



# A review of the use of genetic markers in orchid systematics with emphasis on allozymes

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## ABSTRACT

Conservation of orchids is sometimes hampered by taxonomic problems, primarily due to the difficulty in delimiting species and/or genus boundaries. In this respect, a summary statistics for Nei's genetic identity (*I*) for conspecific orchid populations and congeneric species pairs could be useful to delimit species boundaries. In this review, we summarized Nei's genetic identity for conspecific populations and congeneric species by performing a literature survey. Average *I* values for conspecific populations ranged from 0.756 to 1.000 with a mean of 0.95 from 84 allozyme-based studies. In contrast, average *I* values for congeneric orchid species considerably varied, ranging from 0.000 to 0.978 with a mean of 0.453 from 190 allozyme-based studies. Most orchid species examined so far exhibit 'diagnostic alleles' at several allozyme loci, which strongly suggests that allozyme markers are still useful for delimiting species boundaries.

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## 1. Introduction

Allozyme genetic markers have traditionally proven useful in solving taxonomic problems at or below the species level (e.g., delimitation of species) in a variety of plant groups and for addressing questions in plant systematics (reviewed in Gottlieb, 1977, 1981, 1982, 1983, 1984; Crawford, 1983, 1985, 1989; Giannasi and Crawford, 1986). In recent times, however, allozymes have fallen out of favor for systematic studies; probably one reason is that it is very difficult to apply them to phylogenetic analyses since allozyme markers do not allow researchers to distinguish between derived and ancestral alleles (Crawford, 1989). Despite this, allozymes can still be very valuable. Allelic frequency data or genotype frequencies are usually employed to calculate either genetic similarity (or identity) or dissimilarity (or distance) among conspecific plant populations and congeneric plant species pairs. Among various genetic identity indices, Nei's (1972, 1978) genetic identity (*I*) and distance (*D*) have been extensively used in plant systematics (reviewed in Van der Bank et al., 2001). Gottlieb (1977, 1981), Crawford (1983, 1989), and Giannasi and Crawford (1986) summarized allozyme-based *I* values for conspecific plant populations and congeneric plant species. For conspecific populations, Gottlieb (1981) reported means of *I* = 0.956 and 0.975 for outcrossers and selfing species, respectively, and similarly, Crawford (1983) reported high *I* values nearly always larger than 0.900. For congeneric species pairs, considerably lower values have been reported compared to conspecific populations: mean *I* = 0.670 (Gottlieb, 1981); mean *I* = 0.789 (Crawford, 1983). More recently, Van der Bank et al. (2001) comprehensively tabulated Nei's *I* values for a large set of conspecific plant populations [average *I* = 0.950 ± 0.059 (mean ± standard deviation, SD), ranging from 0.576 to 1.000, *N* = 1572] and congeneric plant species (average *I* = 0.778 ± 0.180, ranging from 0.167 to 1.000, *N* = 863). These reports support the view that, as expected, conspecific populations are substantially less genetically differentiated than populations of different species.

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The Orchidaceae is one of the largest families of the flowering plants (the number of species has been estimated between c. 19,500 (Peakall, 2007) and c. 25,000 (Chase et al., 2003)). The family provides challenging issues for evolutionary studies, continues to furnish ongoing taxonomic novelties, and many of its members are the focus of conservation efforts (Pillon and Chase, 2007; Hopper, 2009). Nonetheless, application of conservation strategies to this group is sometimes hampered by taxonomic problems. Determining the most appropriate rank for each taxon, which is always a difficult task, is especially controversial within the Orchidaceae; associated problems such as the excessive description of new species (i.e., taxonomic inflation) are particularly serious in Europe and Australia (Pillon and Chase, 2007; reviewed in Hopper, 2009). This situation is primarily due to the application of a too narrow or a too broad species concept and to the paucity of genetic and phylogenetic information, which poses great difficulty in delimiting species or genus boundaries (Pillon and Chase, 2007; Hopper, 2009).

