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GROWTH FORM AND REPRODUCTIVE EFFORT
IN GOLDENRODS (*SOLIDAGO*, COMPOSITAE)

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The optimization of one aspect of genetic fitness, reproductive output, will not necessarily be achieved through extreme fecundity at the earliest possible age of reproductive maturity, but rather through an optimal partitioning of resources among the various reproductive and nonreproductive activities. Species differ in the allocation of resources to these activities (Cody 1966; Gadgil and Bossert 1970; Gadgil and Solbrig 1972). Growth forms and reproductive effort of plants exhibit many interesting patterns when examined from this viewpoint. Thus annual herbs, perennial herbs, and trees allocate a progressively smaller fraction of their resources to reproductive activities (Harper, Lovell, and Moore 1970). In addition, the partitioning of vegetative growth among root, leaf, and stem may vary strikingly. Leaves make up a large fraction of vegetative growth in plant communities in wet areas that are dominated by herbs, stems do likewise in forests, and roots in arid environments (Rodin and Bazilevich 1967).

Although studies such as Rodin and Bazilevich (1967), Cody (1966), and Gadgil and Bossert (1970) reveal much of interest, there is as yet little theoretical formulation which predicts patterns of adaptations resulting in optimal allocation. This study is an attempt to construct such a theoretical formulation and to confirm its predictions from field studies of herbs of the genus *Solidago* (Compositae).

THEORY

First, we will consider the distribution of biomass between the reproductive and vegetative tissues. The theory of *r*- and *K*-selection (MacArthur and Wilson 1967) was used by Gadgil and Solbrig (1972) to postulate that the ratio of reproductive biomass to vegetative biomass will be greater in an environment which imposes a higher degree of density independent (D.I.) mortality. Since the extent of D.I. mortality is expected to decrease as a plant community becomes more mature in a successional sense, the ratio of reproductive to total biomass (vegetative plus reproductive biomass) should be less for plants in a more mature community. This ratio of reproductive biomass/total biomass will hereafter be referred to as “reproductive effort.”

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Second, let us consider the distribution of biomass among the various vegetative tissues. This distribution should depend on the nature of the limiting factor. If water is the limiting factor, a large fraction of the biomass could be in the form of roots. Rodin and Bazilevich (1967) show that roots make up 68% of the biomass in Russian meadow steppeland and 87% in semishrub desert. If light is the limiting factor, then the above-ground stem and leaf tissue could acquire more relative importance.

Since sunlight is unidirectional, it is relatively easy for one plant to withdraw light from another by shading. Plants can respond to shading by (1) allocating more biomass to stems to grow taller and avoid shading, or (2) by allocating more biomass to leaves to intercept more light. How these alternatives will be used depends upon the growth form of the dominant competitor for light. Thus, if herbs are growing with herbs and there is no overhead canopy, the plants could employ the first response. If herbs are growing under a canopy of trees, they could respond by adjusting to the lower light levels by the second response. In this latter situation, stem growth is useless except to avoid self-shading of the herbs' own leaves.

We can therefore predict that if light is limiting and if the competing plants are of a growth form of the same stature, it will be advantageous for a plant to invest relatively more in the stem biomass. If, however, the competing plants are of a growth form of greater stature, then a plant will invest relatively more in leaf biomass. We can suggest three testable predictions. (1) Reproductive effort will decline with increasing successional maturity of a community. (2) The ratio of stem biomass/total biomass will decline for light-limited plant populations as the growth form of competitors increases from the same to greater stature. (3) The ratio of leaf biomass/total biomass will increase for light-limited plant populations as the growth form of competitors increases from the same to greater stature.

MATERIALS AND METHODS

We tested these predictions at a relatively fine level by comparing six populations of four species of *Solidago* (Compositae): *S. nemoralis* Ait., *S. speciosa* Nutt., *S. rugosa* Mill., and *S. canadensis* L. These four species of goldenrods are fall-flowering perennial herbs which die back to the ground during winter. Nearly all the above-ground growth is the product of a given growing season.

