A. Elings

The Use of Crop Growth Simulation in Evaluation of Large Germplasm Collections

Distribution, Variation and Evaluation of Syrian Durum Wheat Landraces

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The Use of Crop Growth Simulation

in Evaluation of Large Germplasm Collections

Distribution, variation and evaluation of Syrian durum wheat landraces

Het Gebruik van Gewasgroeisimulatie

in de Evaluatie van Grote Genenbank Collecties

Verspreiding, variatie en evaluatie van Syrische durum tarwe landrassen

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vakgroep Plantenveredeling.

1. Ook landrassen zijn niet in staat hoge opbrengstniveau's onder ongunstige groeiomstandigheden te handhaven.

   dit proefschrift

2. Een biotechniek die tot doel heeft de genetische variatie te vergroten, heeft alleen toekomst als deze doelgericht kan worden toegepast.

3. Het gebruik van gewasgroeisimulatie bij het beheer van een genenbankcollectie maakt het aanleggen van een 'core' collectie overbodig.

4. Toepassing van gewasgroeisimulatie verbetert de capaciteit en kwaliteit van evaluatieprogramma's voor genenbankcollecties.

   dit proefschrift

5. Tenminste een deel van een genenbankcollectie moet onder verschillende groeiomstandigheden geëvalueerd worden.

   dit proefschrift

6. Het aanbieden van zeer korte arbeidscontracten door overheidsinstanties moet alleen worden toegestaan als de werknemer ook dan ambtenaar in de zin van de Algemene burgerlijke pensioenwet wordt.

7. Het gebruik van Holland en Nederland als synoniemen doet onrecht aan de afkomst van vele Nederlanders.

8. De waarde 0.004 kg kg^{-1} als minimum stikstofgehalte van tarwestro is niet algemeen geldig.

   dit proefschrift

9. Landrasgroepen van Syrische durum tarwe zijn voor een lange periode geteeld in relatief kleine gebieden met specifieke klimaatomstandigheden, gevolgd door een recentere verspreiding van enkele groepen.

   dit proefschrift

10. Het ontwikkelen en uitgeven van nieuwe rassen in ontwikkelingslanden heeft alleen zin als goede zaaizaadvoorzieningsprogramma's aanwezig zijn.

11. Bij sterke droogtestress na de bloei wordt de korrelvulling zowel door de 'sink' als door de 'source' beperkt.

    dit proefschrift

12. The wide adaptability of a variety is different from its local adaptation.

    Nguyen & Anderson, 1991

13. Het gezegde zou tegenwoordig moeten luiden: "Wat de stedeling niet kent, dat eet hij niet", nu deze nog steeds het liefst Bintjes eet.

Stellingen behorende bij proefschrift van A. Elings: The use of crop growth simulation in evaluation of large germplasm collections.

Mon cher seigneur, dit Wiwine, des gens de ma famille sont couchés sous ces dalles, et leur devise est sur oreiller. *Plus est en vous.* Plus est en moi que de rendre oubli pour oubli.

Marguerite Yourcenar,
l'Œuvre au noir.

'From this we may learn two things: first, not to draw general conclusions from a very partial view of nature, and secondly, that trees and fruits, no less than the varied production of the animal kingdom, do not appear to be organized with exclusive reference to the use and convenience of man.'

Alfred Russel Wallace,
The Malay Archipelo.

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ABSTRACT

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Landrace populations of Syrian durum wheat were collected. Regions of collection and landrace groups were described with respect to environmental and plant characteristics, respectively. Phenotypic variation patterns were studied, and agronomic performance under various environmental conditions, frost tolerance and host resistance to three fungal diseases was evaluated.

Evaluation methods were formulated, that allow the utilization of single-evaluation results in forecasting growth and development under different environmental conditions. Use is made of knowledge on the environment of origin, analysis of variance, and simulation models. Herewith, the qualitative and quantitative limitations related to the evaluation of large germplasm collections can be reduced.

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Supervision was provided by my promotor Prof. Dr. Ir. Rudy Rabbinge of the Department of Theoretical Production Ecology (TPE) of the Wageningen Agriculturel University (WAU), co-promotor Prof. Dr. Ir. Herman van Keulen and the late Dr. Ir. Kees Spitters of the DLO Centre for Agrobiological Research (CABO-DLO), Wageningen, co-promotor Dr. Ir. Anton Zeven of the Department of Plant Breeding (IvP) of the WAU, and Dr. Miloudi Nachit of ICARDA. I am very thankful for their combined guiding, which has materialized in this dissertation.

Germplasm was collected in cooperation with the Syrian National Genetic Resources Unit, and evaluation fields were partly located at the Homs and Izra'a Agricultural Research Stations. Parts of simulating and reporting were carried out at TPE, with assistance of CABO-DLO. Final production of this dissertation was done at TPE; I kindly thank Mrs. Gon van Laar for her editorial help.

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Close contacts were maintained with the CPRO Centre for Genetic Resources The Netherlands (CGN-DLO), Wageningen, which also cooperated in research.

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Account

Six chapters of this dissertation are based upon articles that have been published in or submitted to refereed journals in agricultural sciences:

Chapter 3: Elings, A. & M.M. Nachit, 1991. Durum wheat landraces from Syria. I. Agro-ecological and morphological characterization. Euphytica 53 (3): 211-224.

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Chapter 5: Elings, A., 199x. Durum wheat landraces from Syria. III. Agronomic performance. Journal of Applied Ecology (submitted).

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Chapter 7: Elings, A. & M.M. Nachit, 1993. Field evaluation and simulation of frost tolerance in Syrian durum wheat landraces. Netherlands Journal of Agricultural Sciences 42 (accepted).

Chapter 8: Elings, A., O.F. Mamluk & M.M. Nachit, 199x. Distribution of resistance to fungal diseases in Syrian durum wheat landraces, in relation to environmental characteristics of the collection regions. Euphytica (submitted).

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Contents

Chapter 1

GENERAL INTRODUCTION

1.1 Evaluation of large germplasm collections

1.1.1 Limitations to germplasm evaluation

Plant genetic resources centres collect or acquire, characterize, evaluate, maintain and disseminate plant germplasm with characteristics that now or in the future may contribute to improvement and stabilization of yields. The key role of germplasm collections in plant breeding, and their frequent use, puts high demands on their evaluation. This generally comprises two steps: a preliminary evaluation by the genebank's crop curator, in which a limited number of traits of interest to the majority of users is recorded, followed by a more specific evaluation of promising material on the basis of user's specifications.

The number of replications in time and space in a genebank's preliminary evaluation is often limited. The considerable genotype x environment interaction makes extrapolation of single-evaluation results difficult (Ceccarelli, 1989), or even impossible, if location x year interaction is significant (Lin & Binns, 1988). Therefore, evaluation results have often limited applicability. To overcome that problem, extensive multilocational or multiseasonal evaluation would be needed to assess plant characteristics, but this expensive procedure can often not be applied to entire germplasm collections, that may consist of many thousands of accessions. Moreover, extensive evaluations may still not lead to unequivocal results.

Consequently, if germplasm centres are forced to limit their evaluation programmes because of financial constraints (Giles, 1990), assessment of the potentials of germplasm for cultivation under different climatic conditions comes under pressure, so that initial selections have to be made on the basis of preliminary characterization and evaluation covering only one or very few seasons, often at a single location. This involves the risk that part of the useful germplasm may not be recognized as such, and thus not be utilized.

Therefore, an efficient method is required that allows assessment of plant characteristics of large numbers of accessions under various environmental conditions, utilizing a limited number of evaluation results.

1.1.2 Genotype x environment interaction

Results of one or few evaluations can only be utilized in forecasting growth and development under different environmental conditions, if processes underlying genotype x environment interaction are qualitatively and quantitatively understood.

Various techniques have been developed to address the problems created by genotype x environment interaction, and to analyze the effects of environmental factors on plant characteristics. Broadly speaking, three approaches can be distinguished: analysis of variance (ANOVA), calculation of a stability parameter (Gotah & Chang, 1979), and crop growth simulation.

Qualitative analysis

ANOVA tests the significance of the effects of factors and their interactions, and establishes experimental error (Bowman, 1989; Sokal & Rohlf, 1981). This technique analyses effects of population, year, location, fertilizer application, and other environmental factors. An ANOVA provides a qualitative indication of the relative importance of factors, and is therewith a first step in analysis of experiments. However, it does not provide insight in the mechanisms underlying variation, and therefore, it offers little scope for understanding and predicting crop growth under different environmental conditions.

Stability parameters are derived from regression analyses that relate plant characteristics, e.g. yield, to a particular environmental variable, e.g. seasonal rainfall. The difficulty to relevantly characterize environments is in many cases dealt with by defining average population yield as the environmental index. Stability parameters appear in two forms: as regression coefficients (Finlay & Wilkinson, 1963), and as deviations from the regression line (Eberhart & Russell, 1966). Their validity is limited by the range of genotypes and environments tested, and the number of environmental characteristics considered. Such analyses provide some insight in genotype x environment interaction, but remain descriptive, and do not explain plant growth and development. Therefore, their predictive capacity is limited.

Quantitative analysis

Crop growth simulation models describe dynamically dry matter production and phenological development, incorporating plant genetic and environmental characteristics. Crop growth models account for genotype x environment interaction on the basis of quantitative knowledge on the relations between plant genotypic and environmental characteristics. They allow extrapolation of effects at the level of single plant organs to the growth of a complete canopy in a continuously changing field environment (Spitters & Schapendonk, 1990).

In addition to ANOVA, a well-calibrated simulation model offers a comprehensive tool to analyze genotype x environment interaction, which can assist in germplasm evaluation and selection for specific environmental conditions.

