. Since conditions of high D.I. mortality imply less severe D.D. regulation, a high level of rarefaction selectively favors the biotype that allocates a smaller fraction of resources to nonreproductive activities and a greater fraction to reproductive activities.

Thus, a greater allocation of resources to reproduction enhances fitness when D.I. mortality is high, that is, when population density is low. This strategy, however, has the consequence of a lower Malthusian parameter when the D.I. mortality is low and hence population density high.

Characteristics of r- and K-Strategists

Given the concept of r- and K-selection, the various attributes of r- and K-strategists and of the environments favoring them can be deduced. Mac-

Arthur and Wilson (1967), Cody (1966), and Pianka (1970) have already covered some aspects. Attributes of r- and K-strategists may be consequences of differences in allocation of resources to reproductive and nonreproductive activities or may derive from differences in limitation through D.D. factors.

Diversion of a greater fraction of resources into reproduction for r-strategists generally implies (1) production of a larger mass of offspring for any given size of parent and (2) a greater diversion of resources into reproduction throughout the life history. This would lead to earlier sexual maturity. A third attribute of r-strategists which may seem to follow is a shorter life-span. However, it is not obvious why diversion of resources into reproduction as opposed to, say, gaining competitive advantage should be accompanied by a higher death rate. There is, however, abundant empirical evidence and a plausible theoretical justification for a positive correlation between age of sexual maturity and length of life-span (Gadgil, in preparation). Hence, lowered age of sexual maturity in r-strategists may be accompanied by shorter life-spans.

Increased allocation of resources to reproduction is one response of an r-strategist to being less severely limited by D.D. factors such as resources and predation. When food is abundant, an organism often extracts less energy from each item. Thus, copepods feeding at high concentrations of algae pass out a greater fraction of algal substance undigested. This may be one aspect of MacArthur and Wilson's (1967) suggestion that r-strategists maximize productivity and not efficiency. When food is abundant, an animal may restrict the range of items in its diet to those yielding maximal energy per unit effort. The number of offspring produced is determined by: the total amount of resources available, the fraction of these which are devoted to reproduction, and the division of such resources among some number of offspring. Both greater absolute resources and a greater fraction of their resources are devoted by r-strategists to reproduction. The question then arises as to whether these will be partitioned among few large, or many small, offspring. If the advantage of large offspring is mainly their higher competitive ability and better capacity to counter predation, r-strategists produce more, but smaller, offspring. If large or small progeny demand greater or less parental care, then r-strategists expend less parental care per offspring (Cushing 1966).

Relaxed predation pressures on r-strategists need not be identical for various stages of life history. Reproductive effort will be concentrated in the life-history stages with the least predation (Gadgil and Bossert 1970). K-strategists should devote more resources to nonreproductive activities. What these nonreproductive activities specifically are depends on the relative value of the various nonreproductive activities toward enhancing the Malthusian parameter mainly through two mechanisms: (1) the increased survival of the individual and (2) the enhanced ability of the individual to obtain resources from the environment.

Fugitive Species and r-Strategy

We have demonstrated that r-selection is effective in situations where organisms suffer high D.I. mortality. Furthermore, we also showed that in situations of low D.D. regulation, such as fields that become temporarily denuded, r-strategists are favored. This preadapts r-strategists to becoming colonizing species, although they must not be identified solely with colonizers.

Three types of environments could impose high D.I. mortality: (1) habitats which are permanent in space, and also continuously available in time with a high level of D.I. mortality distributed uniformly with time; (2) habitats permanent in space, but discontinuously available in time with a high level of D.I. mortality during an adverse season such as cold winter or a hot dry summer (Roughgarden 1971); (3) habitats temporary in space and time. Only the third of these habitats is that of the fugitive species, characterized by a high degree of dispersibility, as well as other characteristics (Baker 1965). Dispersibility is therefore an attribute of fugitive species but not necessarily of r-strategists.

Once a species invades habitats which are only temporarily available in space and time, selection favors acquisition of a number of other attributes enhancing colonizing ability. Resources may be diverted to nonreproductive activities, such as production of better and stronger wings and associated structures in insects, or production of spines, wings, or other such structures increasing dispersibility of seeds in higher plants. Consequently, fugitive species may allocate smaller fractions of their resources directly to reproduction by comparison with other r-strategists occupying a habitat in space with a high level of D.I. mortality.

