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RECIPROCAL TRANSPLANT EXPERIMENTS WITH DELPHINIUM NELSONII (RANUNCULACEAE): EVIDENCE FOR LOCAL ADAPTATION¹

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ABSTRACT

Reciprocal seed transplants suggest that there is fine-scale adaptation in Colorado populations of the perennial herb *Delphinium nelsonii*. In four experimental plots, seeds planted within 1 m of the maternal parent produced seedlings that began flowering at a younger age and produced more flowers over their lifespan than those derived from maternal parents growing 50 m away. These “resident” seedlings also survived as well or better than the “nonresidents.” Resulting selection coefficients against nonresidents averaged 34%. Species composition of the herbaceous flora was found to vary substantially over short distances in subalpine meadows where *D. nelsonii* grows, indicating that the biotic environment varies and that physical factors probably do as well. Thus, spatial heterogeneity in selective forces may be substantial, which should foster the sort of local adaptation documented for *D. nelsonii*.

PLANT POPULATIONS commonly harbor genetic variation that has a strong spatial component (e.g., Epling, Lewis and Ball, 1960; Jain and Bradshaw, 1966; Levin and Kerster, 1974; Bradshaw 1984). To what extent does spatial genetic variation result from natural selection rather than from stochastic effects of limited gene dispersal and resulting genetic drift (i.e., isolation by distance; Wright, 1943)? Support for the importance of selection dates to the classic studies of Turesson (1922) and Clausen, Keck and Hiesey (1940, 1948), who used transplant experiments to demonstrate genetic variation among plant populations on a scale of kilometers to hundreds of kilometers and who argued on the basis of functional design that this variation is adaptive.

Over the last 15 years, evidence has accumulated for fine-scale adaptation within single plant populations. Some of the best demonstrations again involve transplants (Bradshaw, 1984; Endler 1985). For example, Turkington and Harper (1979) made reciprocal transplants of clover within a pasture and found that each genotype grew best in its site of origin and when competing in the greenhouse with the grass species that dominated that site. Hickey and McNeilly (1975) and Davies and Snaydon (1976) used transplants to demonstrate local

adaptation to abiotic, rather than biotic, conditions. Schemske (1984) detected local adaptation in jewelweeds distributed along a strong gradient of biotic and abiotic conditions, but not in those growing under more uniform conditions. Fowler and Antonovics (1981) and Antonovics and Primack (1982) found little evidence of local or regional adaptive differentiation, but, as discussed later, their results might be due to the methods used.

We report here on reciprocal seed transplants with *Delphinium nelsonii* Greene (Ranunculaceae). Demographic studies of this small perennial herb indicate that several fitness components, especially age at first flowering and lifetime flower production, are sensitive to transplantation over short distances in subalpine meadows. Seeds planted within 1 m of the maternal parent yield seedlings (“residents”) that outperform those planted at the same site but derived from maternal parents growing 50 m away (“nonresidents”). This pattern holds in four replicate plots followed for 6–7 yr. We also report on the relationship between physical distance in meadows and change in species composition of the herbaceous flora, which is a likely indicator of change in biotic and abiotic selective forces impinging on *D. nelsonii* individuals.

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MATERIALS AND METHODS—Basic life history—Demographic results from this and other studies at the Rocky Mountain Biological Laboratory (RMBL) in western Colorado allow us to outline life history features of *D. nelsonii*. There is no clonal growth or seed dormancy;

seeds shed in one summer germinate immediately after snowmelt the following May. Aboveground vegetative parts persist for 2–4 wk, depending on June rainfall, and then wither. First year seedlings produce one small 2–3-lobed leaf. Second year plants produce a single 3–5-lobed leaf, and leaf size and lobe number increase in subsequent years. By the third to fifth year, plants generally produce two leaves. Under optimal growing conditions some individuals flower in the third year, but in the field first flowering is usually delayed. The first flower raceme is small, sometimes containing a single bud. Bud number increases for about 3 yr and then stabilizes at 5–15, produced on a flowering stalk that is 15–25 cm tall. Some individuals survive for at least 9 yr after they start flowering. Plants occasionally skip flowering for one or more years, producing leaves only. Not all flower buds yield fruits; later buds especially may abort before or after they open. Flowering usually begins in early June and lasts about 4 wk. For more information on floral biology and pollination see Waser (1978), Waser and Price (1983), and references cited in those papers.

