Resource choice in *Cuscuta europaea*

(plant distribution/modular autonomy/clonal plants/parasitic plants/host choice)

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ABSTRACT   Individual stems with growing tips of dodder (*Cuscuta europaea*) were transplanted onto host plants (hawthorn) of varying nutritional status. The parasite was more likely to coil on ("accept") hosts of high nutritional status and grow away from ("reject") hosts of poor quality. Dodder exhibits this acceptance/rejection response before taking up any food from the host, so it is possible to dissociate active choice from the passive effects of growth and mortality. Probability of acceptance is gauged to expected reward.

Higher plants vary in size and shape through variation in number or morphology of the repeating subunits (modules) of which they are composed (1–3). Differences among modules have primarily been assumed by population biologists to be the result of changes in growth dictated by changes in local resource uptake (e.g., refs. 4–7), although physiological studies show that plants can make qualitative changes in gross morphology in response to local resource conditions that could be adaptive (e.g., refs. 8–12). Such changes could execute plant "choice": the acceptance or rejection of a resource type or patch based on some criteria of patch value to the choosing plant.

Rejection of a resource in the absence of an alternative would indicate that a plant may strategically take the risk of forfeiting resources for the chance of acquiring better resources later, thus altering resource acquisition patterns. Resource choice could also determine entry of a plant into a resource patch and in this way contribute to the notoriously variable size and shape of plants (13–15), traits that have direct and indirect consequences for plant fitness through their effects on competition, herbivory, and seed set (16–22). Additionally, choice combined with differential mortality of plant parts may affect the distribution of a population among resources.

However, previous demonstrations of the qualitative morphological changes that plant choice would entail have been based on contrasts between high and low values of a nutrient or condition (e.g., refs. 8–12), thus allowing no more than the conclusion that plants do different things in different environments. It is not possible to determine under a two-valued system whether the observed responses are the right (adaptive) things to do with regard to those particular levels of treatment. In order to demonstrate that plants can make adaptive choices among resources, this study uses four levels of treatment and draws upon the same cost–benefit criteria that have been applied to resource choice in animals (23–25).

I show here in experiments with the clonal parasitic plant dodder (*Cuscuta europaea*) an unequivocal demonstration that plants are able to make qualitative morphological changes gauged to the level of expected gain from the resource.

METHODS AND MATERIALS

Dodder (Convolvulaceae) has no roots, only vestigial leaves, and does not photosynthesize. A stem of dodder infests its hosts by forming one or more loops about the host stem or leaf (a coiling bout), after which it sends pegs of absorptive tissue (haustoria) into the host vascular system. Dodder possesses responses that may be used to effect rejection (Fig. 1) and acceptance of resources. These responses are complete prior to any resource uptake and thus cannot be confused with the passive results of uptake (16).

Hawthorn (*Crataegus monogyna*) is a native host of this dodder in Great Britain (26). Six hundred 45-cm rooted cuttings of a single hawthorn genotype were grown for 8 months in John Innes compost no. 2 at Wytham Research Station (Oxon, U.K.). In July 1989, the roots were cleaned of potting material and the plants were repotted in 20-cm plastic pots with John Innes silver sand, a non-nutritive, non-retentive potting medium. Forty-eight similar-sized plants were selected for the experiments and removed to a small glasshouse. In late February 1990 the glasshouse plants were placed on a regime of deionized water to exhaust any internally stored resources, so that subsequent growth would depend only on regulated nutrient supplements. One month later the plants were randomly divided into four groups of 12 each, and each group was subjected to a different nutrient treatment. The nutrient treatments constituted a serial dilution of a balanced, complete nutrient solution (27) supplying 15, 7.5, 3.75, and 1.87 mM nitrogen (N) per week. The treatment levels were chosen to span the range of possible host values: the full-strength treatment was only slightly less than that which induced leaf-burn in the host, and the lowest treatment level produced only minimal amounts of host growth. It was expected either that dodder would show a 0–1 response, in which at some point in the range of host values, dodder would switch from rejecting hosts to accepting hosts (23), or that dodder would exhibit what are termed partial preferences, where host acceptance would rise with increasing host value (28).