These four species are distributed over three communities located on the grounds of the Concord Field Station of Harvard University in Bedford, Massachusetts. Each community was represented by a study site approximately 200 m² in area and within 500 m of one another. The first of these sites, labeled "dry," was a dry and heavily disturbed locality (high D.I. mortality), populated only by herbaceous plants predominantly belonging to the genera *Rumex*, *Oxalis*, *Potentilla*, *Achillea*, *Hypericum*, *Rubus*, and *Solidago* (*S. speciosa* and *S. nemoralis*). The herbs did not grow densely enough to shade each other appreciably. This community was clearly the

least advanced in a successional sense. The second community, labeled "wet," was a moist meadow site populated by *S. rugosa* and *S. canadensis*, along with a few shrubs of the genera *Sambucus* and *Spiraea*. The limiting factor for these herbs was probably light, as the growth was very dense and herbs shaded each other appreciably. The third, "hardwood," community was dominated by trees of the genera *Betula*, *Quercus*, and *Acer*. Shrubs of the genus *Vaccinium* were also present. The forest floor was occupied by *Maianthemum canadense*, grasses, *S. speciosa*, and *S. rugosa*. The goldenrods were shaded appreciably by the trees. The herbs themselves were sparse and did not shade each other. This site was little disturbed and should have had the least amount of D.I. mortality. The three communities were arranged according to increasing maturity in a successional sense: "dry," "wet," and "hardwood." There are six populations: *S. nemoralis* and *S. speciosa* at the "dry" site; *S. canadensis* and *S. rugosa* at the "wet" site; and *S. rugosa* and *S. speciosa* at the "hardwood" site.

These six populations were studied during the peak of flowering in the third and fourth weeks of September 1970 and during the entire growing season in 1971. Sampling during the 1971 growing season was done every 3 weeks beginning June 15 and continuing until September 7. From September 7 through October 5, the populations were sampled every 2 weeks. Randomly chosen plants (six plants in the 1970 study, five in 1971) from each population were cut at ground level and separated into stems, leaves, and inflorescences. These tissues were dried at 100° C for 24 hours and weighed. Calories per gram dry weight were determined by burning ground samples in a Parr bomb calorimeter. In addition, a random sample of 30 plants from each population was measured in the field for several characters including plant height, amount of branching, height of the lowest leaf, height of the lowest flower heads, and stem diameter. Field observations were made during the 1971 growing season noting the stage of flowering in each population (i.e., budding, full bloom, seed set, etc.). In the laboratory, the floral structure, seed size, and seed weight of each population were determined. Another random sample of five plants from each population was transplanted to the greenhouses of the Harvard University Biological Laboratories. Observations were made concerning the general growth form of the plants for 1 year.

DIFFICULTIES

A major disadvantage of determining reproductive effort by the above techniques is the neglect of underground tissue, which is difficult to sample. A second disadvantage is that dry weight does not necessarily represent the limiting resource in a given community, which might have been a particular soil nutrient.

Here too, we would like to comment on the use of floral and seed biomass combined rather than seed biomass alone as a measure of reproductive effort. Our studies of floral structure and seeds of these species indicate

extreme similarity in seed shapes and weights. The flower heads are also quite similar with respect to size and number of disk and ray florets. Given these similarities in seed weight and the reasonable assumption of a good positive correlation between floral and seed biomass, the use of total reproductive tissue appears justified. We recognize these difficulties, but we think that our methodology suffices for an initial study.