Reciprocal transplants—Around the RMBL, *D. nelsonii* is abundant in habitats ranging from rocky hillslopes dominated by *Artemisia tridentata*, to aspen woodlands, to meadows lacking woody vegetation. In the last of these habitats we chose three study sites designated Upper Slope, Lower Slope, and Flat Meadow (hereafter US, LS, and FM) along an elevational gradient running from NW to SE. Adjacent sites are separated by 50 m. The US site (2,920 m elevation) is on a steep south-facing slope. Snow usually melts in late May, and the vegetation is dominated by *Lomatium dissectum* and *Erigeron speciosus*. The LS site (2,900 m elevation) is on a gentler south-facing slope. Snow melts about one week later than at the US site, and the vegetation is dominated by *Viola nuttallii* and grasses. The FM site (2,890 m elevation) is at the bottom of the slope containing the other sites. Snow melts about 2 wk later than at the US site, and the vegetation is dominated by *Potentilla gracilis* and grasses. At each site we characterized soil depth by pounding in a steel stake until bedrock was encountered. This was repeated 10 times for each site, at intervals of 5 m along a line at right angles to the slope and at the appropriate elevation for the site. The proportion of soil surface area turned over by gophers was also estimated within a 1 m² area at each of these 10 sampling points.

To look for local adaptation, a 1 m × 1 m

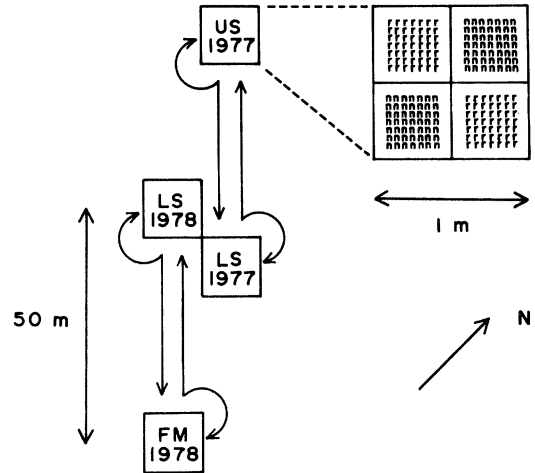


Fig. 1. Reciprocal transplant experiments. US = Upper Slope site; LS = Lower Slope; FM = Flat Meadow. Each plot was planted with 98 resident and 98 nonresident seeds (labeled "r" and "n") as shown in the blowup. Seeds were separated by 5 cm.

transplant plot was established in 1977 at each of the US and LS sites, and in 1978 two more plots were established, one adjacent to the 1977 LS plot and one at the FM site (Fig. 1). Plots were seeded as follows: To ensure that no extraneous *D. nelsonii* seeds would contaminate plantings, all flowers within 2 m of each plot were removed annually; seed dispersal is <1 m (Waser and Price, 1983). In July 1977 mature open-pollinated seeds were pooled from six individuals growing within 1 m of the US plot and from six growing within 1 m of the LS plot. From each of these separate bulked seed collections 196 normally pigmented, apparently viable seeds were chosen, and half were planted in the US plot and half in the LS plot (Fig. 1). Each seed was placed in a hole 5 mm deep and covered with soil to reduce winter displacement. We did not remove vegetation in plots before planting. In July 1978 identical transplants were carried out between the FM plot and the second LS plot. Thus, there were two replicate reciprocal transplant experiments and four replicate plots in terms of treatments received. In all we planted 784 seeds.

Plots were censused in June of each year following planting, using a 1-m² wooden frame divided into 100 10-cm × 10-cm squares. The frame was positioned over permanent corner markers of a plot, and for each individual we recorded leaf size (number of lobes and radius of largest leaf), leaf number, and number of flower buds. Relocation between years was accurate: most individuals were found within 2 cm of their previous positions. However, a small fraction of surviving plants was not re-