EMPIRICAL EVIDENCE: DANDELION POPULATIONS

The common weedy dandelion (*Taraxacum officinale sensu latu*) is a plant that produces seeds parthenogenetically, without recourse to fertilization. It has therefore lost the ability of acquiring new genotypic variability through recombination. This characteristic makes it an ideal subject for the investigation of intra- and interpopulation variability of life-history parameters, since the investigator does not have to contend with the problem of recombination and can follow the various biotypes both in time and in space. We shall examine data on seed production and competitive ability of biotypes found in populations with different degrees of D.D. and D.I. mortality and correlate them with the strategy of allocation of resources between reproductive and nonreproductive tissues.

Material and Methods

The three populations chosen were located within 500 m of one another on the grounds of the Mathei Botanical Gardens of the University of

Michigan. Each site was a quadrat of 10×10 m, which was subdivided into 100 squares measuring 1×1 m from which one dandelion plant was chosen at random. Biotypes were identified using isozyme patterns as well as morphology (Solbrig 1970). Competition experiments between the two main biotypes were performed under a variety of growth chamber, greenhouse, and experimental field conditions (Solbrig and Vuilleumier, in preparation). Seed production estimates were obtained from single plants in both greenhouse and field conditions; germination experiments were performed under both controlled growth chamber and greenhouse conditions, using a variety of temperatures and soils (Solbrig and Vuilleumier, in preparation). Resource allocation was obtained estimating dry weights of various plant parts as well as leaf surfaces (Muenchov, in preparation).

Description of the Sites and Genotypic Composition of the Populations

The three populations will henceforth be called 1, 2, and 3; the four biotypes A, B, C, and D.

Population 1 is situated immediately behind the main building of the Botanical Gardens in the path of people and equipment, resulting in patches of bare ground (high D.I. mortality). Furthermore, it is closely mowed approximately once a week. The area is not watered and, lying in a relatively high place, the soil tends to be dry and hard.

Population 2 lies in the same general area but to one side and under an oak tree, approximately 150 m from the first. It partakes of the same physical conditions as population 1, but it is not frequented as much by people and equipment; it is mowed occasionally but not as frequently as population 1.

Population 3 lies in a depression by the bank of a creek 100 m south and 3 m below population 2. Population 3 is relatively undisturbed: it is mowed once a year with a hay mower at a height of 20 cm from the ground; it is only infrequently visited by people. The area is periodically flooded, particularly during spring thaws, and the soil tends to be wetter than in populations 1 or 2.

The vegetation covering the area of populations 1 and 2 is formed largely by annual and perennial weeds and some short grasses; the vegetation of population 3 is formed largely by grasses about 50 cm in height with some *Rumex*, *Amaranthus*, and other broad-leaved species of that size. The density of dandelions is greatest in populations 1 and 2 and lowest in population 3. The density of dandelion plants fluctuated between 230 plants of dandelion per square meter for the densest 1-m² quadrat and five plants for the quadrat with lowest density. All quadrats had dandelion plants.

All of the area of the present Mathei Botanical Gardens was a pasture until approximately 10 years ago. Sheep and other domestic animals were kept on the premises then and the area was very overgrazed (high D.I. mortality; low plant cover). The three populations, therefore represent

stages in an old field succession: population 1 is very close to the original old field, while Population 3 is the most mature one.

Analysis of the populations showed at least four biotypes (Solbrig 1970). Three of these (A, B, C) were found in all three populations, and one (D) only in populations 2 and 3. The abundance of the various biotypes varied greatly from population to population (table 1). Several hypotheses might account for the uneven distribution of the biotypes over the area. The two most plausible are: (1) The various biotypes are differentially adapted to different microhabitat characteristics (soil, water, nutrients, light). (2) The various biotypes differ in the way they allocate their energy between reproductive and nonreproductive tissues (r- and K-strategies), making each optimally adapted to sites with different amounts of D.I. mortality.

Competition Experiments and Seed Productivity

To discriminate between the two hypotheses, a series of competition experiments was designed. Details of these experiments, which tested the performance of the genotypes under different soil temperatures and light conditions, will be reported elsewhere (Solbrig and Vuilleumier, in preparation). The results are summarized in figure 3. It can be seen that the D biotype outcompetes the A biotype under all environmental conditions tested.

