diejenigen Provenienzversuche, in denen die gleichen oder benachbarte Provenienzen verwendet wurden. KRAMER (1979, 1980) erhielt in seinen, in Niedersachsen angelegten Provenienzversuchen ähnliche Ergebnisse, wie sie hier besprochen wurden. Durch gutes Wachstum zeichneten sich die Herkünfte Stará Voda und Bardejov aus. Die Provenienz Bardejov ist mit der hier verwendeten Provenienz Zborov vergleichbar. Diesen Trend zeigen auch die englischen Versuche, in denen neben kalabrischen Provenienzen diejenigen aus dem östlichen Teil des Slowakischen Erzgebirges (Stará Voda) an der Spitze stehen (LINES, 1979). Zu ähnlichen Schlußfolgerungen kommen auch MAYER et al. (1982) aufgrund der Ergebnisse des österreichischen Versuchs.

Alle erwähnten Versuche haben den Nachteil, daß sie nur vergleichsweise wenige Provenienzen enthalten. Dies erlaubt es nicht, von einem West-Ost-Klin hinsichtlich des Höhenwachstums zu sprechen. Es scheint aber wahrscheinlich, daß die Provenienzen mit dem besten Wachstum aus dem östlichen bzw. nordöstlichen Teil des Verbreitungsgebietes (Ostpolen, Ostslowakei) stammen. Andererseits sind auch die trockenresistenten Provenienzen aus Kalabrien und die Herkunft aus dem Lăpuş-Gebirge besonders hervorzuheben.

In der Slowakei sind in der Vergangenheit die ersten Provenienzversuche erst in den 60er Jahren angelegt worden (LAFFÉRS 1978, KORPEL and PAULE 1981). In diesen Versuchen konnte das Wachstum und die Phänologie von osteuropäischen Provenienzen, insbesondere solchen aus dem Karpatengebiet, nicht studiert werden. Die neueren Versuche sollten eine bessere Grundlage für das Studium des geographischen Variationsmusters der Tanne geben. Die hohe Vitalität der Tanne in ihren natürlichen Beständen in der nordöstlichen Slowakei (Bardejov - Zborov, Ulič) und im östlichen Teil des slowakischen Erzgebirges (Košice, Stará Voda und Murán) ist nicht nur in den hier beschriebenen, sondern auch in den von LAFFÉRS begründeten Versuchen zu beobachten. Zu den besten Provenienzen gehören ferner solche aus der Kleinen Fatra und dem östlichen Teil der Niederen Tatra (Poprad und Beňuš).

Abschließend ist anzumerken, daß außer der hier beschriebenen, Variation diese auch in anderen Untersuchungen festgestellt worden ist, wie z. B. in der Phänologie (KOCIOVA 1976) oder dem Chlorophyllgehalt und dessen

Reaktion auf veränderte ökologische Bedingungen (PAULE 1976). Im allgemeinen dürften die Übergänge zwischen benachbarten Provenienzen graduell sein (MAYER et al. 1982).

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Sexual Breeding System and Morphological Variation in Some Stands of Fraxinus syriaca Boiss.*)

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Summary

Fraxinus syriaca BOISS. is diploid (2n = 46), andromonoecious and protogynous. Size and germination of pollen grains from various provenances, from hermaphrodite and staminate flowers, and from a mutant with yellow anthers, are similar. Pollen germination was highest on a medium containing 15% sucrose. Morphological variation was analyzed by factor and cluster analysis to show patterns of relationship among 12 measured traits and the various groupings recognized within a given population.

Key words: Fraxinus syriaca, breeding system, chromosome number, pollen, variation.

Zusammenfassung

Fraxinus syriaca BOISS. ist diploid mit 2n = 46, andromonoezisch, wobei Protogynie besteht. Die Größe und der

Keimungsverlauf von Pollenkörnern verschiedener Herkünfte, bei zwittrigen und mit Staubgefäßen versehenen Blüten, wie von einer Mutante mit gelben Antheren sind gleich. Die Pollenkeimung war am höchsten, wenn das Medium 15% Rohrzucker enthielt. Die morphologische Variation wurde durch Faktoren- und Cluster-Analyse ermittelt, um die Muster der Beziehungen zwischen 12 bonitierten Merkmalen und den verschiedenen Gruppierungen, die in einer gegebenen Population erkannt werden konnten, aufzuzeigen.