1.2 Environmental characterization

Environmental characterization of the collection region may be used in assessing plant genotype and forecasting growth under different climatic conditions. Provided that the germplasm originates from the collection region, agronomic practices and ecological characteristics during domestication and cultivation have influenced its genotypic constitution: variation has narrowed, and landraces adapted to cultivation have developed. Hence, a relation exists between the agro-ecological conditions of the region of provenance and the morpho-physiological make-up of the plant. It may be expected also, that the former can be related to phenotypic plant characteristics at locations with different environmental conditions. Such relations are used, for instance, when a breeder requests seeds from 'a desert area' in search for drought tolerance.

Elucidation of such relations may contribute to understanding of plant performance in different environments. However, establishment of unequivocal relations is hampered by environmental interactions associated with plant phenotype.

Accessions can be classified on the basis of differences in their agro-ecological background, which requires detailed characterization of the environment of provenance. It is possibly more efficient to evaluate a representative sample of a germplasm collection in a number of distinctly different environments, possibly over a number of years, than to evaluate the entire collection in a single environment.

1.3 Variation

The evaluation of genotype x environment interactions may be complicated by genetic heterogeneity, as in the case of landraces. Plants within populations differ genetically, while also variation can be observed among populations and population groups, e.g. populations from specific regions. The degree of variation varies, presenting germplasm curator and plant breeder with problems with respect to collection strategies, and description, evaluation and selection of germplasm.

Assessment of, mostly phenotypical, diversity forms an essential part of plant germplasm evaluation, as it indicates the breeding value of observed plant characteristics. Also, knowledge of variation patterns aids in planning future collection missions, and variation in plant characteristics and in environmental conditions in the collection region can be related.

The complex interplant relations within a landrace population are balanced towards long-term yield stability in the environment of origin. Intrapopulation variation can be quantified with ANOVA, but this is of little predictive value for different environmental conditions. Also, regression analyses and crop growth simulation models at the population level, do not incorporate intrapopulation variation and do not explain therefore the consequences of heterogeneity in different environments.

1.4 Problem definition

The overall objective of the present study was development and testing of a method allowing rapid identification of agronomic characteristics of accessions, and application of single-evaluation results for analyzing crop behaviour in other years and at other locations with different climatic conditions.

Three research phases were distinguished, each with a number of intermediate objectives:

i. Collection and description of germplasm.

- collect germplasm,
- provide a description of environmental conditions in the regions of provenance,
- provide morphological characterization of the germplasm.

ii. Phenotypical characterization:

- establish relations between environmental characteristics of the region of provenance and plant characteristics at other locations,
- study diversity patterns.

iii. Agronomic evaluation:

- carry out multilocational, multiseasonal agronomic evaluations,
- perform statistical analyses of the agronomic trials,
- analyze the agronomic trials through crop growth simulation,
- develop a suitable evaluation method.

1.5 General overview

A collection of durum wheat landraces from Syria was considered suitable as research material, and missions were organized to collect new germplasm (Chapter 3).

The domestication of durum wheat and the role of wheat landraces in Near Eastern agriculture are briefly discussed in Chapter 2. The evaluation study on Syrian durum wheat landraces is presented subsequently: Chapter 3 reports on the collection missions, and gives environmental and morphological descriptions of regions of collection and durum wheat landrace groups, respectively. Patterns of phenotypic diversity are analyzed in Chapter 4. Chapters 5 and 6 deal with agronomic field trials, descriptive statistical analyses, explanatory analyses by simulation models, and the establishment of relations with environmental conditions in the regions of collection. Chapters 7 and 8 illustrate the establishment of relations between plant characteristics and environmental characteristics of the regions of provenance; Chapter 7 treats evaluation of frost tolerance, and in Chapter 8 fungal disease resistances are related to the environmental characteristics of the regions of origin. Chapter 9 finally contains a general discussion.

Chapter 2

DURUM WHEAT

2.1 Domestication of wheat

Domestication of plants in West Asia started in the Late Stone Age (Neolithic) in the so-called Fertile Crescent, i.e. present northern Israel and Jordan, Lebanon, western and northern Syria, southern Turkey, and the Euphrates/Tigris basin in Iraq and Iran, where rainfall sufficed for non-irrigated agriculture. Initially, wild plants were selected, which adapted to human needs. In the process, cultivable types emerged, differing from their wild relatives to such an extent that now they are sometimes considered as distinct species.

The Triticeae annuals show greatest species diversity in the eastern Mediterranean semi-arid lowlands and the mountain areas of Turkey, Iran and the Caucasus (West et al., 1988). In this main centre of diversity, wheat was domesticated, as were many more plant species, such as barley, chickpea, lentil, peas, clovers, faba bean, onion, flax, olive, apple and pear (Simmonds, 1976; Vavilov, 1951; Zeven & de Wet, 1982). Vavilov (op. cit.) identified the region as the fourth centre of origin, 'The Near-Eastern Centre of Origin of Cultivated Plants', and emphasized its wealth of varieties of cultivated wheats.

Cultivation of wheat and barley started towards the end of the 8th millennium B.C., which enabled man in the Near East to transfer from hunting and food collecting to farming (Harlan & Zohary, 1966), and to expand its Neolithic agriculture to West Asia, Europe and North Africa (Zohary & Hopf, 1988). The first evidence of free-threshing tetraploid wheats (of which durum wheat [Triticum turgidum L. var. durum (Desf.) MK.] is the main representative) dates from 7th to 6th millennium B.C. sites in Syria, Turkey, Iraq and Iran (Zohary & Hopf, 1988). During the Neolithic and Bronze Age, their importance increased. Bread wheat (T. aestivum L.) is currently the most important wheat species.

From the Fertile Crescent, wheats spread over Europe, North Africa and Asia. After introduction of tetraploid wheats in Ethiopia, a secondary centre of diversity developed (Zeven & de Wet, 1982). In recent centuries, wheats have spread to larger parts of Africa, the Americas and Australia.

Ever since the start of domestication, wheats have evolved, while agriculture diffused from its location of origin (Harlan, 1986). Mutations and gene combinations with favourable properties were preserved, while cultivated species in the centre of origin remained in close contact with their wild relatives, and absorbed new genes through introgression. Exposure to new environments and developing agricultural systems resulted in new genotypes and widening variation. In the 20th century, modern breeding techniques substantially contributed to development of genotypes with higher yield potentials. Therefore, crops cultivated presently, including landraces, differ considerably from the types domesticated millennia ago.

2.2 Wheat landraces in Near Eastern agriculture

Constraints for wheat production in the arid regions of West Asia and North Africa (WANA) are low and erratic rainfall, limited irrigation possibilities, low soil fertility, low winter temperatures and high temperatures during the grain filling period, poor management practices, and occurrence of pests and diseases (Ceccarelli et al., 1987b; Miller, 1987; Osman, 1986; Stapper & Harris, 1989). As the possibilities for application of external inputs such as irrigation and inorganic fertilizers are limited, introduction of modern varieties that require these inputs to fully realize their genetic potential is feasible only in the higher rainfall zones. Although mainly restricted to these zones, an increasing part of the total wheat area in Syria is planted to modern varieties: currently over 50%, compared to approximately 10% in 1973 (Belaid & Morris, 1991). As rainfed agriculture remains important to WANA, which faces a growing gap between wheat production and consumption (Adamowicz, 1988; Belaid & Morris, 1991), germplasm that has been domesticated locally and is adapted to the erratic exposure to growth-limiting factors, may contribute to the improvement of yield level and yield stability.

Maximum yields of landraces are moderate, but average yields are generally more stable under a wide range of environmental conditions than yields of modern varieties. Since the start of domestication, landraces have been cultivated in various agro-ecological niches by farmers who maintained their own seed, and may have traded to other regions (Harlan et al., 1973). This practice has resulted in wide variation in plant characteristics, among and within locations, which are balanced in such a way that unfavourable environmental conditions are generally not catastrophic and do not lead to substantial yield losses. Farmers in marginal environments still adhere to a considerable extent to landraces, as was observed during the collection missions. Therefore, landrace germplasm is extensively used in breeding programmes aimed at environments characterized by high probabilities of growth limitations.

Chapter 3

AGRO-ECOLOGICAL AND MORPHOLOGICAL CHARACTERIZATION

Abstract

A total of 185 durum wheat [Triticum turgidum L. var. durum (Desf.) MK] landraces was collected from 166 sites in the Syrian Arab Republic. With K-means clustering the collecting sites are grouped based on four climatological variables to create relatively homogeneous regions of origin with respect to agro-ecological characteristics. Stepwise Discriminant Analysis confirmed the minimization of variation within regions.

Regional description with respect to agro-ecological characteristics is given. According to farmers' estimations, average grain yield is lowest in western mountainous regions, and highest in southern parts of the country, which illustrates the tendency of landraces to produce more straw rather than grain dry matter under high rainfall conditions. Other data, however, show that farmers in southern regions supposedly have overestimated yield levels.

Landraces groups as distinguished by farmers are morphologically identified, to provide a sytematical description of visable variation. Distribution patterns of the various landrace groups are indicated. Only few landrace groups are widely distributed, whereas most others are regionally concentrated. Genetic diversification is found in the heterogeneous nature of landraces and in the cultivation of different landraces per region or village. Large proportions of T. aestivum were found in T. durum populations in the mountainous regions in the west of the country, where farmers apparently desire a species mixture.