Table 2 shows the number of flowering heads produced by plants of all biotypes from all three populations when grown in individual pots under uniform greenhouse conditions. It can be seen that the A biotype produces approximately three times as many heads (and seeds) as the D biotype. Furthermore, experiments with plants grown from seed indicate that plants of the A biotype germinate in the spring and bloom and seed 4 months after germination, while plants of the D biotype do not bloom until the second year.

Table 3 and figure 4 show the difference between plants of biotypes A and D in number, size, shape, and surface of leaves. It can be seen clearly that plants of biotype D of the same age produce more leaf biomass than plants of biotype A.

Discussion

Dandelions are fugitive species and, therefore, basically r-strategists. However, the habitats they occupy differ greatly in their degree of per-

TABLE 1

PERCENTAGE OF EACH OF FOUR DANDELION GENOTYPES IN
THREE ANN ARBOR POPULATIONS

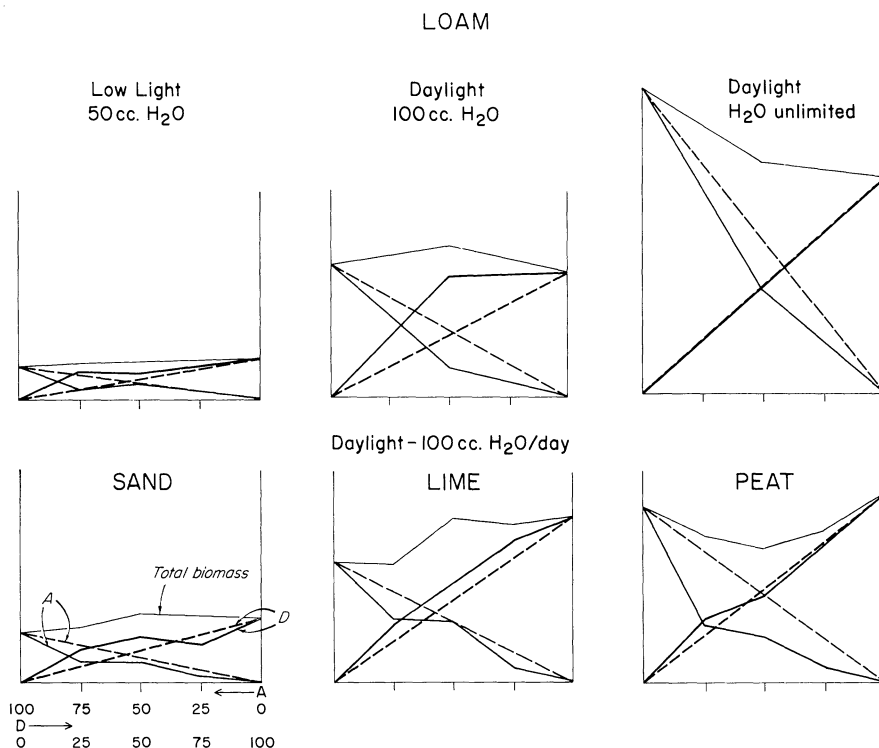| POPULATION NO.	N	BIOTYPE			
		A	B	C	D
1	94	73	13	14	...
2	96	53	32	14	1
3	94	17	8	11	64

FIG. 3.—Replacement diagrams to show the result of competition between two dandelion biotypes under various light and soil regimes. Each experiment was replicated twice, the diagrams depicting the average values after 1 year of competitive growth. Each experiment consists of five flats with the following initial mixture of seedlings (from left to right in each diagram): (1) 80 plants of A genotype and 0 of D genotype (100%:0%); (2) 60 of A and 20 of D (75%:25%); (3) 40 of A and 40 of D (50%:50%); (4) 20 of D and 60 of A (25%:75%); and (5) 0 of D and 80 of A (0%:100%). The ordinate indicates total biomass. The solid lines indicate the observed values, the dashed line the expected values, under a model of no competition. As can be seen, the values for the D genotype are consistently above expectation, while those for the A genotype are below expectation. All three experiments depicted in the upper row were grown in loam; the three in the lower row were grown in daylight with 100 cm^3 of water a day. Other conditions are indicated immediately above each graph.

manence. In arctic regions, where dandelions are very abundant, the habitat may be quite permanent in time and space; in a well-cared-for lawn, suitable habitats may be very transient. There is consequently ample latitude for differences to evolve in the degree of resource allocation between reproductive and nonreproductive tissues.