RESULTS AND DISCUSSION

The first prediction tested was that reproductive effort, estimated as the ratio of dry weight of inflorescences to the total dry weight (of aerial parts), would decrease when compared over populations ordered from dry to wet to hardwood communities. Figures 1 and 2 illustrate the data. Figure 1 shows the data taken during the peak of flowering while figure 2 illustrates the data throughout the growing season. The six populations can be ranked in terms of their reproductive effort in the order: *Solidago nemoralis* (dry), *S. speciosa* (dry), *S. canadensis* (wet), *S. speciosa* (hardwood), *S. rugosa* (wet), and *S. rugosa* (hardwood). Differences in figure 1 are significant at the .005 level as tested by the Mann-Whitney one-tailed *U*-test for 11 of the 15 population comparisons. Differences between *S. speciosa* (dry) and *S. speciosa* (hardwood), and *S. speciosa* (hardwood) and *S. canadensis* (wet) are significant at the .05 level. Differences between *S. speciosa* (dry) and *S. canadensis* (wet), and between *S. speciosa* (hardwood) and *S. rugosa*

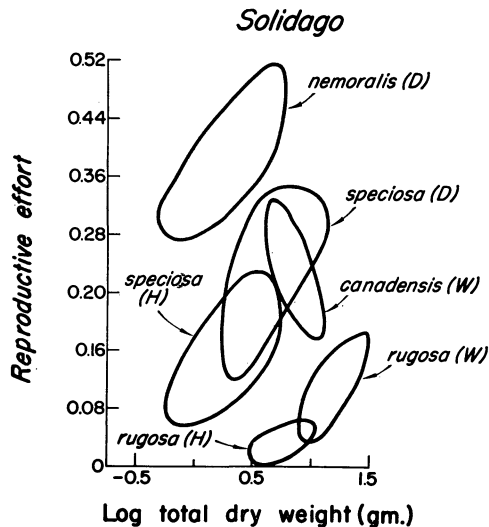


FIG. 1.—Reproductive effort (ratio of the dry weight of reproductive tissue to the total dry weight of above-ground tissue) plotted on the ordinate as a function of the log of the total dry weight (plotted on the abscissa) for the six populations of goldenrod. Each closed curve embraces all points representing the individuals included in a single population. *D* = dry field site; *W* = wet meadow site; *H* = hardwood site.