3.1 Introduction

Efficient use of germplasm requires characterization and evaluation. The latter is normally performed in two steps: a preliminary evaluation, which concentrates on recording a limited number of traits thought to be desirable by a consensus of users (IBPGR, 1985), followed by a more specific evaluation of promising material. While the large quantity of accessions limits multilocational preliminary evaluation, information resulting from one-site evaluation cannot be used to predict performance in other environments due to genotype x environment interactions (Ceccarelli, 1989). In addition, further evaluation may not include useful material that has not been recognized as such in the preliminary evaluation. Part of the problem is the restricted use of environmental parameters of the collection region in germplasm evaluation. Agronomic and ecological characteristics have influenced the genotypic constitution of landraces during domestication (Harlan et al., 1973), and hence a relation exists between the agro-ecology in the collection region and the morphophysiological make-up of the plant.

This study aims to provide a method to define regions of collection whereby agro-ecological characteristics, in combination with multilocational evaluation results, can help in understanding crop performance under various growth conditions. This knowledge can be utilized in selecting for different agro-ecological zones, thus reducing the exclusion of valuable germplasm.

A collection of durum wheat [Triticum turgidum L. var. durum (Desf.) MK] landraces from the Syrian Arab Republic was considered suitable for this purpose for the following two reasons:

- Syria is situated in the "Fertile Crescent," where the first cereals were domesticated by ancient civilizations about 10,000 years ago in the late Mesolithic Period and the early Neolithic Age (Hawkes, 1983; Harlan, 1986), and where tetraploid wheats are cultivated since the 7th millenium B.C. (Zohary & Hopf, 1988). Up to the present wheat and barley have been grown here (Vavilov, 1951; Zeven & de Wet, 1982), and have spread to many other parts of the world (Bell, 1987; Yamashita, 1980).
- Although landraces are outyielded by newly-developed varieties under favourable conditions, they may yield higher under stress due to heterogeneity (Hawkes, 1983; Nachit et al., 1988).

However, no existing collection could be identified that met the following necessary requirements for an eco-geographic study: a) regular distribution of collection sites over the regions of collection, b) representation of various agro-ecological zones, c) availability of information on agro-ecological site parameters, and d) availability of seed samples representative of the populations in the field. The first three requirements were not met due to the dearth of information on the precise origin of available Syrian accessions (Toll, 1984), while the fourth implied access to bulk samples. An entire new collecting mission was made, which paid attention to record of passport and collection information (IBPGR, 1985), and which provided an agro-ecological description of each site.

Evaluation results have often been interpreted in relation to the origin of the material. Morphological and agronomic crop characteristics were presented per country or group of countries (Asins & Corbonell, 1989; Gallagher & Soliman, 1988; Erskine et al., 1989; Jain et al., 1975; Kato et al., 1988; Narayan & Macefield, 1976; Porceddu, 1976; Spagnoletti Zeuli & Qualset, 1987; Spagnoletti Zeuli et al., 1984), or per region or site within countries (Bekele, 1984; Bogyo et al., 1980; Ceccarelli et al., 1987a; Damania & Porceddu, 1983; Murphy & Witcombe, 1981; Weltzien, 1988). Isozyme frequencies were similarly presented (Asins & Carbonell, 1989; Nakagahra et al., 1975). Although such groupings elucidate the structure of data sets, they are less satisfactory in interpreting the agro-ecological background of germplasm. On the other hand, Burt et al. (1980) provided networks of floristic, soil and climatic characteristics of collection sites and correlations between environmental characteristics. Allozyme frequencies were related to environmental factors (Nevo et al., 1986, 1988) and the ecogeographical distribution of glutenin alleles was studied (Levy & Feldman, 1988).

When regions of collection have to be defined independently from evaluation results, only site characteristics can be considered, whereas crop characteristics can be related to the regions only afterwards. Burt et al. (1979) identified regions in South and Central America most likely to provide the legumes required for Northern Australia, before plants were explored.

In this study, K-means clustering of collection sites on the basis of independent environmental characteristics was tested. The K-means clustering procedure is well adapted to large data sets (Lebart et al., 1984) and partitions into groups such that cases within a group are relatively homogeneous and cases in different groups are relatively heterogeneous for the characteristics involved (Press, 1982). Also, regions formed by clustered sites were described for agro-ecological characteristics.

This study also seeks to provide a brief morphological description of the Syrian durum wheat landrace group as distinguished by farmers. Each group has its specific morphological characteristics and geographical distribution pattern, and is referred to by a local name that is often derived from a striking character or supposed origin. Jacubziner (1932) studied the Syrian durum wheats and developed a detailed taxonomic key based on detailed morphological observations. However, this approach is less useful for studying population performance, which requires identification of a particular landrace rather than the genotypes that compose it.

3.2 Materials and methods

The Syrian Arab Republic is situated on the eastern side of the Mediterranean. It has parallel mountain ranges in the west and, in the southeast, is incorporated in the Arabian Desert (Anonymous, 1977). Extensive parts of the country consist of plains interspaced by river valleys and mountain ridges. The year can be divided into four seasons: a cool and rainy winter, a hot and dry summer, and short transition periods in spring and autumn. Three climatic regions can be distinguished: a) coastal area with high relative humidity (mean annual relative humidity 60-75%), mild winters (mean January temperature 4-12°C), warm summers (mean August temperature 22-26°C) and relatively high annual rainfall (up to 1400 mm), b) desert area with low relative humidity (45-55%), cool winters (3-8°C), hot summers (24-32°C), and low precipitation (less than 300 mm annual rainfall); and c) areas located between the first two regions and in an about 50 km-wide strip along the northern border, characterized by relatively moderate relative humidity, temperature, and rainfall conditions (50-60%, 5-7°C (Jan.) and 25-31°C (Aug.), and 300-500 mm, respectively) (Rafiq, 1976).

In June 1987 and June 1988, ICARDA's Genetic Resources Unit conducted collecting missions for Triticum durum in cooperation with the Genetic Resources Unit of the Syrian Agricultural Research Centre, Douma, in most of the regions of Syria where landraces of this species were known or expected to be cultivated. A total of 185 landraces was collected from 166 sites (van Slageren et al. 1989). The geographical distribution of the collection sites is presented in Figure 3.1.

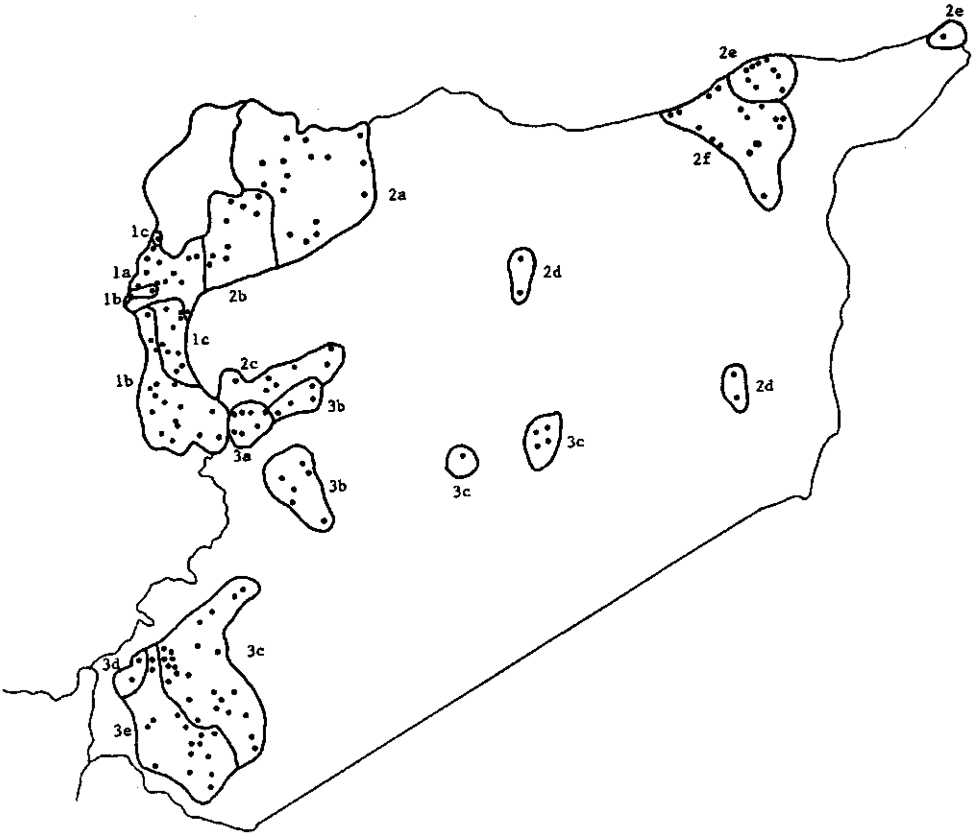


Figure 3.1. Geographical distribution of the collection sites (indicated as dots) of durum wheat landraces in the Syrian Arab Republic.

1a = Lattakia	2a = Aleppo	3a = Homs
1b = Tartous	2b = Idleb	3b = Qaryatain
1c = Central Mountains	2c = Hama	3c = Damascus
	2d = Central Area	3d = Quneitra
	2e = Northeast	3e = Hauran
	2f = Hassake	

Two random samples were taken per population : 100 individual spikes, and 100 spikes in bulk (Marshall & Brown, 1975). The individual spikes were used for evaluating genetic variation, while the bulk samples were multiplied, characterized and evaluated for agronomic traits, and stored. Standard passport and collection information (IBPGR, 1985) was recorded at each site, using ICARDA's collecting forms, which provide geographical and ecological features, as well as qualitative and quantitative information on the collected seed samples (Elings, 1989). Farmers, who were present at 132 sites, were asked for information on the landraces and their farm management practices: local name of the landrace; origin of the seed (own farm, another farm in the same village, another village in the same region, another region, market); number of years the seed had been used locally; rotation scheme; irrigation practice; average sowing date and rate; average harvesting date; estimated grain and straw yields (lowest, average and highest); frequency of grazing by sheep instead of harvesting (indication of crop failure); fertilizer (N,P) and manure application; and means of weed, disease and pest control. Although the resulting data were possibly biased, they seemed sufficiently reliable for comparative purposes. Some soil characteristics were recorded (stoniness, cracking, soil type, and soil layer depth), and soil samples from the 20 cm soil surface were taken at three arbitrarily chosen spots in each field. The three samples were mixed and analyzed for organic matter content, total N (Kjeldahl, Bremner method) and extractable P (Olsen). Tiller density was also determined at three randomly chosen sites in the field. The number of seeds per spike, seed weight per spike, and the thousand kernel weight of the single heads collected were determined.