Hawthorn growth was recorded at 10-day intervals from the beginning of nutrient applications. Growth was calculated as change in volume on a branch-by-branch basis for all branches (and main stem) more than 0.5 cm long; branches and stem were assumed to be cylinders. Because primary meristems had been removed, there was no growth in main-stem length during the course of the experiment. Main-stem length did not differ among treatments ($F_{3,47} = 0.143$, $P = 0.9336$), and overall average length from soil surface to tip was 32.9 ± 1.83 cm (mean ± SE).

Parasite stems collected from a single naturally occurring parasite were transplanted onto the nutrient-regulated hosts on two separate runs, 7 July and 11 July. Transplants were performed after the host plants showed significant differences among nutrient treatments in individual growth for two measurement periods (ANOVA; $F_{3,47} = 2.98$, $P = 0.04$ for

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Ecology: Kelly

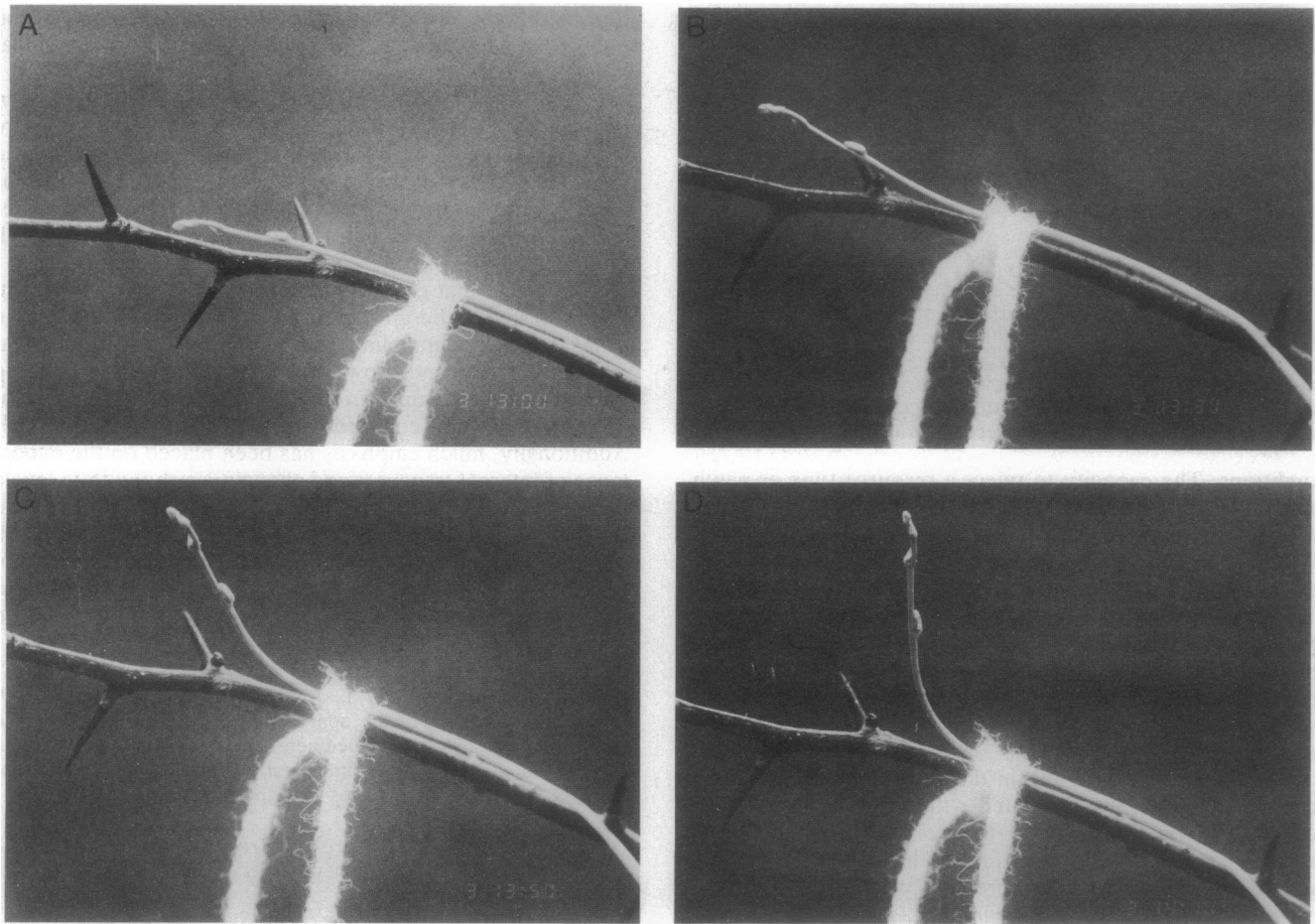*Proc. Natl. Acad. Sci. USA 89 (1992)* 12195

