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Janzen's Dandelions: A Criticism

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Source: *The American Naturalist*, Vol. 114, No. 1 (Jul., 1979), pp. 152-156

Published by: [The University of Chicago Press](#) for [The American Society of Naturalists](#)

Stable URL: <http://www.jstor.org/stable/2460296>

Accessed: 12-08-2014 14:09 UTC

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Submitted December 29, 1977; Accepted June 5, 1978

JANZEN'S DANDELIONS: A CRITICISM

Janzen (1977) has produced a model of the structure and growth of dandelion populations based on the following assumptions: (1) nearly all seed is produced by apomixis and (2) sites colonized by individuals of a single population are highly invariant for spatial variables of the environment; therefore, (3) dandelion populations are comprised of many replicates of a single or very few biotypes and thus show a markedly low genetic variance.

With regard to assumption (1), Janzen provides no details of which species or sections of the genus *Taraxacum* he is considering, despite the fact that the genus contains an estimated 2,000 microspecies (Richards 1973) with a diversity of breeding systems. From available chromosome counts within the genus, Richards (1973) has calculated that 13% of species are diploid, 52% triploid, 27.5% tetraploid, 7% pentaploid and 0.5% hexaploid. All diploids are obligate sexuals and therefore

exceptions to Janzen's first assumption. Of the rest, it is the common view that reproduction occurs by near obligate apomixis. This certainly seems true for most polyploid dandelions including those North American representatives of *Taraxacum officinale* (see Solbrig and Simpson 1974), which Janzen may have had in mind when formulating his model. However, it should not be overlooked that reasonably extensive surveys of populations of certain European triploid microspecies (including some that have been traditionally placed within *T. officinale* agg.) have shown that diploid sexual individuals and triploid facultative apomicts may exist alongside triploid obligate apomictic individuals (Richards 1970, 1973; Sørensen and Gudjons-son 1946; Malecka 1971, 1973). Richards has advanced that such sexuality within triploid species is very limited, the vast majority of species being obligate apomicts. However, such a belief must be born more from hearsay than fact, as only a very few triploid species of *Taraxacum* have so far received the required detailed investigation to reveal sexuality (see Richards 1970). Indeed, Richards (1970, p. 771) has pointed out that, "It may be that facultative agamospermy remains to be discovered in a number of other *Taraxacum* species." Where facultative apomixis is reported its expression seems flexible and, having a genetic basis (Sørensen 1958; Richards 1970), will be subject to selection. Such a system may allow certain *Taraxacum* populations to achieve that fine measure of control over degree of outcrossing that exists in many species of predominantly self-pollinating sexual species (see Jain 1975; Campbell and Abbott 1976).

Turning to Janzen's second assumption, it is difficult to understand why he states "the habitats and resource bits for an EI [evolutionary individual] dandelion are highly invariant. I have trouble thinking of a more monotonous resource than 6 square inches of new mud" (Janzen 1977, p. 586). It is a well known fact that, even when the environment is uniform within a microsite, in most habitats there are likely to be disparities between sites. Russell (1961) and many other authors too numerous to quote here have made it abundantly clear that "mud"/soil, be it new or old, may show marked variations for compactness, water and nutrient content, pH, etc., over short distances. Add to this the great range of species, each of varying form, that can be present around each patch of mud, and it is clear that the type of sites occupied by dandelions in a particular area will often be highly heterogeneous. Such heterogeneity could generate considerable genetic differentiation within a population due to the selection of highly localized adaptive forms which are in the main self-perpetuating. It is worth noting that this might be expected even in such species as dandelions which show a capacity for wide phenotypic plasticity (see Abbott 1976a, 1976b).

In situations where Janzen's assumptions (1) and (2) are correct we must still ask the question whether near obligate apomixis is sufficient to suppress the presence of overt (between plant) genetic variability in dandelion populations. Again, the existing literature suggests it would not. First, Solbrig and Simpson (1974) have drawn attention to the evidence of a high rate of somatic mutation within dandelions. Indeed, it is well known that various chromosomal changes such as loss of individual chromosomes (Sørensen 1958) and polyploidy (Kappert 1954) readily occur in dandelions, and in the case of chromosome loss the affected plants may produce offspring sexually rather than by apomixis (Sørensen 1958; Richards 1970). In

addition to mutation, Briggs and Walters (1969, p. 144) have pointed out that the condition of diplospory in *Taraxacum* species (leading to the production of an unreduced gametophyte) allows for "some pairing of the chromosomes in the embryo sac mother cells and crossing over may take place giving rise to plants of different genotype from that of the parent." (See especially the recent work of Malecka [1971, 1973].) Such genotypic differences will, of course, only affect gene position. The total genotype will remain the same, although rearranged. Nevertheless, as Briggs and Walters suggest, such complexities "may be more widespread and more important in their effect on variation patterns than has yet been established."