Data were analyzed using the BMDP statistical software package (Dixon et al., 1985). The 166 collection sites were grouped following the K-means clustering method (Lebart et al., 1984) so that variation is minimized within and maximized among groups. The analysis was based on a set of four climatological variables, viz. the difference between the longest and the shortest daylength in the course of a year ("daylength amplitude"), annual precipitation, and maximum and minimum annual monthly temperature. All other observed variables were assumed dependent. The daylength amplitude is the difference between the daylengths at June 21st and at December 21st. Latitude was considered an unsatisfactory parameter, as it is not a driving force in crop development, and in choosing daylength itself definition and determination of the optimal date, which would need to be related to plant development, was problematic. Temperature was described by the mean maximum temperature in August and the mean minimum temperature in January. In these two months, the highest and lowest values are reached, respectively. Nearly all rain falls during the growing season, and was therefore supposed to be totally available to the crop. The rainfall figure for irrigated sites was not adjusted since it is believed that domestication has occurred under rainfed conditions, which therefore represents the agro-ecological background of the concerned populations.

Values were standardized to unit variance, and the Euclidean distance was used to measure distances between each case and the centre of a cluster. In subsequent steps, Syria was divided into regions and then further sub-divided into subregions. Variables highly discriminative in the first step could lose this characteristic in favour of other variables in the following step, causing a "fine-tuning" effect: the smaller the geographical scale, the more accurate and hence realistic the descriptive value of the discriminating variables (Press, 1982).

To verify the consistency of the constructed clusters, a spanning tree based upon the same cases was formed, using the centroid method. This agglomeration method is preferable to the other technique available to BMDP, the single linkage (H. Nilwik, personal communication); furthermore, in a comparative study by Peeters and Martinelli (1989), centroid and average linkage, rather than single linkage, confirmed expectations. The pattern of amalgamation was considered: it was tested whether sites belonging to the same cluster merged before merging with sites belonging to other clusters. A parallel between the K-means clustering and spanning tree would indicate consistency of the clusters.

Stepwise Discriminant Analysis (SDA) was used to describe the variation between the collection sites in terms of linear combinations of the original variables.

In addition to the four climatological variables mentioned above, several other ecological and agronomic characteristics (Table 3.1) were defined for the regions formed during the first clustering step. The significance of differences between the latter cluster means was tested by analysis of variance.

Only landraces were selected of which the same farm or village had been indicated as indicated source. Of 89 landraces, 50 single spike progenies were sown separately at ICARDA's main farm, located 32 km south of Aleppo, Syria. Each single head line was taxonomically identified, as some populations were mixtures of _T_. _durum_ and _T_. _aestivum_.

A taxonomic description of the species _T_. _durum_ has been given by Bor (1968) and Tan (1985). For landrace groups description, three to four specimens were randomly selected per population, and a number of morphological characters was recorded: pubescence of leaves, spike density, spikelet attitude, glume colour, lemma colour, awn colour, and glume

Table 3.1. Mean values of variables describing the three initial clusters (standard deviations in brackets). Climatic characteristics are retrieved from the Climatic Atlas of Syria (Anonymous, 1977).

Variable+	West		South		Centre/North		p
Daylength amplitude (hrs)	4.8	(0.0)	4.5	(0.1)	5.0	(0.1)	****
Altitude (m)	386	(269)	754	(169)	445	(94)	****
Rainfall (mm $year^{-1}$)	1045	(215)	267	(115)	357	(120)	****
Max. temperature (°C)	29.0	(1.8)	33.8	(1.6)	37.6	(2.1)	****
Min. temperature (°C)	5.4	(2.0)	2.1	(0.9)	2.2	(0.7)	****
Potential evaporation (mm)	1273	(101)	1734	(227)	2052	(326)	****
Texture[1]	4.8	(0.6)	4.5	(0.9)	3.9	(1.4)	****
Stoniness[2] (%)	42	(30)	19	(25)	13	(23)	****
Cracking[3]	1.2	(0.4)	1.6	(0.5)	1.6	(0.5)	****
Surface soil depth (cm)	69	(104)	239	(319)	459	(424)	****
Organic matter (%)	3.1	(1.4)	1.4	(0.8)	1.5	(0.8)	****
Nitrogen (ppm)	1632	(779)	823	(438)	939	(413)	****
Phosphorus (ppm)	12.7	(15.3)	13.0	(13.0)	15.8	(23.4)	*
Inputs[4]	1.9	(0.3)	1.5	(0.5)	1.9	(0.4)	****
Sowing rate (kg ha^{-1})	195	(53)	112	(68)	131	(36)	****
Rotation[5]	2.8	(0.8)	2.2	(1.1)	2.3	(1.1)	**
Average grain yield (t ha^{-1})	1.1	(0.6)	1.9	(1.4)	1.5	(0.7)	**
Max. grain yield (t ha^{-1})	1.8	(0.8)	2.9	(1.7)	2.3	(1.1)	***
Average straw yield (t ha^{-1})	1.5	(0.7)	1.3	(0.7)	1.3	(0.8)	*
Max. straw yield (t ha^{-1})	2.3	(1.6)	2.2	(1.2)	1.8	(1.2)	*
Crop growth duration (days)	216	(25)	205	(33)	201	(26)	*
Spikes m^{-2} (-)	115	(39)	109	(74)	138	(67)	*
Seeds per spike (-)	27.8	(6.4)	31.3	(4.6)	27.0	(4.3)	**
Spike weight (g)	1.3	(0.4)	1.1	(0.3)	1.0	(0.3)	*
Thousand kernel weight (g)	45.0	(4.9)	35.9	(6.2)	37.7	(7.0)	****

(+): 1 = Symbols used for texture: 1 = sand, 2 = sandy loam, 3 = loam, 4 = clayloam, 5 = clay.
2 = Symbols used for cracking: 1 = no cracking, 2 = cracking.
3 = Stoniness is expressed as percentage soil cover.
4 = Inputs considered are: N and P fertilizer manure, fungicides, pesticides and herbicides. Scale: 1 = no inputs used, 2 = one or more types of input used.
5 = To quantify the rotation-schemes, the following symbols have been used: 1 = cereals + fallow, 2 = cereals only, 3 = cereals + legumes, 4 = cereals + legumes + other crops.

****: $0 < p \leq 0.001$
***: $0.001 < p \leq 0.005$
**: $0.005 < p \leq 0.05$
*: $0.05 < p$

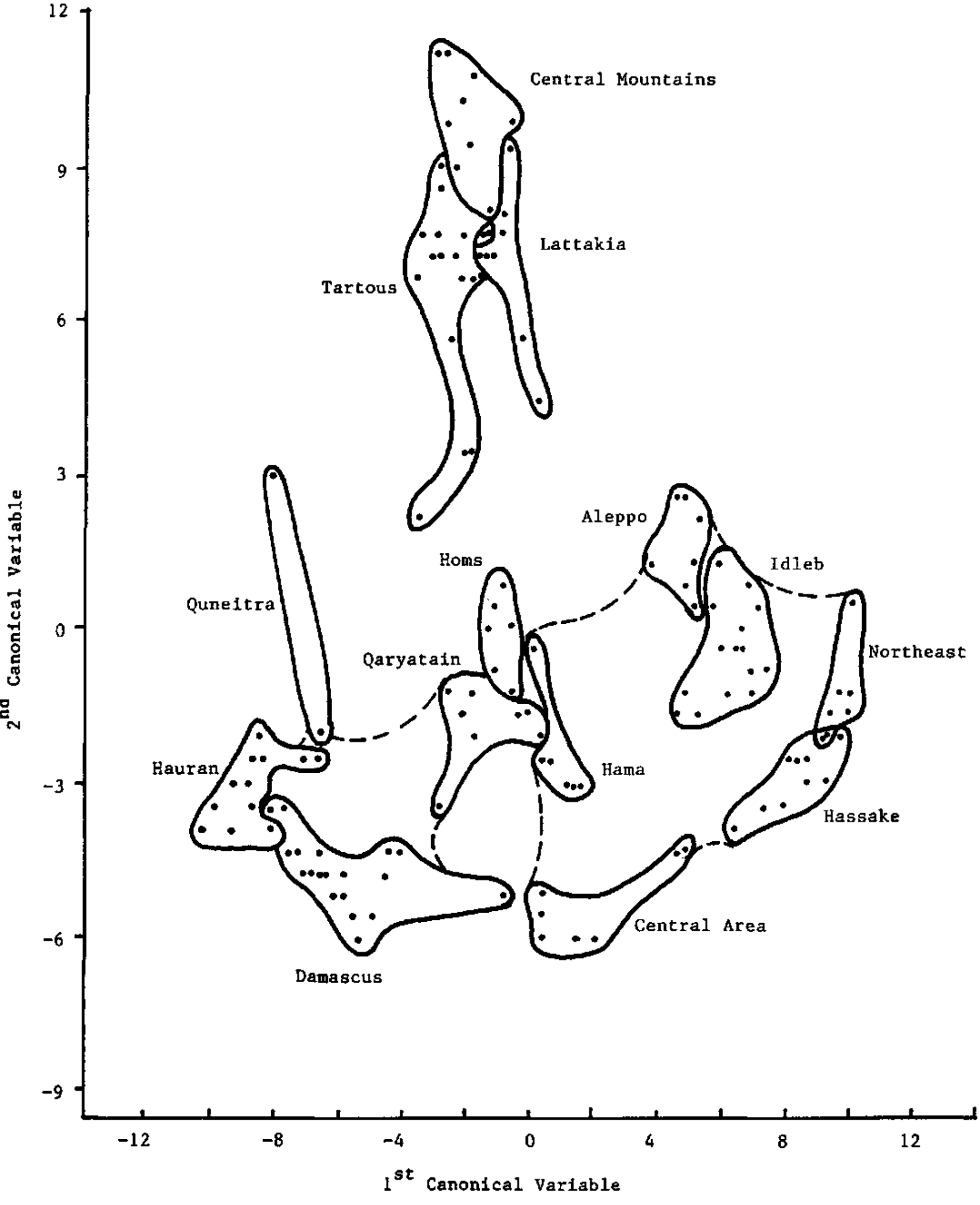


Figure 3.2. Collection sites, constituting 14 regions, plotted against the first two canonical faviables formed in Stepwise Discriminant Analysis.