FIG. 1. Parasite rejection response. A transplanted parasite stem tied parallel to a host branch may reject a host by turning at right angles to the host plant and elongating in a trajectory directly away from the host. This response is complete within ≈3 daylight hours after initial contact between host and parasite. There is a 30-min interval between the first 2 exposures, and 20-min intervals between subsequent exposures.

measurement period 8; $F_{3,47} = 3.93$, $P = 0.01$ for measurement period 9). Transplantation consisted of trimming each parasite stem to 15 cm in the morning, recording the diameter of the parasite stem at its base, and placing the stem in a water-filled plastic test tube taped to the target host. Test tubes were positioned so that the growing tip of the parasite stem could be tied to the newest tissue on the host. Only one parasite stem was transplanted to each host at a time, allowing 96 replicates overall for the 2 runs of the experiment. The experiment was considered complete when 95% of the parasite stems had either rejected or accepted their hosts. The two stems that did not respond (i.e., did not show active rejection) were coded into the analysis as having accepted the host. After the second run, the host sections with which the parasite stems had come in contact were collected and assayed for concentration of Kjeldahl-determined total organic N (29), as an indicator of host metabolic status.

Data were analyzed by fitting a logistic regression using a generalized linear model, assuming a binomial distribution of the dependent variable (30). The independent variables were experimental run, nutrient application level, percent host stem nitrogen, and parasite stem diameter.

RESULTS

Dodder was more likely to accept a host that had received higher nutrient supplements (Tables 1 and 2). The parasite was able to distinguish differences within as well as among host nutrient categories: individual measures of host nutrient status (percent N) accounted for significant variation in

parasite response after host treatment category had been entered into the model, but if percent N was added to the analysis prior to host treatment category, the latter had no significant effect. Parasite stem diameter did not affect host acceptance by dodder (Table 2). All conclusions held regardless of order of entry of the variables ($\chi^2 = 0.64$ when parasite stem diameter was entered into the model first), other than that noted above. There was no significant difference between the two runs of the experiment in parasite response ($\chi^2 = 1.72$, $P > 0.1$).

DISCUSSION

Arguments for non-seed choice by plants have relied upon observations of directional growth along a resource gradient (5) or the previously mentioned differences between responses to two treatment levels (e.g., refs. 8–12). Gradient-oriented growth can show only that a plant will utilize available resources; two-value tests can demonstrate no more than that plants do different things under different

Table 1. Summary of raw data

Treatment	No. of stems accepting hosts	No. of stems rejecting hosts	Average N content
1.87 mM N	9	15	0.727
3.75 mM N	10	14	0.749
7.5 mM N	14	10	0.796
15 mM N	19	5	0.983

Each host plant received 1 liter of treatment solution per week.