As explained in the introduction, a large number of seeds is not sufficient evidence of *r*-selection. It must be shown that the difference is genetically fixed, that it represents an actual difference in resource allocation between reproductive and nonreproductive tissue, and that these changes are cor-

TABLE 2
AVERAGE No. OF HEADS PER PLANT PRODUCED BY EACH DANDELION BIOTYPE

POPULATION No.	BIOTYPE			
	A	B	C	D
1	3.6	2.3	1.5	...
2	2.6	2.1	1.9	...
3	3.8	2.3	0.5	1.2

related with increased D.I. mortality. All this we have been able to show. We were also able to show that the D biotype, which allocates more resources to leaf biomass at the expense of seed production capacity, gains a direct competitive advantage in conditions of higher density (because of its capacity to shade other plants). Furthermore, it was demonstrated (Solbrig and Vuilleumier, in preparation) that the two biotypes do not respond differentially to any of the microenvironmental factors tested. From all these considerations, we conclude that the A biotype is more of an r-strategist than the D biotype, which is more of a K-strategist, and that the decreasing order of D.I. mortality from population 1 to population 3 accounts for the decrease in the frequency of the A biotype from 0.7 to 0.1 and the increase of the D biotype from a frequency of 0.0 to 0.65.

EMPIRICAL EVIDENCE: HERBACEOUS COMMUNITIES

The second of the two empirical studies presented in this paper comprises a comparison of species belonging to different communities which could be ranked as more or less "mature." It is thus analogous to Cody's (1966) study of clutch size in birds. The present study, however, attempts to collect data not on clutch size (reproductive output) alone, but on reproductive output in relation to the total amount of resources available, that is, on the strategy of allocation. Herbaceous plant communities provide by far the most suitable material for such a study.

Methods and Localities

We selected three communities which could be easily arranged in a hierarchy with respect to decreasing harshness and increasing stability of the environment, resulting in decreasing amounts of D.I. mortality. This ranking was based on estimations of (a) degrees of physical disturbance and (b) position on a scale of plant succession.

The communities chosen were located within half a kilometer of one another on the grounds of the Concord Field Station of Harvard University in Bedford, Massachusetts. Each site covered an approximate area of 300 m². The first site has been labeled as the dry site in the diagrams. It is the least advanced site in a successional sense, the only life forms present on it being herbaceous plants. It is also physically most disturbed, being surrounded by large cleared areas and being trampled on a great deal.

TABLE 3

LEAF NUMBER AND LENGTH OF LARGEST LEAF OF 1-YEAR-OLD A AND D BIOTYPES OF DANDELIONS GROWN UNDER VARIOUS CULTURAL CONDITIONS WITHOUT AND WITH COMPETITION

SOIL CONDITIONS	LEAF NUMBER				LENGTH OF LARGEST LEAF (cm)			
	A Biotype Competition		D Biotype Competition		A Biotype Competition		D Biotype Competition	
	No	With	No	With	No	With	No	With
Loam soil, 50 cm^3 H$_2$O/day	9.3	8.9	8.0	10.6	9.9	10.9	12.1	12.7
Loam soil, 100 cm^3 H$_2$O/day	9.0	5.6	5.9	8.6	16.5	10.7	18.2	20.3
Loam soil, H$_2$O unlimited	8.1	3.7	5.6	7.4	13.5	13.2	17.2	16.9
Sand soil, 100 cm^3 H$_2$O/day	2.6	2.1	2.5	3.7	12.9	10.1	13.4	14.0
Lime soil, 100 cm^3 H$_2$O/day	4.2	2.2	3.8	5.1	15.6	9.0	16.0	15.0
Peat soil, 100 cm^3 H$_2$O/day	2.5	2.6	3.0	5.2	15.5	9.4	14.8	17.4