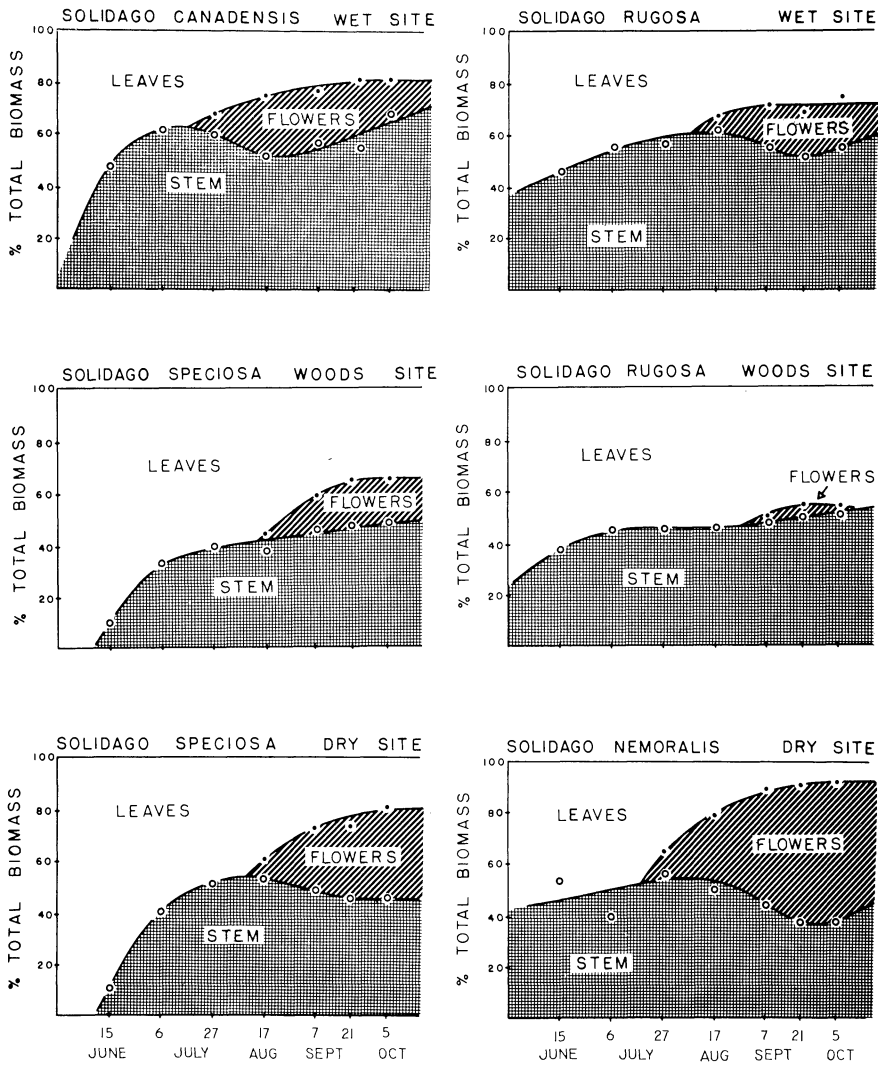


FIG. 2.—Percentage total biomass of stem, leaves, and flowers (buds, flowers, pappi, seeds) plotted on the ordinate as a function of time (plotted on the abscissa) during the growing season for each of the six goldenrod populations. Each point represents the mean of the individuals included in a single population.

(wet) are not significant. This satisfies the theoretical prediction. The only exception being the higher reproductive effort value for the hardwood population of *S. speciosa* when compared with the wet-site population of *S. rugosa*. It is evident that the goldenrods are allocating a lesser proportion of their resources to reproductive activities in the order of dry site, wet site, and hardwood site. This provides evidence that species of goldenrods adapted to conditions of higher D.I. mortality allocate a greater proportion

of their resources to reproductive activities than the same or related species of goldenrods adapted to conditions of lower D.I. mortality.

Similar results were found in two biotypes of the common dandelion (*Taraxacum officinale*) growing in a disturbed site and an undisturbed site (Gadgil and Solbrig 1972). The dandelions at the disturbed site produce approximately three times as many heads and seeds. In addition, the dandelions of the disturbed site bloom in their first year while those of the undisturbed site bloom only after their second year. Quinn, Rotsettis, and Fairbrothers (1972) found *Danthonia sericea* populations growing in dry upland sites have greater seed number and weight than populations growing in wet sites. However, these commitments to reproductive tissues were not correlated with total plant biomass which would have provided an index of reproductive effort. Abrahamson (in preparation) found dewberry (*Rubus hispidus*) populations in a dry field community allocate approximately 2.3 times as much biomass to reproductive activities (seed and vegetative) as do dewberry populations growing in a forest community in Massachusetts.

Another possible index of reproductive effort is provided by the fraction of the total height of the plant occupied by the inflorescence. This index is not as reliable or accurate as the dry-weight studies and depends on how densely the flowering spikes are aggregated. Table 1 presents the mean values and standard deviations for this index based on 30 plants per population. The data conform to the theoretical prediction. The fraction of height with inflorescence varies from 0.25 in *S. nemoralis* (dry) to only 0.03 in *S. rugosa* (hardwood).

Our second prediction would suggest that the goldenrods from the wet meadow site, which compete with other herbs of a similar growth form for light, show higher stem biomass than those in the hardwood area. The mean of the ratio of stem biomass to total biomass decreases in the following order for the four populations pertinent to this prediction: *S. rugosa* (wet), *S. canadensis* (wet), *S. rugosa* (hardwood), and *S. speciosa* (hardwood). Figures 2 and 3 illustrate the data supporting this prediction. Differences in figure 3 are significant at least at the .01 level as tested by the Mann-Whitney one-tailed *U*-test for eight of the 15 population comparisons. Differences between *S. rugosa* (hardwood) and *S. speciosa* (hardwood), and