hairiness. The spike density classes distinguished were intermediate, dense, and very dense, representing the number of spikelets per cm (1.75 - 2.75, 2.75 - 3.50 (- 3.75), and (3.50 -) 3.75 - 5.00, respectively). Spikelet attitude was expressed as the angle between rachis and spikelet. Three angles were distinguished: 45°, 30°, and very acute, with the spikelets almost parallel to the rachis. If discriminating, other characters were observed: kernel colour, kernel shape, spike shape, stem width and stem solidness.

Farmers sometimes gave landraces double names (e.g. Baladi Bayadi, Suweidi Abassieh). In these cases, the first name was considered an indication of the relevant landrace group, and the second name describing an inherent character, an area of cultivation or another subdivision to which no further attention was paid.

3.3 Results

3.3.1 Agro-ecological characterization

K-means clustering on the basis of daylength amplitude, annual precipitation and maximum and minimum annual monthly temperatures of all 166 collection sites resulted initially in three regions: a) the mountainous western part of the country, b) the eastern part of the province of Homs, together with southern areas (Damascus, Sweida, Dara' and Quneitra), and c) the remaining inland areas in the north, centre and east. For convenience, the regions will be referred to as "West", "South", and "Centre/North", respectively. In the next step, each of the regions was further subdivided, as presented in Figures 3.1 and 3.2. The sites were thus clustered into 14 regions, each of limited size. At that stage, the clustering process was stopped, because a large number of small regions, each one comprising of only a few sites, would complicate rather than simplify the analysis.

The relative importance of the clustering variables in each step is indicated in Table 3.2 by their univariate F-values. In the first step, which divides Syria into the three major regions, rainfall is the most influential variable, followed by daylength amplitude and minimum temperature. However, if each regions is subdivided, rainfall would lose importance. Clustering the collection sites in "West" is strongly based on maximum temperature, closely followed by minimum temperature, whereas in "South" daylength amplitude is the most important variable, followed by rainfall. In "Centre/North" maximum temperature again dominates clustering.

Table 3.2. The univariate F-values of the clustering variables in the course of the clustering process. For each step, the relatively most important variable is printed in bold.

	Step *			
Variable	1	2a	2b	2c
Daylength amplitude	265	15	**94**	82
Rainfall	**380**	29	42	45
Max. temperature	28	**37**	9	**188**
Min. temperature	112	33	27	40

* : Step 1 = clustering of all Syrian sites, step 2a = clustering of western sites, step 2b = clustering of southern sites, step 2c = clustering of central sites.

The consistency of the 14 clusters was tested through spanning tree construction. The tree diagram, starting with 166 branches merging one by one, and therefore not presented here, showed in general the same picture as the K-means clustering, which started from the other end. Ideally, the sites belonging to one cluster would have combined before the 14 main branches merge in two steps. The tree diagram was not completely consistent in this, but parallels with the clustering appeared clear enough to confirm the consistency of the K-means clustering.

SDA resulted in four canonical variables, of which the first two accounted for 93% of the total variation (Table 3.3). The first canonical variable was related to daylength and maximum temperature and the second to annual rainfall and maximum and minimum temperature. Plotting the first two canonical variables (Figure 3.2) yielded a picture in which geographical patterns could be recognized. Latitude, via daylength amplitude, dominantly determined the position on the X-axis. Since the isohyets in most collection areas run parallel to the longitude, the latter influenced the position on the Y-axis. The group formed through clustering appeared with only minor overlap.

Table 3.3. Correlation coefficients between the canonical and the dependent variables and the cumulative proportion of the total dispersion for each canonical variable.

Canonical variable	Correlation coefficient				Cumulative dispersion(%)
	Daylength amplitude	Rainfall	Maximum temperature	Minimum temperature	
1	0.98*	-0.04	0.57*	-0.19*	56
2	0.22*	0.98*	-0.78*	0.72*	93
3	-0.03	0.11	-0.14	-0.66*	98
4	-0.003	0.19*	0.24*	0.12	100

*: Significant at $p \leq 0.01$

"West", "South", and "Centre/North" clusters could be defined on the basis of Table 3.1, where cluster means of these groups are given for a set of 25 climatic, ecological and agronomic variables. All the climatic variables had significantly different mean values. In "West", annual precipitation was high, combined with relatively warm winters, cool summers, and low potential evapotranspiration. Mean altitude was low, due to the collection sites near to the sea. "South" was characterized by a short daylength amplitude, low rainfall, mild winters, and moderately high summer temperatures and evaporation. In "Centre/North", maximum temperature and evaporation reached their highest values, while annual rainfall was slightly higher than in "South" owing to the relatively high values for Aleppo and Hassake.

"South" and "Centre/North" had similar soil parameters, whereas "West" showed relatively high values of organic matter and nitrogen contents. In "South", input use was limited, and sowing rate was lowest. "West" had the highest sowing rate and the most diversified rotation scheme, which was narrowest in "South".

Average and maximum grain yields were highest in "South", average and maximum straw yield in "West", where the crop growth duration was longest. The yield components did not show a consistent pattern.

Table 3.4. Percentage of Triticum aestivum plants in T. durum landrace populations; the individual observations and mean value are given per agro-ecological region.

Agro-ecological region	Percentage of T. aestivum per population+	Percentage of T. aestivum mean value
1a Lattakia	2, 9*0	0.2
1b Central Mountains	52, 50, 46, 2*2, 0	25.3
1c Tartous	54, 30, 28, 20, 12, 6, 4, 3*0	15.4
2a Aleppo	2, 6*0	0.3
2b Idleb	8, 2, 0	3.3
2c Hama	0	0.0
2d Central Area	13*0	0.0
2e Hassake	3*0	0.0
2f Northeast	28, 18, 8, 4*0	7.7
3a Homs	2*2, 2*0	1.0
3b Qaryatain	36, 4*0	7.2
3c Damascus	24, 12, 8, 3*6, 2*0	6.2
3d Quneitra	6	6.0
3e Hauran	14, 2*0	4.7

+ : 9*0 = 9 fields without T. aestivum plants
3*6 = 3 fields with 6% T. aestivum plants

3.3.2 Morphological characterization

In the mountainous area along the Meditteranean several populations were collected that were mixtures of T. durum and T. aestivum (Table 3.4). Landrace populations collected in other provinces generally showed much lower frequencies of species mixutures, although high impurities (more than 8%) were occasionally found. In Table 3.5, the proportion of bread wheat plants is given per landrace group. Baladi landraces in particular comprised high amounts of bread wheat plants, which corresponded with the high percentage for the Tartous region.

A uniformly solid stem was observed only once in the case of Sheirieh. In the other landraces the stem was generally solid just below the spike,

Table 3.5. Comparative morphology and distribution of Syrian durum wheat landraces groups.

Landrace groups	Spike[(1)] density	Spikelet attitude	Glume[(2)] hairiness	Glume[(3)] colour	Lemma[(3)] colour	Awn[(3)] colour	Other[(3)] characters	% bread wheat
Haurani	v. dense	45°	gl	y-1b	y	y	-	4.6
Halabi	v. dense	45°	gl	y	y	y	-	0.0
Baladi	int.- v. dense	45°-0°	gl, pb	ly-y; po. black tips + nerves	y; po. bl tips	y-p. bl	-	22.4
Bayadi*(a)	dense	0°	gl, pb	ly	ly	ly	kernels ly	0.4
(b)	dense	30°	gl	ly-y; po. bl tips	ly-y	y; po. p. bl	kernels lb	
Sweidi	int.-dense	30°	gl	lb; bl. tips	lb; po. bl tips	p. bl	-	3.5
Shihani	int.-dense	30°	gl, pb	ly-lb; po. bl tips	y; po. bl tips	b-p. bl	-	9.0
Sin Al Jamal	int.	0°	pb	ly; po. bl tips	ly-y	lb-b	kernels long & slender; spike bowed	0.0
Saglouweh	v. dense	30°	pb	ly-y	ly	y	-	0.0
Juda	dense	30°	pb	ly-y	ly	p. bl	-	0.0
Shamieh	dense	30°-0°	gl	ly; po. bl tips	ly	p. bl	kernels ly; large spike; thick stem	0.0

Nabi Jamal	dense	30°	pb	ly; po. bl tips	ly	p. bl	-	0.0
Abassieh	dense	30°	gl	y-lb; po. bl tips	y-lb	y, bl	-	0.0
Mousseirieh	int.	30°	gl	y; bl tips	y; bl tips	p. bl	-	0.0
Sheirieh	int.-dense	0°	gl	ly	ly-y	y	solid stem	4.0
Surieh	int.	30°	gl, pb	y-lb, po. bl tips + nerves	y-lb, po. bl tips + nerves	y-p. bl	-	0.0
Tounsieh	dense	30°	gl	y-lb, po. bl tips	y-lb; lb patches	p. bl	-	0.0
Haririeh	dense	30°	gl	y-lb; po. bl tips	y-lb; lb patches	p. bl	-	0.0
Harari	dense	30°	gl	y; po. bl tips	y; lb patches	p. bl	-	0.0
Ahmar	int.-dense	30°	gl	y-lb; po. bl tips	y-lb	y-p. bl	kernels dark reddish	0.0

(1): v. = very, int. = intermediate.
(2): gl = glabrous; pb = pubescent.
(3): ly = light yellow; y = yellow; lb = lightbrown; b = brown; bl = black; po. bl tips = possibly black tips; p. bl = partly (1/2-3/4) black coloured.
* : two groups are distinguished; glume hairiness and % bread wheat combined.

but hollow further down. Stem wall thickness in the lower half of the stem varied considerably, both within and among populations.