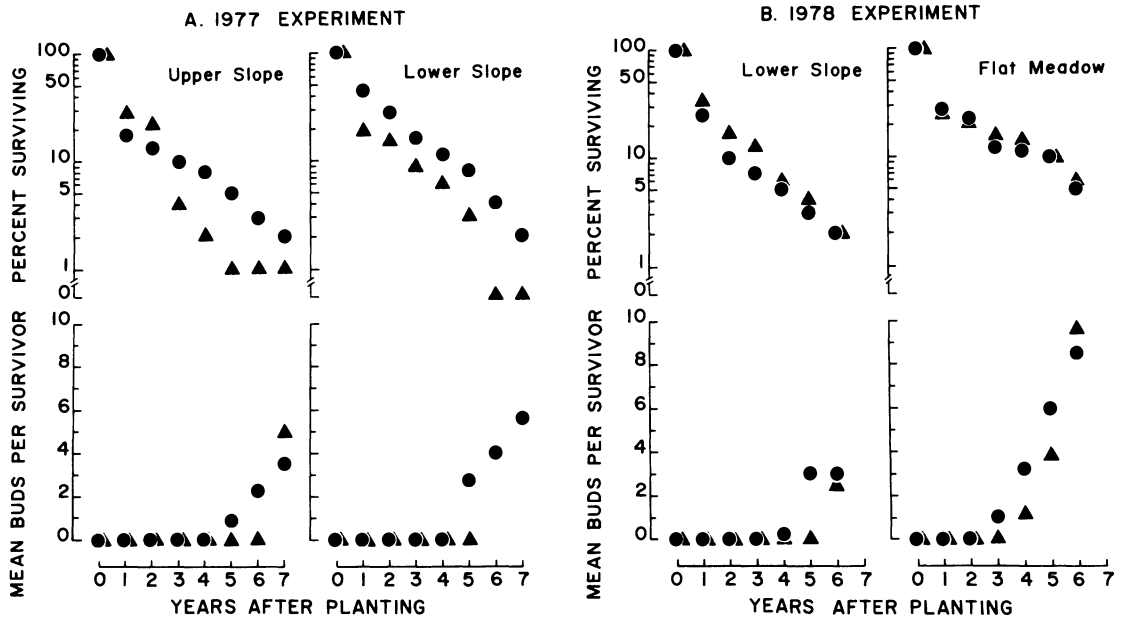


Fig. 2. Survivorship curves and age-specific fecundity estimates (mean number of buds produced per surviving plant) for residents and nonresidents in each plot. A. Values for the 1977 transplants between US and LS sites. B. Values for the 1978 transplants between LS and FM sites. Residents are shown as circles, nonresidents as triangles.

corded in some years, presumably because leaves had withered before the census was conducted.

Censuses yielded values for age specific survivorship (l_x) and reproduction (m_x), from which fitness estimates were derived. We estimated m_x as the average number of flower buds produced at age x rather than as seed set, for two reasons. First, flowers may contribute genes through pollen independent of seed production. Plants that perform poorly as seed parents might do well as pollen parents, which would be obscured by simply counting seeds. Second, nonresident plants experienced a foreign pollen environment, which is expected to reduce seed production (Waser and Price, 1983). This reduction appears to be caused by a prefertilization barrier, and the barrier appears to have evolved to prevent wide crosses, which yield offspring of low fitness (Waser and Price, in prep.; also see Discussion section). This is a complication we do not wish to incorporate in estimating the degree of local adaptation. For our purpose, estimating fecundity as bud number will yield qualitatively correct relative fitness values so long as we assume that buds of residents and nonresidents have equivalent intrinsic abilities to transmit genes; i.e., equivalent ovule numbers, pollen production, pollinator attractiveness, and so on.

Survivorship and fecundity values were used

to calculate the net reproductive rate, R_0 , for residents and nonresidents. This is the total expected number of offspring produced by an individual, or $\sum l_x m_x$. We also calculated dominant eigenvalues (λ) of Leslie matrices containing age-specific survivorship and fecundity estimates. As a fitness measure λ is more complete than R_0 because it incorporates the substantial effect of age of first reproduction (Leontin, 1965). A computer was used to calculate eigenvalues by iterative multiplication of an initial uniform age vector by survival and fecundity estimates through Year 6 or 7, as appropriate for each plot. This assumes that fitness contributions beyond Year 6 or 7 are negligible. Convergence on stable age distribution often took several hundred iterations. In two cases, both involving nonresidents, there was only one reproductive age class. Convergence cannot occur under this condition, so it was necessary to switch a minimal fraction or reproduction from the reproductive age class to the next earlier age class in order to obtain convergence and a λ estimate. This inflates λ slightly, but the effect was conservative because if anything we were reducing the chance that resident fitness estimates would exceed nonresident values.

