POPULATION VARIATION IN THE *ONCOCYCLUS* IRISES ALONG A GEOGRAPHICAL GRADIENT IN ISRAEL

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ABSTRACT – The section *Oncocyclus* of the genus *Iris* L. comprises eight species in Israel, which are among the most beautiful and important plants for conservation. Three of the dark-coloured species (*I. haney*, *I. atrofusca* and *I. petrana*) are distributed along the North-South climatological gradient in Israel. Although many taxonomists have dealt with this section in the last century, no quantitative research has been done. Many transitional forms between species or populations are known from the field. The purpose of the current reaearch was to test quantitatively, by using inter and intrapopulation variation, the relationship among those species, and to examine whether morphological traits changed along the ecogeographical North-South gradient. Morphological traits were measured in eleven populations along this gradient. Intrapopulation variation is significantly higher than variation between each nearest population for most characters. Morphological distance was calculated using the Pearson distance coefficient, and is significantly correlated with geographical distance. Regression of all traits against latitude revealed that diagnostic characters, especially flower size, stem height and leaf characters, change along the aridity gradient.

KEY WORDS - Irises, *Oncocyclus*, populations, Israel, morphological distance, gradient.

INTRODUCTION

The section *Oncocyclus* of the genus *Iris* comprises eight species in Israel (Feinbrun-Dothan, 1986). More species and micro-species of the section have been determined in the past 120 years (e.g. Post, 1932 see Davis, 1946), but most of them are now considered subspecies or synonyms (Feinbrun-Dothan, 1986; Rix, 1997). Three of the species in Israel have light coloured standards and five have purple to black standards. The light species grow in the north, Mediterranean regions of Israel, while the dark ones grow in the south or in semi-arid environments (Avishai, 1977; Shmida and Ivri, 1996). Avishai and Zohary (1980) found that speciation in the *Oncocyclus* section did not involve the development of post-zygotic reproductive isolation barriers. All species in the section interbreed freely, and have the same number of chromosomes (2n=20) (Avishai and Zohary, 1977).

Three of the black species, *Iris haynei* Baker, *I. atrofusca* Baker (including *I. «loessicola»* Kushnir) and *I. petrana* Dinsmore (only the Negev populations – *I. «hieruchamensis»* Avishai - have been studied) are distributed in the semi desert strip in the eastern part of Israel. The populations of these three species, hence called "atrofusca group", distribute from the Golan Height and Mt. Gilboa in the north, through the Shomron and Judean desert, to Arad and Yeruham in the south. The atrofusca group belong to the *Haynei* aggregate in the section *Oncocyclus* (Avishai, 1977). In the field a very wide range of colours can be seen: in the same population, flowers are pink to black and blue to deep purple. Flower colours are often used as diagnostic characters (Post, 1932; Zohary, 1976; Feinbrun-Dothan, 1986), but due to the high variability and overlapping we could not use them.

The habitat of the atrofusca group is in open areas of semi arid and transitional zones (Fragman and Shmida, 1995). The vegetation is marginal batha, composed of perennial herbs and dwarf shrubs. The dominant species composition in each location changed along the transect. One dominant species that occurred in all locations is *Asphodelus ramosus*, which indicates a high grazing pressure (Waisel, Pollak and Cohen, 1982).

The *atrofusca* group replace each other along a north – south gradient. Although diagnostic characters were given (Feinbrun-Dothan, 1986), transitional populations and great variation were observed in the field. The aim of this paper is to test those three *Oncocyclus* species, using variation in morphological traits inside and between populations, according to the phylogenetic species concept, determining species as «the smallest diagnosable unit» (Luckow, 1995).

Materials and Methods

Field measurements - Populations list is given in Table 1. The distances between the populations studied along the gradient were approximately 30 Km (Fig. 1). Thirty individuals (if present) were measured in each location. Only one individual was measured in each clone, under the assumption that the members are genetically similar

Table 1 - Populations measured (Longitude and Latitude are according to the Israeli system)

Location	Longitude	Latitude	Altitude (m a. s. l.)
South Golan	213	238	250
Gilboa	188	213	450
Um Zuka	199	189	70
Kubet Najme	183	149	580
Rimonim	181	146	550
Tekoa	172	117	620
Tel Arad	161	075	535
Mar'it Wadi	154	074	450
Goral Hills	130	080	320
Rotem Plain	163	051	390
Yeruham	147	048	560