Spike density and spikelet attitude were interrelated: angles of 45^{o} occurred in combination with very dense spikes, angles of 30^{o} with all density classes - although mainly with dense spikes, and a very acute angle coincided generally with intermediate spike density.

Glume, lemma and awn colour were a highly variable, both within and among landrace groups. Two basic colours were found: yellow and brown to black. Glumes and lemmas varied from light yellow to light brown, and could possess black tips and blackish nerves. Awns were either completely (light) yellow, or (light) yellow only at the terminal part, with a brown or black colouration at the base.

Within the landrace groups of Bayadi, Shihani and Surieh both plants with glabrous glumes and plants with pubescent glumes were observed. The other landrace groups were characterized by only one form of glume hairiness.

Kernels were yellow, except in the cases of Bayadi (partly yellow, partly light yellow), Shamieh (light yellow) and Ahmar (reddish; ahmar = red in Arabic).

Morphologically, the Haurani and Halabi groups (from Hauran and Aleppo region, in Arabic, respectively) appeared to belong to the same type of landrace, which was also indicated by the farmers, who sometimes combined both names. Only the suggested geographical origins differed.

The variation in spike density was a clear first character to differentiate, since it dominated the visual impression of a landrace. The Haurani/ Halabi landraces were predominantly characterized by very dense spikes and yellow to light brown colouration of the glume, lemma and awn.

Baladi (from balad = locality, native to in Arabic) showed a wide range of forms, and was difficult to describe accurately, and gave the impression that many landraces may be called Baladi, implying that this landrace group may actually comprise more than just one group.

Most other landraces had an intermediately dense to dense spike, and had to be differentiated on the basis of other characteristics. Bayadi (from abiad = white in Arabic) landraces could be divided into two groups on the basis of spike type: very acute angles or 30^{o} angles, the latter group tending to be darker. Sweidi (from aswad = black in Arabic) was easily recognizable because of the completely brown or black colouration of the entire spike, in contrast to Shihani, which was only partly black. Sin Al Jamal (= tooth of the camel in Arabic) was characterized by a long and slender kernel in combination with a long, bowed and slender spike. Shamieh could be uniquely characterized by its broad stem, and Surieh by its reddish seeds.

Table 3.6. Number of collected populations (in brackets) per agro-ecological region, per landrace group.

Landrace group	Number of accessions per region
Haurani	Damascus (23), Hauran (16), Hassake (6), Northeast (5), Qaryatain (4), Quneitra (2), Aleppo (2), Hama (1), Homs (1)
Halabi	Hassake (4)
Baladi	Tartous (13), Aleppo (8), Central Mountains (6), Qaryatain (4), Hama (1), Damascus (1)
Bayadi	Palmyra (6), Hama (4), Homs (4), Qaryatain (2), Aleppo (2), Tartous (1), Hassake (1)
Suweidi	Idleb (7), Lattakia (4), Central Mountains (3), Tartous (1), Homs (1)
Shihani	Hassake (6), Northeast (5), Palmyra (1)
Sin Al Jamal	Hassake (3), Northeast (2)
Saglouweh	Palmyra (1)
Juda	Palmyra (1)
Nabi Jamal	Palmyra (1)
Mousseirieh	Palmyra (1)
Sheirieh	Tartous (1)
Abassieh	Tartous (1)
Shamieh	Idleb (2)
Hamari	Aleppo (4), Tartous (2), Idleb (1), Hama (1), Homs (1), Palmyra (1)
Zaraa	Damascus (1)
Kendahri	Northeast (1)
Haririeh	Lattakia (2)
Tounsieh	Lattakia (1), Tartous (1)
Ahmar	Lattakia (1)
Surieh	Lattakia (3), Central Mountains (2), Tartous (1)
Hredieh	Lattakia (1)
Harari	Lattakia (1)

Table 3.6 lists the principal regions of geographical distribution, and in Appendix I, distribution of all encountered landrace groups is mapped. Haurani was the most widespread landrace, both in number of populations and in distribution. It was collected in most durum wheat production regions, in the Hauran region itself and in Damascus region

at a high frequency. Baladi and Bayadi were widespread as well, with concentrations in the regions of Tartous, Central Mountains and Aleppo, and in the regions of Homs, Hama and Palmyra, respectively. All other landraces were regionally concentrated. Some were cultivated in rather extended areas, such as Hamari, while others were limited to a much smaller region, such as Sin Al Jamal. Surprisingly, Halabi was not found in the province of Aleppo, but was concentrated in the east. An explanation may be that in Aleppo this group is called "Baladi", since the Baladi landraces in this region are all of the Haurani/Halabi type.

3.4 Discussion

3.4.1 Agro-ecological characterization

Dividing the regions of collection helped define sub-regions with more or less uniform climatic conditions. Although high homogeneity for all characteristics could not be expected, since variation was minimized in a multidimensional space, the majority of mean values differed significantly (Table 3.1). The minimization of within-group variation was confirmed by SDA, which separated regions by formation of two canonical variables. The small inconsistencies between the two analyses can be caused by variation in climatic conditions determined by local factors such as topography, vegetation and the presence of bodies of water.
Differences in agronomic characteristics are of particular interest. In "Centre/North" yields are lower than in "South", in spite of higher rainfall (Table 3.1). Regional durum wheat nurseries (Yau, 1987, 1988, 1989) indicate that as annual rainfall increases from 200 to 500 mm, seed yield also increases. Grain yields were also calculated from the number of seeds per spike and thousand kernel weight of the individual spikes collected and the number of spike-bearing tillers m^{-2} (Tables 3.1 and 3.7). These values differed considerably from farmers' estimates (Table 3.7): in "West", the calculated value is 0.3 t ha^{-1} higher than the estimated value, in "South" 0.7 t ha^{-1} lower, whereas in "Centre/North" they approximately match. It is unlikely that not randomly collecting accounts for the whole difference. This suggests that in "South", the farmers have reported overestimated yield levels.

Straw yields and harvest indexes are biased by harvesting methods:

while in "West" harvesting by hand is a common practice, resulting in low loss of straw, in other parts harvesting is mostly done by machine, which causes loss of the stubble. Consequently, straw yield is lower and harvest index higher.

Table 3.7. Grain, straw and total yield, and harvest index for the three subregions, under favourable and average growing conditions.

	West		South		Centre/North	
Favourable						
Grain yield (t ha^{-1})	1.8		2.9		2.3	
Straw yield (t ha^{-1})	2.3		2.2		1.8	
Total yield (t ha^{-1})	4.1		5.1		4.1	
Harvest index	0.44		0.57		0.56	
Average						
Grain yield (t ha^{-1})	1.1	(1.4)*	1.9	(1.2)*	1.5	(1.4)*
Straw yield (t ha^{-1})	1.5		1.3		1.3	
Total yield (t ha^{-1})	2.6		3.2		2.8	
Harvest index	0.42		0.59		0.54	

* = normal grain yield as calculated from observed yield components.

Therefore, it is questionable whether under favourable growing conditions, performance is best in "South", where the highest grain and total yield and harvest index are reached (Table 3.7). In "West" and "Centre/North", total yields are equal under favourable conditions, but grain yield in "West" is considerably lower, illustrating the tendency of landraces to produce more straw rather than a higher grain weight under high rainfall conditions.

Noteworthy differences were found between seed rate (in kernels m^{-2}) and number of spikes m^{-2}. For "West", "South" and "Centre/North", these are 433 and 115, 312 and 109, and 347 and 138, respectively. Evidently, emergence and crop establishment are poor. Frost and drought at early development stages could account for this, in combination with the commonly used split ridge sowing technique and bird damage.

Yield trials, with focus on the interaction between crop and climate characteristics, are necessary for clearer interpretation of observed trends. Then also the relevance of the demonstrated clustering to crop characterization on basis of field evaluations can be investigated, if clustering on basis of agronomic and physiological traits has parallels in the clustering of environments.

3.4.2 Morphological characterization

Durum wheat landraces in Syria are threatened with extinction (van Slageren et al., 1989). The dangers of disappearance of germplasm have been pointed out repeatedly (Bennett, 1965; Dahlberg, 1983; Feldman & Sears, 1981; Mooney, 1979), and it is therefore important to ensure the preservation of the Syrian T. durum genepool, which may hold yet unknown genes and gene complexes.

Large proportions of T. aestivum were found in T. durum populations only in the regions of Tartous and Central Mountains. The lower proportions inland could be related to the lower annual rainfall, which favours the better adapted durum wheat. However, the high purity of the landraces collected in Lattakia province, where annual rainfall is also high, indicates that other factors play a role. Impurity is apparently accepted and desired by farmers, who otherwise would produce a purer crop. Human diet preferences and differential disease resistance may be of influence.