TABLE 1
MEAN AND STANDARD DEVIATION VALUES FOR FOUR PARAMETERS OF GROWTH FORM
OF PLANTS BELONGING TO THE SIX *Solidago* POPULATIONS, 1970 STUDY

SPECIES AND SITE	HEIGHT	NO. OF BRANCHES	FRACTION OF HEIGHT OCCUPIED BY:	
			Leaves	Inflorescences
<i>S. nemoralis</i> (dry)	53. ± 10.6	0 ± 0	0.62 ± 0.102	0.25 ± 0.068
<i>S. speciosa</i> (dry)	72. ± 15.2	1.6 ± 2.47	0.92 ± 0.115	0.25 ± 0.106
<i>S. rugosa</i> (wet)	128. ± 15.2	7. ± 3.3	0.59 ± 0.078	0.15 ± 0.052
<i>S. canadensis</i> (wet)	109. ± 14.5	4. ± 3.4	0.59 ± 0.099	0.12 ± 0.046
<i>S. speciosa</i> (hardwood)	52. ± 13.2	0.1 ± 0.36	0.91 ± 0.134	0.13 ± 0.059
<i>S. rugosa</i> (hardwood)	74. ± 28.9	1.1 ± 1.68	0.66 ± 0.109	0.03 ± 0.041

NOTE.—Sample size of each population is 30 plants.

between *S. rugosa* (hardwood) and *S. rugosa* (wet) are significant at the .025 and .1 levels, respectively. Differences between *S. nemoralis* (dry) and *S. speciosa* (dry) or *S. speciosa* (hardwood), *S. speciosa* (dry) and *S. speciosa* (hardwood), *S. canadensis* (wet) and *S. rugosa* (wet) or *S. rugosa* (hardwood) are not significant.

A study of the growth form of the various populations also verifies the second prediction. The plants from the wet meadow site are the only ones assumed to be competing with other plants of the same growth form for light. Such plants are expected to show a number of features which enhance the ability of the plant to shade other plants while minimizing being shaded by others (Donald 1963). These features include: tall stem, branching at the top, and presence of leaves largely towards the apex since the lower leaves are quickly shaded. Table 1 shows the values for height, number of branches, and the fraction of the plant height occupied by leaves. It can be seen that the two wet-meadow-site populations are the tallest, most branched forms with their leaves mainly restricted to the upper portions of the plant. Branching of the inflorescence allows for complete coverage of the canopy so the plant can intercept more incident sunlight while shading shorter plants.

Our third prediction implies that the goldenrods from the hardwood site, which are shaded by trees, should adjust to the lower light level and should have high leaf biomass. Figures 2 and 4 illustrate the empirical data which provide evidence for this prediction. The mean of the ratio of leaf biomass to total biomass decreases in the following order for the four populations pertinent to the third prediction: *S. rugosa* (hardwood), *S. speciosa* (hardwood), *S. rugosa* (wet), and *S. canadensis* (wet). Differences in figure 4 are

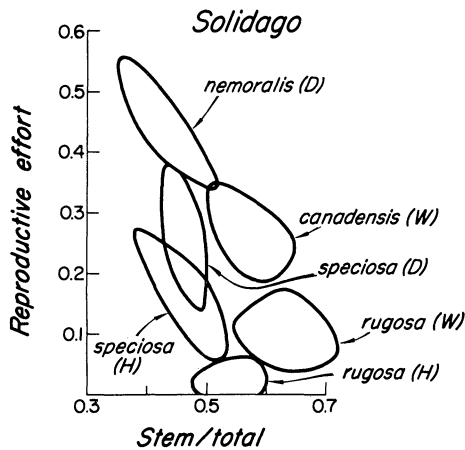


FIG. 3.—Reproductive effort (ratio of the dry weight of reproductive tissue to the total dry weight of above-ground tissue) plotted on the ordinate as a function of the ratio of stem tissue weight to total dry weight of above-ground tissue (plotted on the abscissa) for the six populations of goldenrod. All other information as in figure 1.