Censuses of herbaceous vegetation—To characterize biotic differences between transplant plots, their herbaceous vegetation was cen-

TABLE 1. *Fitness estimates for residents (R) and nonresidents (N) in transplant plots. US = Upper Slope site, LS = Lower Slope, FM = Flat Meadow. R_0 is net reproductive rate and λ the dominant eigenvalue of the Leslie matrix for each treatment*

Fitness measure	Plot and treatment							
	1977 US		1977 LS		1978 LS		1978 FM	
	R	N	R	N	R	N	R	N
R_0	0.18	0.05	0.51	0.0	0.16	0.05	1.56	1.18
λ	0.79	0.67	0.91	0.0	0.75	0.66	1.08	1.03

sused in June 1982. In each plot we counted the proportion of the 10 cm × 10-cm subdivisions of the sampling frame that contained a given species. Euclidean vegetational distances were calculated by squaring the difference between paired plots (US and LS, LS and FM) in proportional occurrence of each species, summing across species, and taking the square root.

The relationship between physical distance and vegetational distance in a representative subalpine meadow was also characterized. In June 1981, two 160-m-long transects were established in a meadow containing *D. nelsonii* about 200 m north of the US plot. The transects formed an “L.” Census points were chosen at 5-m intervals, but only where transects traversed relatively dense *D. nelsonii* stands (>3 flowering individuals within 50 cm of the census point). A 25-cm × 25-cm quadrat was placed 1 m from each census point in each compass direction, and the proportion of these four quadrats containing each herbaceous species encountered in the census was recorded. We calculated vegetational distances between all possible pairs of census points as before.

RESULTS—Reciprocal transplants—Resident seedlings were surviving better than nonresidents in both 1977 reciprocal transplant plots by Year 3 (Fig. 2). There were no marked survival differences in the 1978 plots. In all four plots, residents flowered earlier and produced more flower buds over the span of the study than nonresidents (Fig. 2). Net repro-

ductive rates of residents usually exceeded those of nonresidents by 200% or more (Table 1), largely because residents produced more buds. Residents usually outperformed nonresidents by 20% or more in terms of λ , which takes into account earliness of flowering and stable age distribution (Table 1).

Because m_x was defined in terms of flower buds rather than seeds, most λ values were less than 1. This does not mean that populations are declining and does not influence qualitative conclusions about fitness differentials of residents and nonresidents. Also, fitness differentials appear to be larger if estimated by R_0 than by λ . This can be explained by the two measures having different units. Both are rates of change in population size, but the units of R_0 are change per generation, where generation time is longer than 1 yr for *D. nelsonii*, whereas the units of λ are change per reproductive episode, which is 1 yr. These units are related by a power of T , the generation time (Elseth and Baumgardner, 1981, p. 275 ff., p. 455).

The success of residents is not related to their having achieved larger sizes than nonresidents as young seedlings. During the first 3 yr, nonresidents actually produced larger leaves than residents in 8 of 12 cases (Table 2), although this majority is not significant ($P = 0.39$, two-tailed sign test). Either earliness of flowering is unrelated to our index of leaf size, or residents overtook nonresidents by growing more rapidly in subsequent years. Samples of older seedlings are too small to explore the second possibility.

Overall seedling emergence averaged 28%

TABLE 2. *Leaf size index (number of lobes multiplied by leaf radius) for residents (R) and nonresidents (N) in the first 3 yr of the study. US = Upper Slope site, LS = Lower Slope, FM = Flat Meadow. No plant produced more than one leaf until Year 4. Values are means; italics indicate nonresidents larger than residents*

Year since planting	Plot and treatment							
	1977 US		1977 LS		1978 LS		1978 FM	
	R	N	R	N	R	N	R	N
1	6.0	5.7	8.6	9.3	11.3	10.0	10.1	10.6
2	27.3	34.6	25.2	35.3	29.5	24.0	25.2	38.8
3	35.3	43.0	45.8	97.0	76.0	43.1	94.7	122.5