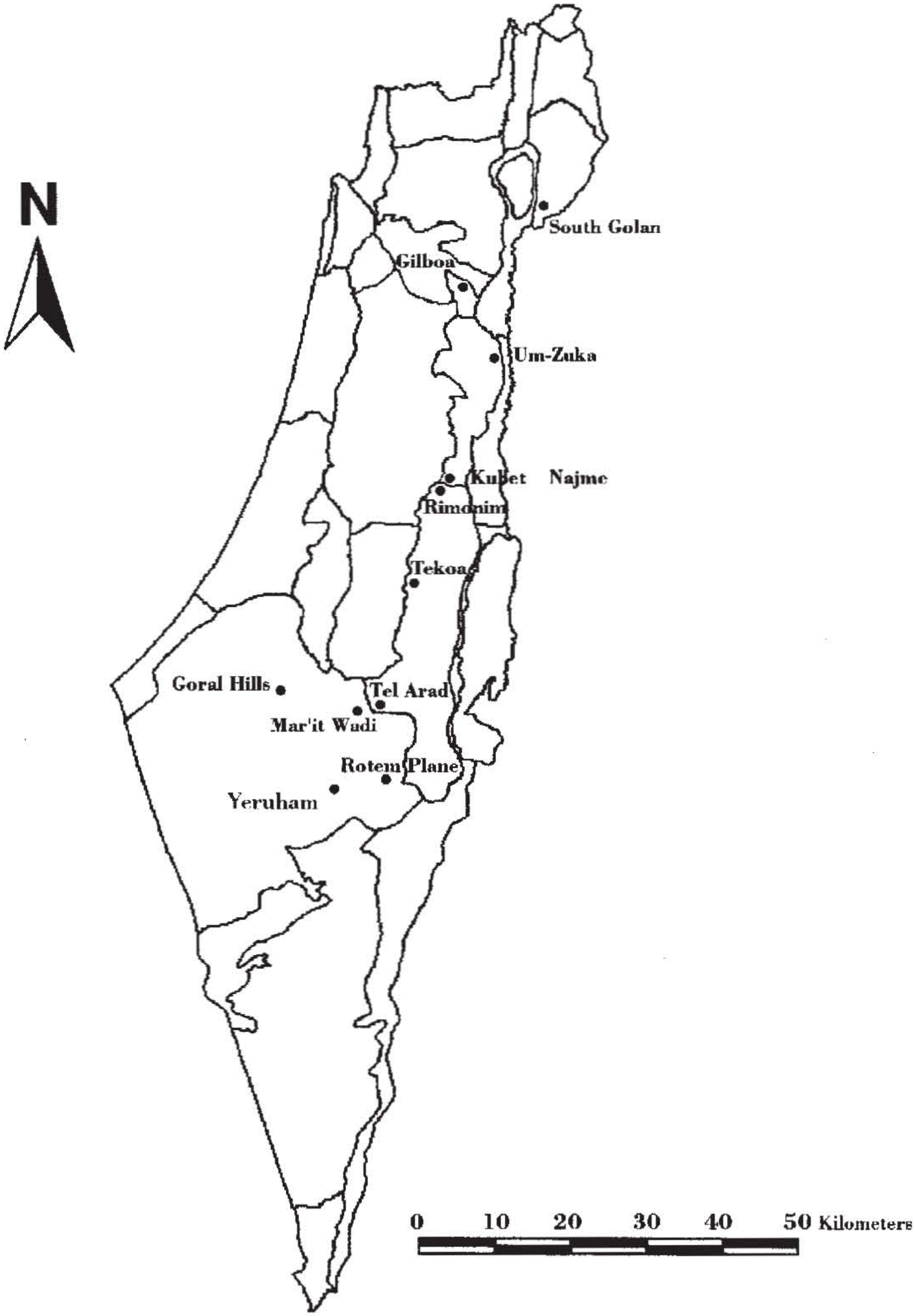

Figure 1 - Iris populations along the North-South gradient in Israel

(Tucic *et al.*, 1990). The individuals measured were chosen randomly in each clone, along a line transect that began at a random starting point.