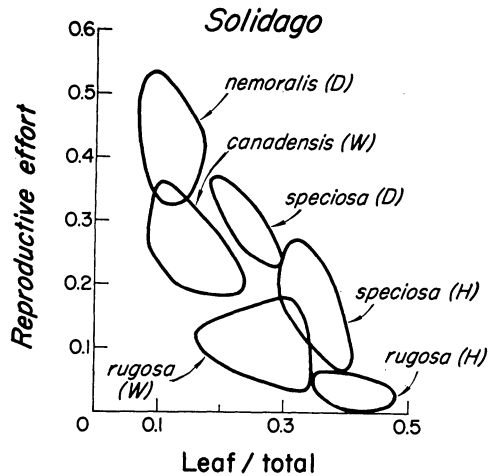


FIG. 4.—Reproductive effort (ratio of the dry weight of reproductive tissue to the total dry weight of above-ground tissue) plotted on the ordinate as a function of the ratio of leaf tissue weight to total dry weight of above-ground tissue (plotted on the abscissa) for the six populations of goldenrod. All other information as in figure 1.

significant at the .005 level as tested by the Mann-Whitney one-tailed U -test for 9 of the 15 population comparisons. Differences between *S. speciosa* (hardwood) and *S. speciosa* (dry), *S. rugosa* (hardwood), or *S. rugosa* (wet) and between *S. rugosa* (wet) and *S. canadensis* (wet) are significant at least at the .025 level. Differences between *S. nemoralis* (dry) and *S. canadensis* (wet), and between *S. speciosa* (dry) and *S. rugosa* (wet) are not significant.

Gadgil and Solbrig (1972) found similar results in dandelion populations. The biotype from the undisturbed site has a higher ratio of leaf biomass to total biomass than the biotype from the disturbed site.

The observations made on the goldenrods grown in the greenhouse confirmed the findings in the field that the leaves of plants from the wet meadow site were restricted mainly to the upper portions of the plant. As the plants in the greenhouse grew in height their lower leaves died even though they were not shaded. We can hypothesize that, owing to shading, the lower leaves usually receive such low levels of light that the energy accumulated by photosynthesis is less than the energy necessary for maintenance of these leaves. When this occurs, it would become advantageous for the plant to lose these leaves rather than divert energy to them for respiration (Donald 1961). Presumably shedding of lower leaves has become genetically fixed in the wet populations, as the plants manifest this characteristic even in the absence of shading in the greenhouse. However, more evidence is necessary for a conclusive test of this hypothesis.

The greenhouse-grown plants showed the same basic patterns of resource allocation as the field populations, even though some plasticity was noted.

This posed the problem of how the same species growing in different habitats, but within 500 m of each other, maintain these ecotypic patterns of adaptation. Observing these populations throughout the growing season allowed us to consider the degree of overlap in flowering times among populations. As is seen in figure 5, blooming times correlate more closely with site than with species of *Solidago*. Thus we observed "full bloom" on the wet meadow site for one species about August 17, 1971 and the other about September 7, 1971; about September 21, 1971 on the dry field site; and about September 29, 1971 on the hardwood site. This indicates that, even though there is some overlap in flowering times, there is some degree of isolation of the same species at different sites. Particularly noteworthy is the situation of *S. rugosa* which flowers much earlier at the wet site than at the hardwood site (fig. 5). The plants at the wet site are setting seed as those at the hardwood site begin to make pollen available to pollinators. Goldenrods are insect pollinated with the most frequent floral visitors being honeybees and bumblebees. Given the usual constancy of these floral visitors, we might expect a lessening of the potential for hybridization even among the different species of a given site.