TABLE 3. Soil depth (in cm) and turnover by gophers (in % of soil surface area) at each transplant site. Values are means \pm 1 SE. Sample sizes were 10 depth measurements and 10 lm^2 areal measurements at each site

Soil characteristic	Site		
	US	LS	FM
Depth	17.6 \pm 2.45	54.3 \pm 3.66	37.2 \pm 5.96
Turnover	9.5 \pm 4.86	22.9 \pm 5.03	20.2 \pm 3.90

across all resident and nonresident plantings (SD = 8%, N = 8). Final survival to Year 6 averaged 3% (SD = 2%). Geometric mean survival between years, including the year of seedling emergence but excluding the zero values for nonresidents in the 1977 LS site, averaged 56% (SD = 4%). Excluding the emergence year it averaged 64% (SD = 7%). As a comparison, the value for reproductively mature individuals in a dry open meadow 100 m NW of the US site was 74% over 9 yr of censuses (Waser and Price, unpubl.). There were differences in performance between transplant sites (Fig. 2; Table 1); survival and reproduction generally decreased from the FM plot to the LS plots to the US plot. This corresponds to a general gradient in soil depth and gopher disturbance (Table 3).

Spatial changes in herbaceous vegetation—The Euclidean vegetational distance (defined above) between the 1977 US and LS plots was 1.14, and that between the 1978 LS and FM plots was 0.68. These different values are not due to different numbers of species being involved in the two pairwise comparisons. Rather, the difference confirms the impression based on slope characteristics, soil depth, and gopher disturbance (Table 3) that the LS and FM sites are more similar than the LS and US sites. Species number does indeed influence the magnitude of the vegetational distance measure; the maximum value is the square root of total number. Species numbers in all reciprocal transplant plots were around 25, while that in the transect meadow was 49. This accounts for the smaller vegetational distance values in the former case (see below).

In the transect meadow there was a general divergence in the composition of the herbaceous flora, as measured by an increasing vegetational distance, with increasing physical distance between two points (Fig. 3). The relationship is fit slightly better by a logarithmic than a linear function, suggesting a decelerating increase in vegetational distance. Both functions explain over 20% of the variance in vegetational distance. Testing the significance

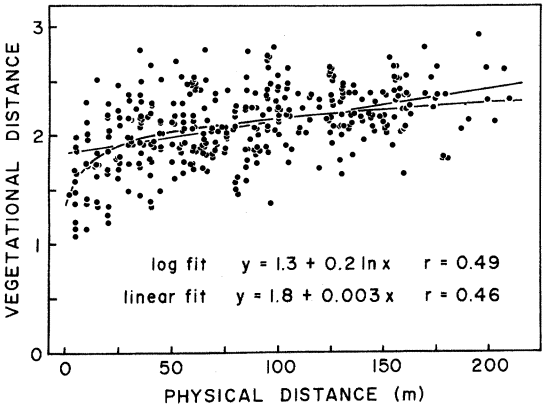


Fig. 3. The relationship between physical distance and Euclidean vegetational distance in a meadow containing a dense *D. nelsonii* population. Each point is a pairwise comparison of two sampling stations along a transect; there were 27 stations in all. Linear and logarithmic regression equations and correlation coefficients are shown.

of the correlation coefficients is not straightforward, because different pairwise comparisons that include a given transect sampling point are not independent. One way to calculate significance is to compare the actual relationship between physical and vegetational distances with a null expectation derived by computer simulation. A simpler alternative, adopted here, is to deflate the degrees of freedom used in a significance test. We used 26 degrees of freedom, one less than the number of sampling points, which yields $P < 0.05$ for correlations using both untransformed and log-transformed physical distances.

DISCUSSION—Reciprocal transplants suggest that fine-scale local adaptation occurs in our *D. nelsonii* populations. In four of four cases, fitness estimates for resident plants exceeded those for nonresidents from 50 m away (P = 0.06, one-tailed sign test). This was largely a consequence of earlier and more prolific flowering of residents, although residents also out-survived nonresidents in 1977 transplants. Fitness differentials were large: selection coefficients against nonresidents, based on λ values (Table 1), ranged from 0.05 to 1.0 with a mean value of 0.34. This is in keeping with the common finding of large selection coefficients in natural plant populations (Antonovics, 1971; Davies and Snaydon, 1976; Bradshaw, 1984; Endler, 1985).