When these sources of variation are taken into account and considered with the existence of facultative apomixis in the dandelion genus it is to be expected that a significant amount of genetic variability may well occur within many dandelion populations. Nevertheless, the existing literature remains confused on this point. On the one hand Nilsson (1947) and Kappert (1954) suggest that apomictic dandelion populations in Europe are comprised of many disparate microspecies (genotypes) and thus are highly variable, while a survey by Solbrig (1970) of three North American dandelion populations comprising a total of several thousand individuals has established the presence of only four major genetically distinct biotypes, indicating relative genetic uniformity. Such low genetic variance within populations in the United States of America could be attributable to the fact that dandelions are adventive there. It is noteworthy, however, that Solbrig (1970) classified plants into biotypes by means of a survey of isozyme variation. Recent work (Levin 1975; Steiner and Levin 1977) has shown that the results of such isozyme surveys may lead to a serious underestimate of the amount of genetic variability within plant populations. Such underestimation may stem from the rather crude methods that have often been employed in the surveys. (See Coyne [1976] and Singh et al. [1976] for more critical approaches.) It is possible, therefore, that the use of improved techniques of gel electrophoresis combined with other methods of genetic analysis may in fact show far greater levels of genetic variation to exist within North American dandelion populations than Solbrig's work has so far indicated.

I arrive at my final point. Our present knowledge of the population genetics of dandelion populations is about equivalent to that for predominantly self-pollinating species at the time when Darlington and Mather in 1949, Baker in 1953, and Stebbins in 1957 suggested models for the genetic structure of populations of inbreeding species. As Janzen (1977) does now for dandelions, these workers advanced that populations of predominantly selfing species would be genetically uniform and comprised of many replicates of one or a few biotypes. For a variety of reasons (see Allard and Kahler 1971; Jain 1975; and Abbott 1976*a*, 1976*b*) we now know that the very opposite situation is true, and that most predominantly inbreeding species contain at least some populations in which there are considerable amounts of between-plant variation. Even within species where outcrossing has yet to be detected, e.g., *Festuca microstachys*, high levels of intrapopulation genetic variation exist for a range of morphological traits (Kannenberg and Allard 1967). One is left with the notion that at the present stage it would seem more profitable to gather relevant data on the biology of dandelion populations than accept generalized

models of their biology based on what must be described as somewhat superficial assumptions.

ACKNOWLEDGMENTS

The preparation of this letter benefitted from discussions with Peter Gibbs and George Sheperd during a sabbatical period spent at the Departamento de Botanica, Universidade Estadual de Campinas, Brazil. The award of a Fellowship tenable in Latin America by the Royal Society and the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) is gratefully acknowledged.

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Submitted October 25, 1977; Accepted June 21, 1978

JANZEN'S REPLY

Abbott (1979) states that "Janzen (1977) provides no details of which species or sections of the genus *Taraxacum* he is considering." The last three sentences of the first paragraph of my note are a succinct ecological description of the kind of organism I am considering; what Latin binomial has been attached is absolutely irrelevant. Incidentally, by Abbott's cited calculation it appears that my model dandelion is representative of 87% of the 2,000 microspecies in the genus, which is considerably more in focus than nature allows most ecological models.

It is very easy to see why I stated "there should be selection for only minimal outcrossing among EI [evolutionary individual] dandelions, since the habitats and resource bits for an EI dandelion are highly invariant. I have trouble thinking of a more monotonous resource than 6 square inches of new mud." I'll bet Abbott a case of beer that the traits of 6 square inches of new mud have not changed since the Cretaceous, or at least the Pliocene, if you must. Of course there is marked variation between this and that small patch of bare ground; but the EI dandelion is trying to harvest all or most patches of a certain kind within its reach, and there is no evidence that this resource in aggregate changes over a time scale such as to select for constant high levels of outbreeding to keep the genome picking up new genetic information required to deal with an ever-changing environment. While the environment "new diseases, new competitors, new pollinators, new herbivores, new dispersal agents, and the loss of any or all of them" is in a constant state of flux, the environment "specializing on harvesting new bare bits of earth" has probably not changed in a good 50,000,000 yr or more. Even with global changes in climate all that changes is the location of the bare bits of earth, not the essential trait of being bare.

I think I remain quite happy with Abbott's observation through Solbrig (1970) that there are only four genetically distinct types of dandelions in North America; this is, irrespective of the character states used to ascertain it, rather less variation than I would expect to be found in a continent-wide genus of regularly outcrossing