The term "landrace group" was used by Zeven (1986) for landraces derived from one another or sharing a common origin. In Western Europe, it was possible to group landraces with different names, but in Syria it is still not known how landraces of different names are related, and therefore only landraces carrying the same name were grouped. This empirical division was thus based purely on identification by farmers.

Mac Key (1966) noted the continuity of morphological traits among T. turgidum convarieties, which has a parallel in the morphological variation among the T. durum landrace groups, to such an extent that clear distinction between groups could not always be made. The grouping should therefore merely be considered as a systematical description of visable variation.

Depending on environmental influence, the expression of characteristics in the region of origin may differ from that in the evaluation site, and therefore the descriptions may not be completely accurate in giving the morphology of landraces in their original habitat.

Geographical distribution patterns can be recognized within the total germplasm collection of Syrian durum wheat landraces. Only three landrace groups, viz. Haurani/Halabi, Baladi and Bayadi, were really widely distributed, whereas others, although found outside the principal regions of collection, should not be considered as such, as they were encountered only occasionally. The reason for the success of Haurani can only be speculated upon. Possibly, the intermediate climatic conditions of the supposed region of origin, Hauran, gave the landrace a relatively easy access to other climatic conditions. It should be noted that Haurani is not cultivated in the western part of the country. Apparently, the landrace had a competitive disadvantage that prevented its spread into mountainous areas.

Besides regional diversification, genetic diversification is found in the heterogeneous nature of the landraces and in the cultivation of different landraces per region or village. Apart from the Hauran and Quneitra region, where only Haurani landraces were collected, three or more landrace groups were sampled per agro-ecological region.

Chapter 4

PATTERNS OF VARIATION

Abstract

Phenotypic variation components were estimated with respect to days to heading, flag leaf length and width, plant height, awn and spike length, awn and spike colour, spikelets per spike and seed shrivelling of 84 Syrian durum wheat landrace populations. Multivariate patterns of variation were established through principal component analysis to describe relationships between landrace groups and regions of collection. Agro-ecological site characteristics and plant traits were compared with respect to patterns of geographical variation. Grouping on the basis of landrace groups proved more discriminative than on the basis of regions of origin. Landraces originating from sites characterized by favourable growth conditions tended to be later in heading and to have longer spikes with longer awns but with less spikelets. The observed relation between favourable growth conditions in the region of origin and smaller flag leaves may be caused by genotype x environment interaction.

Among populations variation was high, and amounted to 96% of the total variation, whereas the remnant 4% was contributed to differences within populations and among lines. Variation among landrace groups and among regions was calculated as 79% and 75% of total variation, respectively.

4.1 Introduction

Rainfed agriculture in West Asia and North Africa is influenced by variation in environmental conditions among localities and years, such as rainfall, summer and winter temperature, nutrient level, diseases, pests and management practices (Ceccarelli et al., 1987b). This restricts the use of modern varieties that require inputs such as fertilizer and supplementary irrigation to exploit fully their genetic potential. Landraces, although moderate in maximum yield, generally offer a more stable yield over a wide range of environmental conditions (Hawkes, 1983). Since domestication, landraces of a particular crop have been cultivated in various agro-ecological niches by farmers who maintained their own seed and applied so-called "unconscious selection" (Harlan et al., 1973; Heiser, 1988). This process has resulted in a wide variation of plant characteristics, among and within locations, which are balanced in such a way that environmental pressures are generally not catastrophic to the crop and do not lead to great loss of harvest. The variable genetic composition of landraces is an important factor in stress tolerances, which can be utilized by breeding programs aimed at the production of varieties suitable to areas where biotic and abiotic stress conditions are regularly encountered (Ceccarelli et al., 1987a; Nachit et al., 1988).

Breeding programs often face the problem of evaluating large germplasm collections to identify entries carrying promising traits as potential parents. It may be more efficient to evaluate a representative sample of a collection at a number of sites with distinct environmental characteristics, possibly over a number of years, than to evaluate the entire collection in a single environment. However, dividing accessions into groups that represent diverse backgrounds requires detailed knowledge of the original environments and diversity pattern of the material under evaluation. Also, Brown (1989) argues that carefully chosen subsamples of a species will contain more genetic diversity than randomly chosen subsamples.

This study describes phenotypic variation components for a collection of durum wheat, and relates variation in plant and environmental characteristics among populations, among landrace groups and among regions of collection.

4.2 Materials and methods

Germplasm collecting missions for landraces of durum wheat [*Triticum turgidum* L. var. *durum* (Desf.) MK] in 1987 and 1988 in the Syrian Arab Republic (van Slageren et al., 1989) yielded 59 and 25 landrace populations, respectively. These had most probably evolved at or near the site of collection, as farmers had declared that the seed was not recently or in the past obtained from other regions. The collection sites represented a wide range of agro-ecological areas. Four climatic characters, viz. maximum and minimum annual monthly temperature, annual precipitation and the difference between the longest and shortest day length in the course of a year, were used to cluster collection sites into geographical regions that were relatively stable for these characters as compared to differences between regions. The regions were described for a set of climatic, ecological and agronomic characteristics, and landrace groups as distinguished by farmers, who identify them with different names, were morphologically described (Chapter 3).

Each accession was collected both as a bulk sample and as randomly selected spikes. Bulk samples were multiplied for agronomic evaluation, and the single head progenies were evaluated for variation components.

After collection, the seed samples were fumigated with aluminum phosphide (6 g m^{-3} Phostoxin) to control insect infestation, and before sowing the threshed seeds were treated against common bunt (*Tilletia caries* and *T. foetida*) by application of Vitavax 200 (2.5 g carboxine and thiram per kg seed). The crop was sprayed at regular intervals with Bayfidan (250 g Triadimenol l^{-1}, 0.5 l ha^{-1}), a broad spectrum fungicide.

Fifty spikes as single head progenies were sown in a randomized complete block (RCB) design with one landrace population per block. Since the number of seeds per collected spike was in most cases small, no replications were possible. The 1987 collection was evaluated in the 1987/88 season, the 1988 collection in the 1988/89 season. A local landrace, Haurani, was used as check, with one and three lines added at random per evaluated population, in 1988 and 1989, respectively.

Evaluation fields were situated at the farm of ICARDA's headquarters near Tel Hadya, Syria, located at 36°01' N and 36°56' E, and 284 m elevation. The fields had not received fertilizer for some years, and contained at sowing in november 1987 0.89% organic matter, 590 ppm N and 2.4 ppm P, and at sowing in november 1988 0.88% organic matter, 677 ppm N and 5.2 ppm P. Total annual precipitation amounted to 504 mm and 234 mm, respectively, and seasonal minimum air temperature was reached at -7.4 °C and -9.7 °C, respectively.

The number of days from emergence to heading was recorded for all lines. After flowering, observations were made on 25 single head progenies and all check lines for flag leaf length and width on five plants per line, and for plant height on three plants per line. A higher number of observations on the flag leaf was considered necessary because of its greater variation than plant height. After maturity, five spikes of each line were harvested at random measured in the laboratory for awn and spike length, awn and spike colour, number of spikelets per spike and degree of seed shrivelling. In Table 4.1 the scale used to quantify spike characters is specified. Awn length (mm) was measured from the top grain to the termination of the longest awn, spike length (mm) from the top grain to the deepest point of the collar, and the number of spikelets per spike included the lowest, aborted spikelet(s).

Table 4.1. Scale used to quantify spike characters (after Mattatia, 1986; Williams et al., 1988).

Awn colour

1 = yellow, straw colour
3 = tan coloured to light beige-brown
5 = mostly darker brown to reddish
7 = purple to black at the base, lighter tan coloured to yellow distally
9 = dark purple to black

Spike colour

1 = cream-white to yellow (straw colour)
3 = darker, beige to brownish or reddish, tips greenish
5 = spike mottled or patched: tips, margins or other parts of glumes and/or lemmas purple to black, the rest yellow
7 = tips, margins or other parts of glumes and/or lemmas darker purple to grey, the rest beige-brown, reddish or greyish
9 = spike mostly dark purple or black

Seed shrivelling

1 = smooth
3 = slightly shrivelled: only one lateral side, possibly slightly on the other lateral side
5 = fairly shrivelled: on both lateral sides
7 = shrivelled: on both lateral sides and bottom side
9 = very shrivelled, deformed

Bread wheat lines, which were identified in some populations, were excluded. Remaining data on durum wheat lines were analyzed using the BMDP statistical software package (Dixon et al., 1985).

Mean values were calculated for each single head progeny, and subsequently population means were established on basis of the landrace single head progenies. Initial analysis showed that landrace group x year interaction was not significant for all characters except for days to heading ($p = 0.03$), and awn and spike colour ($p \leq 0.01$). Although this cannot be interpreted as pure genotype x year interaction, it was decided to rescale population mean values to comparable 1987/1988 values through Analysis of Covariance (ANCOVA) of landrace group on year, using the check values as covariable. Awn and spike colour which characterized landrace groups and regions represented by only one year were not rescaled. Adjustment of these qualitative characters occasionally led to values below one, which on the scale used would be meaningless. Means per landrace group and per region were calculated.

Calculations on population mean values were first performed. Character association was studied through calculation of correlation coefficients between agro-ecological site characteristics and population means of observed traits, and between population characteristics only. Positive correlation between site and plant characteristics would suggest that variation between populations is related to agro-ecological variation between collection sites. High correlation coefficients between plant characteristics would indicate corresponding patterns of geographical variation in phenotypes (Bekele, 1984), as well as genotypes, if the conclusion of Cheverud (1988), based on animal research, also holds good for plant populations. He concluded that "phenotypic correlations are likely to be fair estimates of their genetic counterparts in many situations". If the heritability is sufficiently high, this assumption is likely to be correct.