Our study appears to be unusual in several respects. The plant involved is a native and is not subject to grazing by introduced herbivores. Some transplant experiments have used introduced plants (e.g., Fowler and Antonovics, 1981; Antonovics and Primack, 1982)

growing in grazed or otherwise manipulated habitats (e.g., Hickey and McNeilly, 1975; Davies and Snaydon, 1976; Turkington and Harper, 1979; Fowler and Antonovics, 1981). Our plants grew along an elevational gradient in which environmental features (e.g., soil moisture and depth) varied without obvious discontinuities (contrast Hickey and McNeilly, 1975; Davies and Snaydon, 1976; Lovett Doust, 1981). Environments appeared to differ in overall harshness along the gradient, so we compared residents and nonresidents within plots, rather than asking whether each plant cohort performed best at its site of origin (contrast Turkington and Harper, 1979). What may be most unusual about our method, however, is that we transplanted seeds. Of the studies just cited, only that of Schemske (1984) shares this feature. Transplanting seedlings or mature plants assures larger numbers of survivors than transplanting seeds and is the most practical approach if there is seed dormancy. It has the drawback, however, of obscuring potential differences in early survival. Thus, seedling transplantation may allow only a "one-tailed" test for the presence of adaptation. For example, the failure of Fowler and Antonovics (1981) and Antonovics and Primack (1982) to detect local adaptation is not conclusive since an analysis that included early survival might conceivably have uncovered genotype by environment effects.

The evidence for fine-scale vegetational change in meadows is consistent with the evidence for local adaptation, since it indicates the potential for spatial heterogeneity in selective pressures. Vegetation probably is an accurate, if indirect, indicator of abiotic conditions such as soil depth, moisture, and chemical composition, and of changes in biotic factors such as the disturbance of soil by gophers. Vegetation certainly is a direct and potentially important part of the biotic environment of a *D. nelsonii* plant, since other plant species may act as competitors for space, nutrients, water, light, or pollination services (Waser, 1978) and may influence interactions with herbivores and pathogens. With this in mind, it is interesting that the pair of plots more dissimilar in soil (Table 3) and vegetational characteristics (US and LS) is the pair in which residents more clearly outperformed nonresidents (Table 1).

Spatial change in selection pressures will lead to local adaptation only if gene dispersal is restricted. *D. nelsonii* appears to meet this condition. Seeds are passively shed and the vast majority fall $\ll 1$ m from the plant (Waser and Price, 1983). Ants may subsequently move some seeds further (Turnbull, Beattie and Han-

zawa, 1983), but it is unclear that this is common or that such seeds often survive. The percentage of pollen transported as far as 50 m from the source by hummingbird and bumblebee pollinators is extremely small (Waser and Price, 1983). Theoretical treatments (Jain and Bradshaw, 1966; Dickinson and Antonovics, 1973) suggest that such restricted gene flow will be unable to swamp divergence unless selection coefficients are well below 0.2, a value exceeded in our transplant experiments. An alternative analysis involves the "characteristic length" of a steady-state gene frequency cline expected with given gene flow and selection (Slatkin, 1973; May, Endler and McMurtrie, 1975). Dye dispersal experiments (Waser and Price, 1983, unpubl.) yield an estimated root mean squared pollen dispersal distance of 1.3 m for *D. nelsonii*. Assuming a selection coefficient of 0.2, the characteristic length is about 2.9 m, meaning that local adaptation should be swamped only if populations are separated by less than this distance.

Finally, one effect of local adaptation is that it may lead to reduced success in crosses over short distances within a single meadow, a phenomenon we have called "outbreeding depression" (Price and Waser, 1979; Waser and Price, 1983). Outbreeding depression may occur because the offspring of crosses between differently adapted plants are ill-suited to either parental environment. Such an "ecological" explanation for outbreeding depression is explored by Shields (1982; see also Bateson, 1983), who argues that it cannot provide a general explanation for the phenomenon. His arguments are logical, but our reciprocal transplant results imply that ecological factors are a major contributor to the outbreeding depression we have documented over distances of 10–30 m in *D. nelsonii* (Price and Waser, 1979; Waser and Price, 1983).

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