Table 2.   Statistical results

Model	Residual deviance	df	χ^2 value	Significance
Null model	116.45	94		
+ host nutritional category	106.98	93	9.47	$P < 0.005$
+ host stem [N]	102.22	92	4.76	$P < 0.025$
+ parasite stem diameter	102.22	91	0.02	$P > 0.5$

Shown are residual deviances, degrees of freedom, and χ^2 values indicating amount of deviation from a binomial distribution (accept vs. reject) accounted for by a variable. The initial variable entered explained deviation from the null model attributable to that factor; variables entered subsequent to the first explained the residual variation not attributable to any preceding variables in the model.

conditions. The capacity to reject a resource type or patch may allow a plant to determine the presence of part or all of its body in a resource patch. For clonal plants, with potentially independent subunits (ramets), choice could also alter the proportion of a population in a resource type; a clonal plant has the option, not available to unitary plants, of abandoning the central, colonizing portion of a plant body should it occur in a poorer resource patch. This research thus emphasizes the need for a greater awareness of local habitat patchiness in studies of distribution and demography of modules, ramets, and genets.

The schedule of rejection in dodder, with probability of acceptance positively correlated with resource value, also accords with qualitative predictions of the cost–benefit criteria used to investigate the adaptive value of resource choice in animals (28). Furthermore, previous work has shown that a related species, *Cuscuta subinclusa*, grows significantly larger (and thereby has greater potential seed set) on hosts that have received nutrient supplements (16). Thus there are three lines of evidence supporting an hypothesis of an adaptive value to choice (*cf.* ref. 31).

Several lines of evidence allow the conclusions reached here for detached ramets to be applied to attached ramets and modules. First, detached ramets do not behave significantly differently than attached ramets, by several criteria: neither probability nor rate of coiling differ between attached and unattached dodder stems, nor does length of stem in coil (unpublished data). Second, $^{14}CO_2$ and dye labeling of vascular flow in attached dodder stems shows vascular flow to be almost without exception toward the growing tip (32), so that one might expect gross source–sink relationships to change when one tip "chooses" to coil but not transfer of fine-tuned evaluations of local conditions such as are evidenced here. Finally, detailed demography of dodder ramets (C.K.K. and R. Perez-Ishiwara, unpublished data) reveals no correlation among adjacent ramets that cannot be explained by local resource conditions alone, indicating that a significant portion of modular response may indeed be an independent response to local conditions.

Whether the potentially adaptive ability to choose resources is accessible to all plants or is dictated by the cloning ability or parasitism of dodder is unknown. However, the increased efficiency of resource acquisition that modular "choice" could provide would be beneficial to any plant, parasitic, clonal, or otherwise. For unitary plants, responses have been identified that would allow adaptive choice at the level of the whole plant or for subsections of the plant reacting to small-scale habitat differences. Seedlings can respond to changes in light quality in a way that may allow the mature plant to avoid competition (11–13). Subsections of roots show heightened lateral root proliferation and increases in biomass accumulation in response to locally elevated

nutrient conditions (33–35). Lastly, the argument has been put forth recently that even individual branches of nonclonal trees may respond locally to local conditions (36).

Previously, host preference in parasitic plants has been equated with host use (37, 38). The results presented here also necessarily show active choice on the part of a parasitic plant and outline a means by which choice might be tested for other parasitic angiosperms. By extrapolation from other studies, resource recognition by dodder is by host bark flavonoids (16).

One reason that choice in plants has not previously been demonstrated to be an adaptive strategy is because of the difficulty in disentangling passive growth due to current resource uptake and growth for the purpose of modifying future resource acquisition (5, 32), except under fairly elaborate experimental conditions (refs. 8–12, but see ref. 16). Additionally, much emphasis has been placed on the importance of internal transport and changing carbohydrate levels in determining ramet or module response (4, 6, 39–43). The results of the experiment described here show that such changes in internal state (as indicated here by the lack of effect of stem diameter; ref. 32) can be negligible relative to the influence of external resources in determining adaptive resource rejection or acceptance.

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Ecology: Kelly

Proc. Natl. Acad. Sci. USA 89 (1992) 12197

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