The following traits were measured (all measured in cm):

1. Flower height – fall bottom to standard top.
2. Flower diameter.
3. Fall width – in the broadest place.
4. Standard width – in the broadest place.
5. Black-patch length.
6. Black-patch width.
7. Leaf width – measured in the second branching leaf from stem.
8. Leaf arching – of the same leaf. Scores: 1- straight, 2- medium, 3- arched.
9. Leaf height above the ground – the highest point of the same leaf.
10. Stem height – from the ground to the fall bottom.

CALCULATED RATIOS

1. Flower diameter / flower height (Feinbrun-Dothan, 1986).
2. Flower surface: diameter x height. determine advertisement area. Flower surface affects water loss and is expected to be smaller in arid environments (Shmida *et al.*, 1986).
3. Black patch area – length x width: an important component in pollinator attraction (Avishai, 1977).
4. Black patch area / fall width.
5. Flower height / stem height (Feinbrun-Dothan, 1986).
6. Stem gap – (stem height – leaf height)/ stem height (Feinbrun-Dothan, 1986).

STATISTICAL ANALYSIS - Analyses of variation and Scheffe's test for multiple comparisons were used to evaluate separation of populations with respect to the measured or calculated variables. Significant differences were taken to be those with $p<0.05$, and highly significant differences were those with $p<0.01$. Variables were plotted vs. latitude, and the adjusted R^2 was calculated. The general morphological distance between populations was calculated by the Pearson distance coefficient (Sneath and Sokal, 1973).

$$C.R.L. = \sqrt{\frac{1}{n}\sum_{i=1}^{n}\frac{(\bar{x}_{iJ}-\bar{x}_{iK})^2}{\frac{s_{iJ}^2}{t_J}+\frac{s_{iK}^2}{t_K}} - \frac{2}{n}}$$

We selected this coefficient because it considers population variation (s^2) and size (t). n is the number of characters considered, J and K are the populations compared. Geographical distance between each pair of populations was calculated as the latitudes interval between populations J and K. The correlation between these two distance matrices was plotted and tested statistically.

RESULTS

Average and standard deviation of characters for each population is given in Table 2. Table 3 presents the number of traits in which significant differences were

TABLE 2 - FLOWER AND PLANT CHARACTERS IN THE POPULATIONS, WITH AVERAGE AND STANDARD DEVIATION (BRACKETS)

STEM HEIGHT	ARCH	LEAF WIDTH	STEM GAP	FLOWER HEIGHT/STEM HEIGHT	STANDARD WIDTH WIDTH	PATCH AREA/FALL AREA	BLACK PATCH	FALL WIDTH	FLOWER SURFACE	FLOWER DIAMETER /FLOWER HEIGHT	N=	LOCATION (FROM NORTH TO SOUTH)
42.805 (7.575)	1.11 (0.32)	1.6097 (0.243)	0.0934 (0.133)	0.2261 (0.048)	6.8708 (0.732)	0.6879 (0.159)	2.9915 (0.976)	4.3458 (0.561)	75.63 (15.71)	0.8597 (0.0905)	36	SOUTH GOLAN
37.722 (9.266)	1.31 (0.47)	1.4778 (0.221)	0.1355 (0.126)	0.3202 (0.093)	7.9625 (1.133)	0.568 (0.158)	3.0395 (0.976)	5.3708 (0.812)	103.66 (20.63)	0.7997 (0.0724)	36	GILBOA
39.685 (8.592)	1.37 (0.49)	1.2519 (0.155)	0.2077 (0.091)	0.2627 (0.053)	7.4037 (0.729)	0.6794 (0.2)	3.2606 (1.01)	4.8037 (0.586)	84.73 (12.31)	0.8439 (0.0720)	27	UM ZUKA
30.413 (8.233)	1.3 (0.47)	1.163 (0.217)	0.1696 (0.196)	0.3487 (0.104)	7.0935 (0.823)	0.3832 (0.099)	1.8443 (0.554)	4.7913 (0.742)	88.34 (19.33)	0.8922 (0.0871)	23	KUBET NAJME
25.016 (7.487)	1.2 (0.41)	1.0817 (0.188)	0.0787 (0.156)	0.3791 (0.108)	6.365 (0.685)	0.4186 (0.136)	1.7183 (0.604)	4.0967 (0.599)	66.48 (12.77)	0.856 (0.0788)	30	RIMONIM
34.633 (9.915)	1.37 (0.49)	1.53 (0.394)		0.2614 (0.084)	5.95 (0.537)	0.5485 (0.188)	2.2057 (0.947)	3.9733 (0.495)	69.13 (9.30)	1.0012 (0.0885)	30	TEKOA
22.383 (3.912)	1.27 (0.45)	0.7867 (0.127)	0.0246 (0.134)	0.3504 (0.07)	5.51 (0.668)	0.4259 (0.079)	1.6398 (0.364)	3.8483 (0.457)	54.83 (9.51)	0.9454 (0.1079)	30	GORAL HILLS
19.95 (3.693)	1.87 (0.51)	0.9083 (0.127)	0.2915 (0.144)	0.437 (0.072)	5.96 (0.811)	0.5398 (0.128)	2.096 (0.627)	3.8667 (0.508)	64.75 (11.49)	0.8947 (0.0847)	30	TEL ARAD
21.6 (6.571)	1.63 (0.56)	0.9983 (0.195)	0.1639 (0.172)	0.3851 (0.125)	5.0467 (0.738)	0.469 (0.126)	1.6774 (0.519)	3.5633 (0.52)	55.62 (11.87)	0.9515 (0.0755)	30	MAR'IT WADI
15.290 (4.638)	2.0 (0.73)	0.5452 (0.126)	0.3356 (0.245)	0.3957 (0.106)	3.8387 (0.663)	0.3765 (0.119)	1.1189 (0.499)	2.8952 (0.491)	33.80 (9.81)	1.0442 (0.1082)	31	ROTEM PLAIN
24.566 (4.227)	2.63 (0.56)	0.6933 (0.122)	0.5892 (0.123)	0.2813 (0.061)	4.8183 (0.776)	0.3574 (0.279)	1.1964 (0.846)	3.3933 (0.566)	44.33 (10.40)	0.976 (0.0773)	30	YERUHAM