Introduction

Fraxinus syriaca Boiss. is a handsome, medium-sized tree, much planted locally; its distribution is Eastern Mediterranean - Western Irano-Turanian and extends from Asia Minor and the Near East to Turkmenistan and Afghanistan (Boissier, 1879; Lingelsheim, 1920). Almost no data are available on its breeding system, variation, ecophysiology, etc.

Since *F. excelsior* L. is known to have an extremely complicated breeding system and comprises both dioecious trees and trees bearing unisexual and hermaphrodite flowers in various arrangements of polygamy (Darwin, 1877; Larsen, 1945; Rohmeder et al., 1959), studies were made of the distribution of sexes in *F. syriaca*. In addition, variation of selected morphological characters was studied to quantify descriptions in standard floras (e.g. Boissier, 1879; Post, 1933; Vasil'ev, 1967; Feinbrun-Dothan, 1978; Yaltirik, 1978; see also Lingelsheim, 1920) which often lack accuracy with regard to numerical features.

Materials and Methods

Most of the data were collected from a ca. 30-year-old plantation of 109 trees (from seed presumedly collected from natural stands in northern Israel) at Ilanot (32° 18' N, 34° 54' E). Additional data were obtained from natural occurrences of *F. syriaca* at Banias (33° 15' N, 35° 42' E), Tel Dan (33° 15' N, 35° 39' E), and in the Hula Valley (environs of Gonen, 33° 07' N, 35° 39' E).

Chromosome counts, using squash preparations, were made according to Feulgen at meiosis on anthers, and at mitosis on root tips after pretreatment with alpha-bromonaphtalene for 4 h, hydrolysis with 1 N HCl, and staining with Schiff's reagent.

Pollen grains were examined after staining with acetocarmine or potassium iodide.

Morphological variation of 21 trees selected at random was investigated at Ilanot. From each tree six fully grown leaves were sampled from the middle of the crown, and from each leaf one leaflet of the second pair from the top was taken. Length and depth of the largest serration in the upper third of the leaflet were measured under a magnification of × 30. From the same trees six fruits (samaras), each from the middle of one inflorenscence (raceme), were also obtained.

Colours were measured according to the Munsell system (Munsell Color Co., 1952); for statistical analyses the index of fading (Nickerson, 1936) was calculated as the colour deviation from the arbitrarily set standard 2.5 G 8/8.

Factor analysis of 12 measured traits was carried out by using principal components analysis followed by varimax rotation on the first eigenvectors explaining at least 80% of the variance (Morrison, 1967). Cluster analysis was carried out, using Euclidean distances, on standardized variables; the clusters were constructed by using the maximum distance over all pairs between two clusters (SAS, 1979).

Results

Chromosome Number

F. syriaca is diploid; chromosome numbers are n = 23 at meiosis and 2n = 46 at mitosis.

No abnormalities at meiosis were observed in tree No. 47 with yellow anthers (see below), and no difference in karyotype was recorded between this tree and trees with normal (red) anthers.

Breeding System

F. syriaca is andromonoecious, *i.e.*, the raceme consists of both hermaphrodite and staminate flowers. Sixty racemes from the middle of the crown of 12 trees (five racemes per tree) comprised 958 flowers, 850 (88.8%) of which were hermaphrodite and 108 (11.2%) were male. There are indications of protogyny in hermaphrodite flowers. The staminate flowers are borne at the base of the racemes and their anthesis is slightly delayed in comparison with that of hermaphrodite flowers. The anthers are very dusky red - 7.5 R 2/2—4 in the Munsell system (Munsell Color Co., 1952).

Tree No. 34 has racemes consisting mostly of staminate flowers and few hermaphrodite flowers. The colour of the anthers differs slightly from that of normal anthers and is dusky red, 7.5 R 3/4.

Tree No. 47 is a mutant with lemon-yellow anthers - 5.0 Y 8/6 in the Munsell system (Munsell Color Co., 1952).