NOTE.—"Competition" is defined as equal initial mixtures of A and D plants; "no competition" refers to pure stands of A or D plants
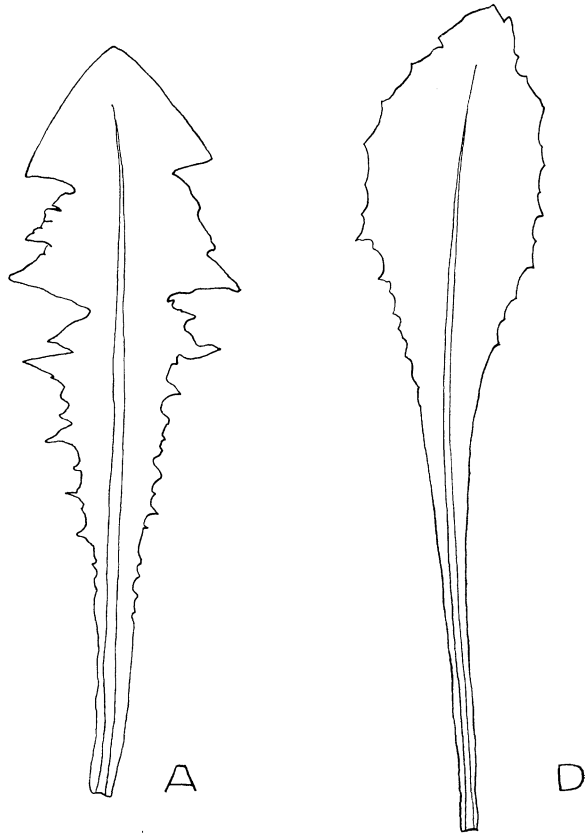
FIG. 4.—Leaf shapes of A and D biotypes of dandelions grown without competition under identical water, light, temperature, and soil conditions.

The second site, which was next to a shallow pond, has been labeled as the wet site. It is somewhat more advanced in successional sense, since in addition to herbs it has a number of shrubs of the genera *Spiraea* and *Sambucus* present on it. It has much less cleared area around it and is trampled on to a lesser degree. The third site has been labeled as the hardwood site. It is the most advanced of the three in a successional sense. The dominant life forms are trees, mostly birches (*Betula* spp.) and some shrubs (*Vaccinium* spp.). It is surrounded by pinewoods and is not subject to trampling. Finally, we also looked at a pinewood site, but the number of wild flowers was so small that it will not be considered here, though it is included in the diagrams.

These three sites can obviously be ranked as more likely to favor *K*-strategists in the order dry, wet, and hardwood.

Herbaceous Components

We decided to study only the herbaceous component excluding the grasses of these communities. That trees would allocate a smaller fraction

of their resources to reproduction than would herbs seems obvious and trivial. What we were interested in was to verify whether even the herbs themselves differed from one another in this manner. Second, the herbs, though mostly perennial, appear to flower every season and hence would be expected to show much less change with age; hence, one source of variation would be removed. Also, the entire above-ground growth is seasonal, and hence the amount of biomass produced in a season can be very easily determined.

We adopted the ratio of dry weight of reproductive tissue to the total dry weight of above-ground tissue as the index of the fraction of total available resources allocated to reproduction. This ratio is henceforth referred to as "reproductive effort." The herb was snipped off at ground level when at least one of its flowers was open. All tissues primarily involved in reproductive functions, namely, flowers and their stalks above the last normal leaf, were separated as reproductive tissue. This tissue and the vegetative tissue were dried in an oven at 100° C for 24 hours and weighed.

Sampling Method

Each site was visited once a week beginning in the first week of May and ending in the last week of September, constituting a total of 22 weeks. On each visit a random strip 5 m $\times$ 40 cm was chosen. From this strip all herbaceous plants, except grasses, in bloom were collected. A total of 423 specimens belonging to 25 species was sampled in this manner.

Difficulties

Although our method has the merit of providing an index of reproductive effort for a number of species and individuals with great ease, and certainly greater accuracy than ever imaginable with animals, it is subject to a number of objections. The first difficulty lies in equating standing crop with production. A second major objection is the neglect of underground tissue. However, sampling underground tissue is beset with so many difficulties that we were forced to neglect it. The third difficulty lies in comparing plants with different life cycles, for example, skunk cabbage (*Symplocarpus foetidus*), which devotes its underground reserves of the previous year to flowering in the spring before it puts out any leaves, with goldenrod (*Solidago* spp.), which devotes its reserves of the previous year entirely to vegetative growth in spring and to flowers in fall. Finally, a fourth objection is that dry weight may not properly represent limiting resources which are particular elements, such as phosphorus. We recognize all these and will attempt to solve them in the future. However, we think that our methodology is adequate for a first study of this type.