TABLE 3 - NUMBER OF SIGNIFICANT DIFFERENCES BETWEEN ALL POPULATIONS. # = P<0.05, ● = P<0.01. EACH SIGN INDICATES SIGNIFICANT DIFFERENCE OF ONE CHARACTER

	SOUTH GOLAN	GILBOA	UM ZUKA	KUBET NAJME	RIMONIM	TEKOA	GORAL HILLS	TEL ARAD	MAR'IT WADI	ROTEM PLAIN
GILBOA	●●●#	-								
UM ZUKA	●	●	-							
KUBET NAJME	●●●●	●●	●●#	-						
RIMONIM	●●●●	●●●●●●	●●●●●●##	●	-					
TEKOA	●##	●●●●#	●●●●●	●●●●#	●●●●	-				
GORAL HILLS	●●●●●●●	●●●●●●●	●●●●●●●##	●●●●	●	●●	-			
TEL ARAD	●●●●●●	●●●●●●●##	●●●●●●●	●●●●#	●	●●●#	●#	-		
MAR'IT WADI	●●●●●●●	●●●●●●●	●●●●●●●##	●●●#	●	●●●#		#	-	
ROTEM PLAIN	●●●●●●●●●●●	●●●●●●●●#	●●●●●●●●●●#	●●●●●●●	●●●●●●●●	●●●●●●●	●●●●●##	●●●●●●	●●●##	-
YERUHAM	●●●●●●●●●●	●●●●●●●●●●●	●●●●●●●●●●	●●●●●●	●●●●●●##	●●●●●●#	●●	●●●●●##	●●●#	●●●●

found. Pairs of populations along the table diagonal represents neighboring the location in the North-South gradient. The table indicates that more variables are significantly different for distant populations than between neighbouring populations.

Fig. 2 presents population averages of the separate variables plotted against latitude. Fig. 3 shows that Pearson distance coefficient between every two populations correlates to the calculated geographical distance on the gradient.

DISCUSSION

Generally, flower, stem and leaves size traits decrease toward the South. This could be an adaptation to aridity by reduction of water loss through reducing the area exposed to the direct sun (Fragman and Shmida, 1995). The Tekoa population of Tekoa is an exception, with wider leaves, probably because the plants grow in cracks in a steep cliff, where conditions are more mesic (Danin, 1972). These conditions mainly influence the leaves (Davis and Jury, 1990).

Geophyte leaves in Israel are more curved and arched towards the South (Fragman and Shmida, 1995). In the populations observed, the change depends also on the microhabitat of the individual plant: In shade, leaves tend to be more straight, and in exposed habitats more arched. This increases the variation in leaf arching within populations.