Flowering occurs before leaf flush and extends from December to February. Dates on flowering at Ilanot are shown in *Table 1*. In both years of the study, the same 30 trees (27.8%) flowered early, *i.e.*, during the first 1—7 days of the flowering period, whereas the same 51 trees (47.2%) were late to flower, *i.e.*, from the 8th to the 18th day; the start of flowering of the remaining 27 trees (25.0%) was early in one year and late in the other. Flowering at Banias, Tel Dan and in the Hula Valley occurred 10—14 days earlier than at Ilanot.

The pollen of *F. syriaca* is yellow, small, usually less than 25 μm in diameter, almost spherical, tricolpate; the exine is reticulate *(Fig. 1)*. Pollen dimensions of the mutant (tree No. 47) are fairly similar to those of trees with normal anthers *(Table 2)*. Differences in size between pollen from Ilanot and from natural populations are small *(Table 3)*, and pollen dimensions are not related to the type of flower (Table 4). Staining showed that percentages of sound pollen grains from hermaphrodite and staminate flowers are practically the same, *viz.* 97.8% in the former and 97.5% in the latter (numbers of grains examined were 650 and 546, respectively).

As shown in *Table 5*, germination of pollen from Ilanot was highest on a medium containing 15% sucrose. There were but minor differences in germination between pollen of trees No. 34 and 47 and that of normal trees.

Morphological Variation

Table 6 shows the mean values and range of 12 morphological traits from randomly selected planted trees at Ilanot. Statistically significant differences were obtained between several of the characters, *e.g.* leaf length and number; length and width of leaflets; number and length, and length and width, of leaflets; length and width of samara and length of seed, etc.

The 12 measured traits *(Table 6)* were analyzed by factor

Table 1. — Dates of beginning and end of flowering at Ilanot.

Year	Beginning of flowering		End of flowering
	1st tree	last tree	
1981/82	20 Dec.	3 Jan.	18 Jan.
1982/83	13 Dec.	1-2 Jan.	12 Feb.

Table 2. — Pollen dimensions of a planted population at Ilanot.

	No. of trees	No. of grains	Largest diameter μm	Smallest diameter μm
Tree No. 47	1	200	23.4±2.0	22.2±1.2
Trees with red anthers	16	3,200	25.6±2.1	24.6±2.1

Table 3. — Provenance means of pollen size.

Provenance	No. of grains	Largest diameter μm	Range μm
Banias	360	21.8±3.0	17.0-24.8
Tel Dan	500	21.7±2.6	19.3-25.6
Ilanot	800	23.4±2.0	18.8-27.9

Table 4. — Provenance means of pollen size from hermaphrodite and staminate flowers.

Provenance	No. of trees	Type of flower	No. of grains	Largest diameter μm
Banias	3	hermaphrodite	186	20.5±3.7
		staminate	176	22.1±3.1
Tel Dan	5	hermaphrodite	300	23.5±2.1
		staminate	300	22.6±2.6
Ilanot	2	hermaphrodite	120	23.3±2.1
		staminate	120	23.1±6.1
Overall means	10	hermaphrodite	606	22.4±1.7
		staminate	596	22.6±0.5

Table 5. — Germination of fresh pollen (% of n) on nutrient medium of sucrose + 2% agar.

Sucrose content %	Tree No. 34		Tree No. 47		Normal trees	
	n	%	n	%	n	%
10	250	34.0	297	37.7	275	38.2
15	215	64.6	197	55.3	240	66.2
20	300	56.7	300	42.0	218	44.5
30	176	14.7	280	8.6	300	16.7

Table 6. — Mean values, standard deviation and range of 12 measured traits of a planted population at Ilanot.