Results for Solidago

The species in bloom at the various sites belonged to different genera for the first 18 weeks. During the month of September, however, four species

of goldenrod belonged to the genus *Solidago* dominated all three sites. The most interesting and clear-cut patterns emerge from comparisons of *Solidago* species and are summarized here. A more detailed account will be given elsewhere (Gadgil and Abrahamson, in preparation).

The four species involved are *S. nemoralis* present only on the dry site, *S. speciosa* present on the dry and hardwood sites, *S. rugosa* present on the hardwood and wet sites, and *S. canadensis* present only on the wet site. We rank dry, wet, and hardwood sites as favoring K-strategists in that order. Therefore, *S. nemoralis* confined to the dry site is expected to possess the highest reproductive effort of all species. We further expect the *S. speciosa* and *S. rugosa* populations from the hardwood site to possess the lowest reproductive efforts of the four populations and *S. rugosa* and *S. canadensis* from the wet site to be intermediate. Figure 5 shows that our data do in fact fit these expectations.

Results for the Entire Community

The overall picture is somewhat more complex than the neat pattern presented by *Solidago* in autumn. Figure 6 shows mean values of reproductive effort for all specimens at each site for each week over the entire season. A comparative measure of reproductive effort over the entire season among the different sites is the area under the reproductive effort curves. Inspection of figure 6 shows that this area is largest for the dry site and smallest
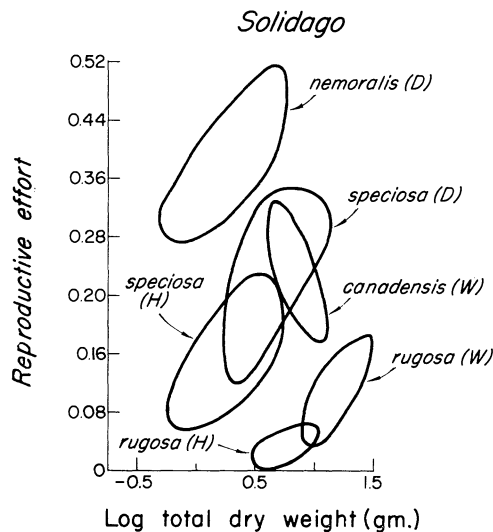

FIG. 5.—Reproductive effort (i.e., ratio of dry weight of reproductive to total aerial tissue) as a function of the total dry weight of the aerial tissue for the various population of *Solidago*. Each closed curve embraces all points representing the individuals included in a single population; D = dry-site population; W = wet-site population; H = hardwood-site population.
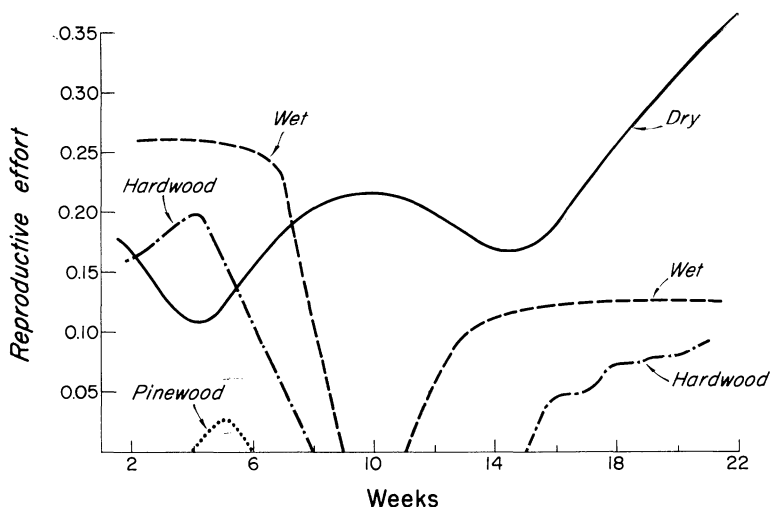
FIG. 6.—Mean of reproductive effort (i.e., the ratio of dry weight of repro-
ductive to total aerial tissue) for all the plants sampled in a given week as a
function of time at three sites in Bedford, Massachusetts. The time axis spans
the interval from the first week of May through the end of September.

for the hardwood site. This corresponds to the expectation that plants in-
habiting the dry site would be mostly r-selected while those on the hard-
wood site would be more K-selected.