The ratio «flower diameter / flower height» is considered a diagnostic sign that separates *I. haynei* and *I. atrofusca*: flower diameter equals flower height in *I. atrofusca*,

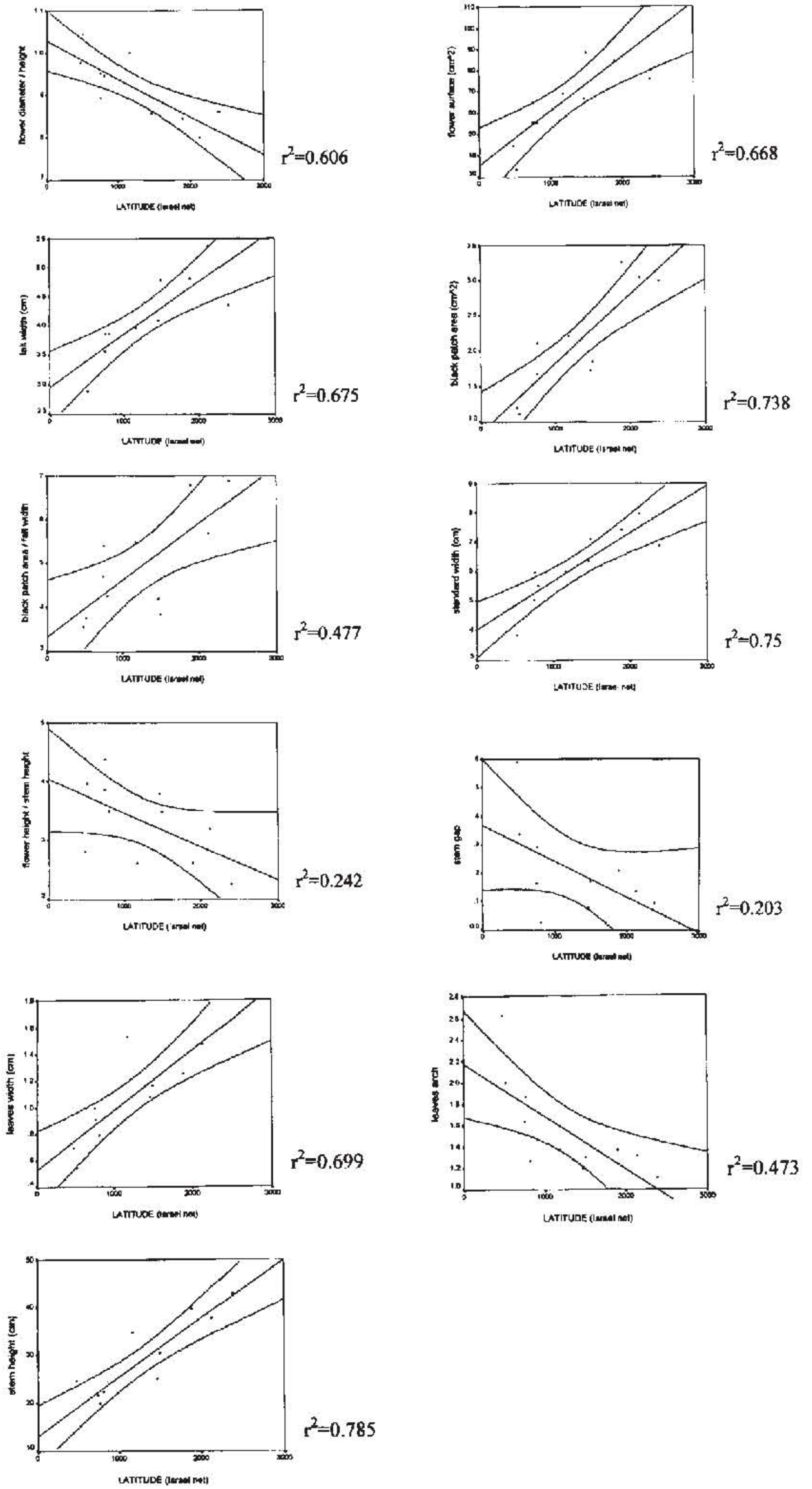

Figure 2 - Morphological characters plotted against latitude in *Iris* populations along the North-South gradient in Israel.