Character	Mean	S.D.	Range
Index of fading	44.85	2.61	40.00-49.00
Length of leaf (cm)	17.41	3.55	10.50-27.00
Length of petiole (cm)	4.04	0.99	2.00- 7.30
Number of leaflets	6.74	2.09	3-13
Length of leaflet (cm)	5.63	1.11	2.80- 8.40
Width of leaflet (cm)	1.93	0.39	1.20- 2.90
Length of serration (cm)	0.57	0.09	0.25- 1.00
Depth of serration (cm)	0.06	0.02	0.01- 0.20
Length of fruit (cm)	3.23	0.75	2.02- 5.00
Width of fruit (cm)	0.69	0.12	0.38- 1.20
Length of seed (cm)	1.55	0.27	0.97- 2.40
Width of seed (cm)	0.35	0.06	0.20- 0.60

analysis (MORRISON, 1967) with 12 factors; five factors were retained which account for 86% of the total variation. The loadings of these factors obtained after varimax rotation (Table 7) show that the first factor is typified by size of samara and seed; factors 2 and 3 are typified by several leaf characters, factor 4 - by the index of fading and width of seed, and factor 5 - by depth of serration.

Grouping of the data into five clusters (SAS, 1979) shows that the population is made up of several distinct phenotypes, with 15 trees (71%) belonging to two clusters with short leaves and relatively few and short leaflets, short and narrow samaras, and short seeds. Trees with longer leaves, larger number of leaflets, longer and broader fruits, and longer seeds, make up only 29% of the population (Table 8).
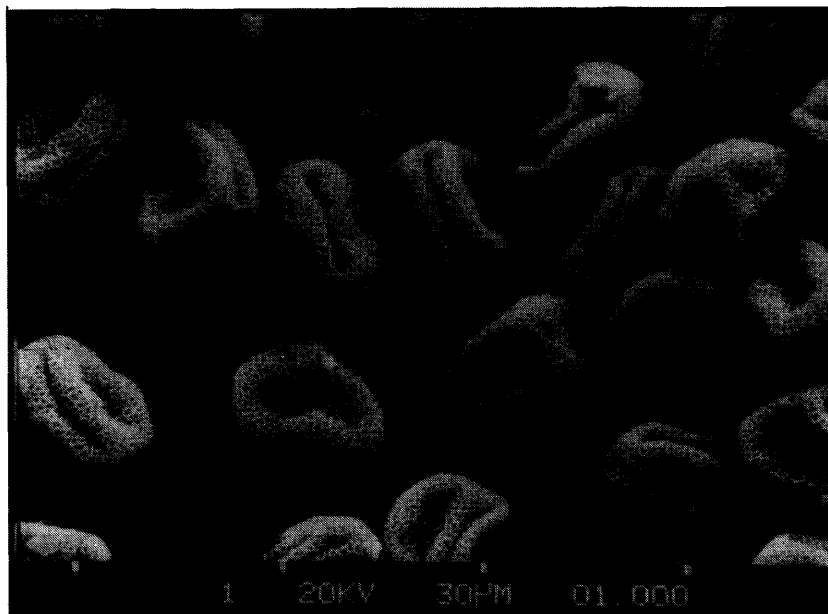

Figure 1. — Pollen grains of *Fraxinus syriaca* Boiss. x900.

Table 7. — Factor analysis of 12 traits of a planted population from Ilanot.

Character	Factor				
	1	2	3	4	5
Index of fading	0.01	0.26	0.22	0.80	-0.24
Length of leaf	0.46	0.11	0.81	-0.07	-0.01
Length of petiole	-0.01	0.86	0.15	0.05	0.03
Number of leaflets	0.54	-0.61	0.51	0.01	0.01
Length of leaflet	0.26	0.42	0.81	-0.01	0.09
Width of leaflet	-0.05	0.07	0.91	0.05	0.08
Length of serration	0.11	0.88	0.19	0.05	-0.08
Depth of serration	0.21	-0.06	0.04	-0.08	0.93
Length of fruit	0.84	0.11	0.16	-0.24	0.29
Width of fruit	0.82	-0.09	0.05	0.44	-0.01
Length of seed	0.69	0.12	0.25	0.01	0.54
Width of seed	0.04	-0.17	0.52	0.72	0.18
Variance explained by each factor	2.50	2.21	2.88	1.43	1.34

Table 8. — Cluster means of 12 measured traits of a planted population from Ilanot.