However, the dry site has the highest values of reproductive effort
only during summer and fall but not in spring. A tentative explanation of
this anomaly is as follows. Resource limitation is not serious on any site
in the spring, since very little plant biomass has been produced. Spring
biomass is small and comparable on all three sites, while differences are
large and striking in autumn. The total above-ground biomass of herbs in
autumn was greatest by far on the wet site, and was comparable for the
dry and hardwood sites. If we regard total plant biomass produced up to
fall as a measure of the resources available for the growth of the herba-
ceous plants, it would appear that the wet site has more such resources
than the dry and hardwood sites. Given this and the fact that plant bio-
masses are comparable in the spring, it follows that resource limitation in
the spring must be least on the wet site and greater on the dry and hard-
wood sites. Organisms less limited by resources are expected to allocate a
greater fraction of their resources to reproduction and therefore to have
a higher reproductive effort. One would thus expect plants on the wet site
to exhibit the highest reproductive effort in spring and those on the dry
and hardwood sites to exhibit comparable reproductive effort. This is
borne out by the data (fig. 6).

Our explanation for the spring anomaly is not entirely satisfactory. We
have not collected precise data on spring and fall plant biomass. More
important theoretically is the question of why the wet site does not have

relatively as large a biomass, compared with the other sites, in the spring as in the fall. Perhaps the spring-flowering plants are more dependent on underground reserves and the neglect of these produces the anomaly. Studies to elucidate this will be undertaken in the near future. Another intriguing problem is the seasonal change in reproductive effort, which increases on the dry site but decreases on the other two sites. An elucidation of what happens in spring should help to clear up this problem as well.

SUMMARY AND CONCLUSIONS

The concept of r- and K-strategies is meaningful only on a comparative basis, there being no absolute criterion to determine whether an organism should be classed as an r- or K-strategist. The most important characteristic of an r-strategist is that it devotes a greater proportion of available resources to reproduction than a related K-strategist. This implies a higher birth rate; however, birth rate in itself does not provide the necessary evidence regarding resource allocation. For a set of environments with equal resources, selective pressures favoring r strategists will exist in those environments imposing greater amounts of density-independent mortality; hence, r-selection need not be restricted to colonizing species.

Empirical evidence is provided through two studies. In one it is shown that populations of dandelions are formed by a mixture of biotypes. In disturbed sites, the predominant biotype is characterized by a higher seed output, a higher proportion of biomass devoted to reproduction, and lower competitive ability than the biotype predominating on the comparatively less disturbed site. In the second study, a comparison of all herbaceous flowering plants from three sites shows that members of the community from the more disturbed site devote on the average a greater proportion of their aerial biomass to reproductive tissue than members of a community from a less disturbed site. The above evidence agrees with the theoretical expectations.

ACKNOWLEDGMENTS

LITERATURE CITED

Baker, H. G. 1965. Characteristics and modes of origin of weeds. *In* H. G. Baker and
    G. L. Stebbins [ed.], The genetics of colonizing species. Academic Press, New
    York. 588 p.
Cody, M. L. 1966. A general theory of clutch size. Evolution 20:174–184.
Cushing, D. H. 1964. The work of grazing in the sea, p. 207–226. *In* D. J. Crisp [ed.],
    Grazing in terrestrial and marine environments. Blackwell, Oxford.
Darwin, C. 1859. On the origin of species by means of natural selection. 1st ed. London.
    593 p.
Gadgil, M., and W. H. Bossert. 1970. Life historical consequences of natural selection.
    Amer. Natur. 104:1–24.
Hairston, N. G., D. W. Tinkle, and H. M. Wilbur. 1970. Natural selection and the
    parameters of population growth. J. Wildlife Manage. 34:681–690.
Harper, J. L., P. H. Lovell, and K. G. Moore. 1970. The shapes and sizes of seeds.
    Annu. Rev. Ecol. Syst. 1:327–356.
MacArthur, H. H. 1962. Some generalized theorems of natural selection. Nat. Acad.
    Sci., Proc. 48:1893–1897.
MacArthur, R. H., and E. O. Wilson. 1967. The theory of island biogeography. Princeton
    Univ. Press, Princeton, N.J. 203 p.
Pianka, E. 1970. On *r* and *K* selection. Amer. Natur. 104:592–597.
Roughgarden, J. 1971. Density dependent natural selection. Ecology 52:453–468.
Solbrig, O. T. 1970. Genotypic variation within and between populations of the common
    dandelion, *Taraxacum officinale* Wigg. Isozyme Bull. 3:43–44.