A summary statistics for Nei's genetic identity for conspecific populations and congeneric species of orchids could be useful to solve uncertainty associated with rank and boundaries of orchid taxa. To date, however, no review is available on orchid literature, which triggered our own review of Nei's genetic identity among conspecific populations and between congeneric species of orchids. The present study represents, thus, the first attempt at a comprehensive literature review and meta-analysis of this genetic parameter.

## 2. Methods

### 2.1. Nei's genetic identity and distance

A number of researchers have proposed measures to quantify the qualitative concept of similarity between populations using allele or genotypic frequency data (Sokal and Sneath, 1963; Cavalli-Sforza and Edwards, 1967; Workman and Niswander, 1970; Hedrick, 1971; Nei, 1972; Rogers, 1972). Among them, Nei's (1972) formula has found the most widespread use based on literature (Berg and Hamrick, 1997; Van der Bank et al., 2001). At a given locus, let  $j_{xx}$  be the probability that two alleles chosen at random from population  $X$  are identical, so that  $j_{xx} = \sum p_{ix}^2$ ;  $j_{yy}$  is the analogous probability for population  $Y$ , and  $j_{xy} = \sum p_{ix}p_{iy}$ . When  $j$ -values are computed for all loci, they are averaged and written as  $J_x, J_y, J_{xy}$ .

The normalized  $I$  for this locus is

$$I = \frac{J_{xy}}{\sqrt{J_{xx}J_{yy}}}, \quad 0 \leq I \leq 1$$

Nei's  $D$  is the negative of the natural logarithm of the genetic identity:

$$D = -\ln(I), \quad 0 \leq D < 8$$

In simplicity, the relationship between  $I$  and  $D$  is  $I \approx 2.7828^{(-D)}$ . Two populations with equal allele frequencies, thus, have an  $I$  of 1.0 and  $D$  of 0, even if they have different genotype proportions or different alleles at given loci. Since Nei's  $I$  uses both monomorphic and polymorphic loci, 'overall genetic similarity' is emphasized rather than dissimilarity at variable loci. This is an important point, as the percentage of polymorphic loci has a big influence on genetic identity values. For a given amount of genetic differentiation among populations at polymorphic loci, species with a higher percentage of monomorphic loci will tend to have higher genetic identity values since  $I = 1.0$  for these loci. Nei (1978) further developed an 'unbiased' formula to correct the systematic bias caused by a small sample size when the ordinary method of estimating  $I$  was used (Nei, 1972). Thus, some authors (e.g., Sun, 1996; Trapnell et al., 2004) used Nei (1972) formula due to relatively even and large sample size (c. 50 individuals per population) across populations of the plants they studied, whereas others (e.g., Azevedo et al., 2007; Chung and Chung, 2007) estimated Nei's (1978)  $I$  primarily due to small and uneven sample sizes.

### 2.2. Literature survey

We searched the published orchid literature that used molecular markers [e.g., allozymes, ISSR (inter-simple sequence repeat), AFLP (amplified fragment length polymorphism), RAPD (randomly amplified polymorphic DNA), microsatellite, and SRAP (sequence related amplified polymorphism)] to assess Nei's  $I$  values published between January 1987 and August 2011. To complement the references contained in Forrest et al. (2004), we further searched in the ISI Web of Knowledge for entries of published papers including the terms 'orchids', 'Nei genetic identity' and 'Nei genetic distances', and the variety of molecular markers above-listed. We screened 46 relevant papers that contain information on  $I$  and/or  $D$  values for conspecific populations [84 allozyme-based entries and 8 DNA-based entries; Tables 1 and 2] and for congeneric species pairs (all the 190 entries from allozyme markers, but no DNA-based studies were available; Table 3). The number of entries was two- to four-times greater than that of published papers (46) because in many papers more than one species is studied (Tables 1 and 3).

### 2.3. Data analysis

We assume that different allozymes encoded by a locus are neutral or nearly neutral. We converted  $D$  to  $I$  values by using the equation,  $I \approx 2.7828^{(-D)}$  for those studies in which the latter were not supplied. When allele frequencies were provided instead of  $I$  or  $D$  values, we used the program BIOSYS-1 (Swofford and Selander, 1981) to estimate average  $I$  values across

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