Character	Cluster				
	1	2	3	4	5
Index of fading	41.33	45.00	46.39	45.00	45.00
Length of leaf (cm)	23.05	17.12	19.47	19.40	15.46
Length of petiole (cm)	5.25	3.78	3.87	4.70	3.93
Number of leaflets	7.10	6.50	8.90	8.00	5.96
Length of leaflet (cm)	7.60	5.87	5.83	5.90	4.93
Width of leaflet (cm)	2.45	2.05	1.87	1.60	1.80
Length of serration (cm)	0.66	0.56	0.55	0.61	0.55
Depth of serration (cm)	0.05	0.07	0.07	0.08	0.05
Length of fruit (cm)	4.27	3.16	4.10	4.03	2.67
Width of fruit (cm)	0.66	0.63	0.94	0.82	0.65
Length of seed (cm)	1.82	1.61	1.83	2.13	1.28
Width of seed (cm)	0.34	0.36	0.38	0.40	0.34
Number of trees in cluster	2	6	3	1	9

Discusion and Conclusions

F. syriaca from Israel is diploid and conforms, therefore, to the majority of species of the genus investigated so far, with a chromosome number of 2n = 46 (Bolkhovskikh et al., 1969). Additional investigations from other parts of the wide geographic range of the tree are, however, desirable, since some species, such as F. americana L. and F. chinensis Roxb., form polyploid series (Bolkhovskikh et al., 1969).

In comparison with F. excelsior (Darwin, 1877; Larsen, 1945; Rohmeder et al., 1959), F. syriaca has a remarkably simple breeding system, as it is strictly andromonoecious, As in the former, the predominantly staminate flowers of tree No. 34 from Ilanot may possibly suggest an incipient trend toward dioecism, though larger numbers of trees need to be examined to support this hypothesis. A further resemblance to F. excelsior (Lingelsheim, 1920; Larsen, 1945) is the apparent prevalence in F. syriaca of protogyny. Time of flowering appears to be genetically controlled, since 75% of the trees investigated over two years were either precocious or late to flower.

Pollen grain dimensions of various provenances, of hermaphrodite and staminate flowers, and of a mutant with yellow anthers, were fairly similar (Tables 2—4) and well within the range for F. syriaca listed by Nikolaeva (1962). In agreement with her findlings, a medium containing 15% sucrose gave the highest germination percentage, but in contrast to her data, germination was severely depressed on a medium containing 30% sucrose (Table 5). Germination rate of pollen from Ilanot (Table 5) was almost double that reported by Nikolaeva (1962).

A mutant with yellow anthers (tree No. 47) did not show any abnormalities at meiosis and did not differ from trees with normal (very dusky red) anthers in size or germination percentage of pollen grains (Tables 2, 5). There are, however, some indications that the tree is more sensitive to drought and, particularly, to sharav conditions - very high air temperatures accompanied by very low relative humidity (C. Grunwald, unpublished data). In future breeding programs of F. syriaca the mutant could possibly serve as a genetic pollen marker (Franklin, 1981), provided that
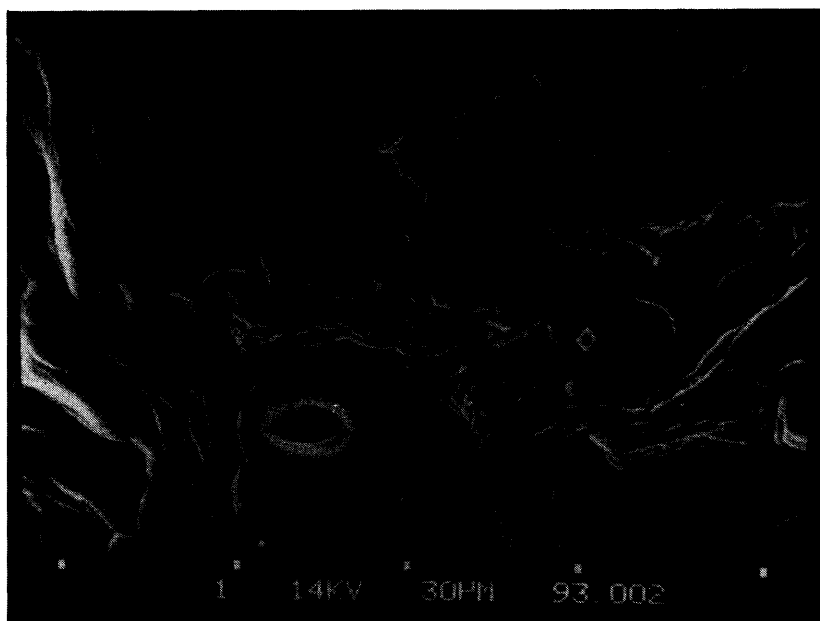