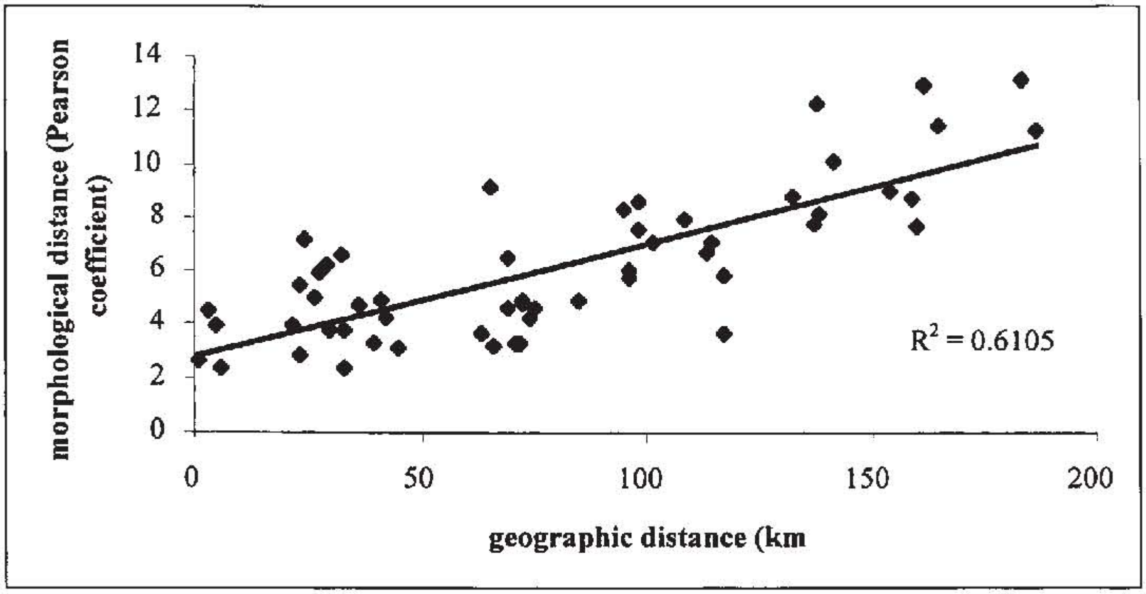

Figure 3 - Pearson distances coefficients of morphology variables versus geographical distances on the north-south gradient.

and the flower height is bigger than flower diameter in *I. haynei* (Zohary, 1976; Feinbrun-Dothan, 1986). Our results show that this ratio changes continuously along the gradient. Northern populations show a low ratio, and in southern populations the population average is close to one. We argue that this ratio is not critical in separating the species. The changes of this ratio along the gradient suggest that flower height may be an important character in adaptation to arid zones. Flower diameter does not change drastically towards the south, and the ratio changes because flower height decreases toward the south. Flower height is determined mainly by the standards. Standard reduction towards the south may result from adaptation to water loss (Fragman and Shmida, 1995), and from the sparse pattern of the vegetation in arid environments, which reduces the necessity for large advertisement, provided by the standards (Shmida and Ivri, 1996).

The «flower height / stem height» ratio and stem gap show very low correlation with latitude and no apparent pattern within the species, suggesting that variables connected with stem / flower ratios and leaves height are related to other conditions, and do not have a role in *Oncocyclus* taxonomy.

According to the classical Biological Species concept (Dobzhansky, 1937; Mayr, 1942), all *Oncocyclus* species belong to one species because of their ability to hybridize (Avishai, 1977; Avishai and Zohari, 1980). Here we argue that the three species discussed above belong also to the same species according to the Phylogenetic Species concept (Nixon and Wheeler, 1990; Luckow, 1995) because of their continuous morphological changes. There are no diagnosable morphological units among populations studied, and intra population variation is higher than the variation between each nearest population.

The correlation of the gradient of characters with the environmental gradient suggests that phenotypic selection created the differences between populations. At present the populations are isolated, but in the past the distribution could have been continuous (Avishai, 1977), and this enabled a great deal of gene flow. With isolation, the phenotype of each population became adapted to local conditions and consequently the morphology changed. DNA sequencing data (e.g.Young, 1998) will determine the genetic distances and genealogical relationships between them, and should combine evolutionary relationships among *Oncocyclus* species in Israel.

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