The reliability of dry-weight measurements as an index of resource partitioning was tested by burning samples of the tissues of the various goldenrod populations in a Parr bomb calorimeter. No variation in a given tissue was noted from population to population in regard to caloric value. There

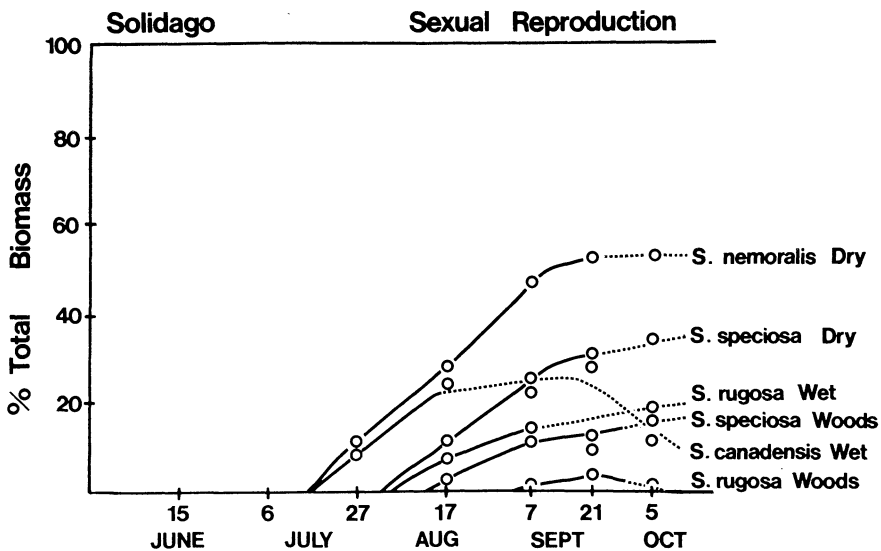


FIG. 5.—Percentage total biomass in sexual reproduction plotted along the ordinate as a function of time (plotted along the abscissa) during the growing season for the six populations of goldenrods. Each circle represents the mean of individuals in a single population. Solid lines trace inflorescences from buds to the full-bloom stage, dotted lines indicate stages past full bloom to mature seeds. Dry = dry field site; Wet = wet meadow site; Woods = hardwood site.

are, of course, differences in the caloric value of the different tissues. However, as a given tissue has the same caloric value in all goldenrods studied, this would only shift the curves in figure 2 slightly up or down. This does not change the conclusions since the reproductive effort, for example, would be increased for all populations in the same proportion.

Stem tissue in the goldenrods tested (sample size = 5) had a caloric value of 4,121 cal/g dry wt, $sd = \pm 194$ cal/g dry wt. Leaf tissue (sample size = 5) had a higher value of 4,479 cal/g dry wt, $sd = \pm 22$ cal/g dry wt. The reproductive tissue (buds, flowers, pappi, seeds, etc.; sample size = 5) had the highest caloric value at 4,561 cal/g dry wt, $sd = \pm 163$ cal/g dry wt. Statistically, the differences between stem tissue and leaf or reproductive tissue are significant at the .05 level as calculated using Student's *t*-test. The difference between leaf and reproductive tissues is not significant.

SUMMARY

Based on Gadgil and Solbrig's (1972) ideas concerning the distribution of resources between the reproductive and vegetative tissues, it is predicted that the ratio of reproductive biomass/total biomass (reproductive effort) will decline with the increasing successional maturity of the community. This prediction was confirmed in field studies utilizing four species of goldenrods.

The distribution of resources among the various vegetative tissues should depend on the nature of the limiting factor and the growth form of the dominant plants competing for this limiting factor. Thus, it is predicted that the ratio of stem biomass/total biomass will decline and that of leaf biomass/total biomass will increase for light-limited plant populations as the growth form of competitors changes from being one of the same stature (herbs with herbs) to being one of greater stature (herbs with trees). These two predictions are likewise confirmed in goldenrods.

The problem of how these differences in the distribution of resources among tissues are maintained in closely growing populations of a single species was examined. It was found that populations of a given species bloomed at different times, thus reducing the gene flow between these populations. This indicates some degree of isolation which could allow for the maintenance of ecotypic variation.

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