Figure 2. — Stomata on upper leaf surface of Fraxinus syriaca Boiss. Note presence of epicuticular waxes. x750.

yellow anthers are subject to the laws of particulate (qualitative) inheritance and behave as a simply inherited Mendelian trait.

Examination of trees planted at Ilanot and of natural populations in northern Israel showed that the leaves can hardly be termed coriaceous and/or subcoriaceous, as stated by several authors (LINGELSHEIM, 1920; POST, 1933; FEINBRUN-DOTHAN, 1978). We also failed to confirm the existence of hairs (POST, 1933; FEINBRUN-DOTHAN, 1978). Confirming to the description of the species by LINGELSHEIM (1920), stomata do indeed occur on the upper leaf surface (Fig. 2).

Standard floras are notoriously short on numerical data describing the range of morphological characters, and those consulted in connection with the present study of F. syriaca (BOISSIER, 1879; POST, 1933; VASIL'EV, 1967; FEINBRUN-DOTHAN, 1978; YALTIRIK, 1978; see also LINGELSHEIM, 1920) are apparently no exception.

The number of leaflets listed ranges from 2—6 in LINGELSHEIM (1920) and VASIL'EV (1967) to (1-) 3 (-11) in FEINBRUN-DOTHAN (1978); in our subjects it varies from 3 to 13, with an average of 6.7. The length of the leaflet ranges from 3—6 cm in VASIL'EV (1967) to 1—10 cm in LINGELSHEIM (1920), and in our study from 2.8 to 8.4 cm with an average of 5.6 cm. The width is given as 2—2.5 cm by VASIL'EV (1967) and 0.8—3.5 cm by LINGELSHEIM (1920), with our data ranging from 1.2 to 2.9 cm, with an average of 1.9 cm (Table 6). Similar differences were found with regard to dimensions of the samara. This implied criticism of the data listed in standard floras does, admittedly, not take into account the possibility of geographic variation, a subject apparently not yet investigated.

Factor analysis (Table 7) leads to a much clearer understanding of morphological variation in F. syriaca and describes total variation better than a series of correlations or scatter diagrams. Cluster analysis (Table 8) used to indicate groupings among the trees examined, provides

further insight into the structure of the population and shows that 71% of the trees belong to two well defined groups, whereas other groups are represented by single or few trees only.

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Genotype-Environment Interactions in Tropical Pines and their Effects on the Structure of Breeding Populations

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(Received 1st September 1983)

Summary

To the tree breeder the many statistical definitions of genotype-environment interaction (gei) can be reduced to the one practical implication that the optimum population or individual on one site is not necessarily the best for others. Various univariate and multivariate techniques are available for detecting and evaluating gei; four methods (PLAISTED's, WRICKE's, joint regression, principal components) were compared with a limited set of data for maximum wood density of Pinus caribaea MORELET and found to provide similar conclusions about the sources of gei but joint regression analysis has the potential for predicting genotypic performance on untested sites.

Gei effects occur at the level of species, provenance, family or clone (and examples of each in tropical pines are given) but few field experiments have been specifically designed to estimate them nor have data been analysed to determine the contributing environments and genotypes.

Gei reduces heritability and hence gain, necessitates the creation and maintenance of separate breeding populations, and requires the integration of genetic and silvicultural research. It is probably only realistic to expect to detect, explain and use gei when a single environmental factor affects an economically important trait in a predictable manner. The decision to use gei effects in breeding strategy becomes more complex when two traits are inversely correlated; the breeder also has to decide between seeking homeostasis at the level of population or individual. This is particularly important in relation to the transience of forest environments due to changing management practices and to the increasing use of marginal sites.