Principal Component Analysis (PCA) on basis of rescaled values was used for definition of multivariate patterns of variation among landrace groups and regions of collection.

Secondly, on the basis of line values the coefficient of variation (c.v.) per landrace group and per region was calculated to express the phenotypic variation. Mean values of both collections were taken.

Contribution to phenotypic variation by populations, landrace groups and regions was analyzed with a nested analysis of variance (ANOVA):

1. Populations
   a. landrace groups
      populations within landrace groups
   b. regions
      populations within regions
2. Lines within populations.

Table 4.2. Regions of origin, landrace groups (Chapter 3) and population means for observed traits per population, after rescaling through ANCOVA.

(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)	(11)	(12)	(13)
1	12	1	152.57	22.49	1.65	86.81	109.94	56.18	17.57	1.17	1.27	3.45
4	14	1	148.17	17.92	1.51	85.12	101.18	48.66	18.77	1.00	1.00	1.76
25	14	1	147.70	17.65	1.23	82.76	91.00	50.58	16.55	1.14	1.14	2.00
32	12	1	149.53	20.88	1.75	96.89	106.20	52.22	19.17	1.04	1.04	2.23
40	13	1	152.89	21.81	1.63	91.83	106.41	53.87	16.52	1.01	1.04	3.93
42	12	1	150.13	19.88	1.59	94.87	97.00	55.69	19.32	1.21	1.23	3.41
44	14	1	146.84	19.25	1.41	90.12	97.09	50.08	19.79	1.00	1.00	2.60
51	12	1	147.45	21.94	1.78	103.90	98.37	57.20	20.17	1.15	1.10	3.15
52	12	1	150.98	22.08	1.83	94.61	92.51	50.43	20.31	1.00	1.00	3.94
54	12	1	152.00	21.88	1.54	94.44	125.95	61.85	20.14	1.01	1.09	2.61
56	12	1	147.37	17.69	1.26	83.97	102.35	53.76	17.98	1.00	1.00	1.55
58	12	2	161.71	20.08	1.55	113.11	112.76	83.36	19.10	1.63	1.05	2.08
70	12	1	148.28	21.06	1.69	98.06	103.50	52.07	19.30	1.04	1.04	2.10
72	12	1	149.07	18.64	1.61	80.93	105.65	44.44	17.75	1.12	1.04	1.60
76	12	1	148.61	18.02	1.48	85.12	94.79	50.41	19.10	1.00	1.01	3.13
94	7	1	149.98	22.55	1.85	94.48	105.64	55.55	19.44	1.00	1.05	2.32
95	7	4	151.43	22.06	1.31	98.86	127.51	68.48	15.68	6.92	2.05	1.43
97	7	1	158.85	21.88	1.56	108.27	96.48	64.35	21.90	1.72	4.89	4.56
99	7	3	158.35	20.93	1.70	118.19	130.56	80.37	20.25	3.29	1.34	2.50
100	7	9	152.77	25.05	1.59	125.09	132.95	80.42	20.00	5.30	2.03	3.73
101	7	10	152.40	23.46	1.34	111.58	135.99	68.70	13.83	6.86	4.72	2.81
102	7	11	148.30	19.16	1.64	71.68	85.99	57.00	15.33	2.68	1.06	1.31
103	7	12	152.30	22.76	1.34	90.58	130.29	67.30	13.33	6.69	3.29	2.41
117	9	1	152.24	18.37	1.43	79.76	104.42	49.59	17.46	1.02	1.05	3.30
119	8	4	153.50	22.66	1.36	93.24	126.72	77.60	17.38	5.94	2.87	2.00
127	8	4	150.72	24.41	1.54	108.53	118.40	83.52	17.26	6.04	2.52	3.35
128	8	9	152.93	18.61	1.25	98.64	-	-	-	-	-	-
135	8	4	150.65	25.94	1.58	115.04	117.46	87.09	18.08	5.76	2.61	4.44
136	8	1	147.45	21.49	1.62	105.16	102.10	47.59	16.63	1.49	1.45	2.98
163	8	1	153.45	22.35	1.82	106.17	99.46	56.78	19.15	1.00	1.02	3.32
167	8	4	152.29	24.93	1.41	107.90	136.25	77.29	18.18	6.74	4.41	3.14
172	9	1	148.73	18.62	1.43	90.50	94.63	49.47	18.92	1.00	1.06	3.48
174	9	4	150.79	25.48	1.48	110.36	130.71	78.52	16.41	6.93	3.61	2.28
203	5	3	149.99	19.85	1.57	79.79	-	-	-	-	-	-
205	5	2	147.84	19.05	1.55	93.58	90.28	53.48	18.54	1.00	1.00	4.47
208	4	6	151.02	23.27	1.72	105.44	109.20	67.27	17.36	3.92	2.94	2.27
209	4	6	153.30	20.86	1.44	93.34	131.04	74.75	17.42	7.10	4.36	2.37
218	5	2	148.76	20.72	1.59	101.80	98.16	56.91	19.24	1.29	1.92	3.30
220	5	5	149.42	19.51	1.43	78.82	85.29	47.07	17.91	2.51	2.87	4.35
222	5	5	147.89	17.27	1.23	74.52	84.68	45.33	19.06	1.95	3.99	3.97
224	5	2	149.61	21.47	1.66	106.57	103.16	53.15	18.10	1.00	1.00	3.84
236	4	6	153.15	16.69	1.44	103.89	115.55	51.52	19.04	7.01	4.44	3.28
245	10	1	161.02	17.83	1.43	75.51	-	-	-	-	-	-
246	10	6	153.28	21.97	1.6	102.60	114.27	65.59	18.56	7.05	6.79	3.20
247	10	3	144.43	19.48	1.46	98.39	90.56	43.52	18.12	2.68	2.68	2.98
250	3	5	154.52	20.26	1.52	93.17	106.18	64.70	17.59	5.90	4.23	3.16
251	3	13	155.30	18.66	1.24	84.78	105.79	65.90	14.83	1.59	1.23	3.11
255	6	3	147.49	22.59	1.78	99.37	97.12	53.11	18.74	1.00	1.02	3.12

269	10	3	152.95	17.79	1.20	81.87	88.35	58.99	16.42	1.22	1.13	2.80
270	3	2	155.28	18.99	1.08	80.10	126.09	79.79	17.36	1.45	1.03	3.24
272	2	2	153.47	16.88	1.16	85.95	97.56	71.28	16.00	1.35	1.17	2.34
274	2	2	156.05	19.66	1.34	89.69	119.51	72.54	16.87	1.83	1.55	3.43
275	2	2	154.67	21.86	1.24	98.58	104.86	92.01	17.49	3.37	3.20	3.70
276	2	2	156.15	18.66	1.19	88.70	119.81	81.23	17.70	1.32	1.19	2.68
277	3	2	152.27	19.14	1.29	107.51	119.45	76.97	16.91	1.46	1.46	3.05
283	3	2	155.37	17.89	1.06	82.09	112.99	79.83	18.64	1.75	1.40	4.04
286	3	2	152.10	21.54	1.29	104.19	105.74	69.65	19.06	1.12	1.14	3.20
287	3	2	156.94	18.34	1.13	86.16	121.39	81.64	19.82	1.67	1.54	4.13
290	3	2	152.79	20.01	1.27	109.41	101.44	73.16	17.03	1.00	1.00	4.55
300	7	3	151.13	20.10	1.58	96.11	102.50	61.78	16.29	1.12	1.05	2.21
301	7	3	150.53	18.78	1.32	97.09	96.79	58.51	18.68	1.78	2.11	3.09
319	7	3	150.53	19.78	1.46	92.61	100.18	57.94	18.09	1.00	2.18	3.78
329	7	3	150.73	20.50	1.58	97.62	101.47	57.50	19.15	1.00	1.00	2.38
332	7	3	149.51	20.38	1.58	97.14	105.84	58.79	18.02	1.04	1.04	2.29
335	11	1	149.51	20.50	1.58	90.05	100.63	54.62	17.81	1.00	1.00	2.58
336	11	1	148.15	19.59	1.57	92.58	95.42	52.55	18.90	1.00	2.44	2.99
342	11	3	151.41	21.21	1.72	93.58	103.11	59.44	19.88	1.01	1.60	3.35
348	11	1	150.15	20.52	1.56	92.97	91.94	52.35	19.68	1.00	1.94	3.10
351	11	2	158.35	14.71	1.38	67.69	114.59	74.73	18.44	3.21	3.09	3.59
357	1	6	151.25	17.94	1.44	91.09	109.94	76.65	17.71	6.30	4.74	3.27
358	1	14	156.50	22.64	1.56	96.12	126.51	65.00	20.37	6.16	4.18	1.89
362	1	8	156.80	21.44	1.65	99.60	122.35	68.70	18.09	5.64	4.43	2.56
364	1	8	158.49	20.91	1.54	93.13	124.03	63.10	19.29	5.76	4.78	2.63
369	1	6	152.19	21.50	1.47	100.14	120.06	61.32	17.79	5.08	3.33	2.22
381	3	2	151.85	21.91	1.31	97.01	109.42	71.86	17.31	6.48	4.77	3.28
385	1	6	154.61	22.65	1.74	98.00	125.38	66.40	18.80	5.66	4.93	2.87
386	1	7	154.85	21.48	1.38	90.22	119.36	72.38	16.64	5.56	3.76	3.01
389	1	7	156.01	20.13	1.32	93.72	113.84	79.63	17.05	2.00	1.79	2.63
393	1	15	157.90	20.94	1.56	99.82	135.41	77.70	21.27	4.30	3.97	2.49
402	2	7	151.84	21.62	1.32	97.68	119.07	75.41	18.25	1.69	4.02	2.90
406	1	7	151.17	21.21	1.24	96.77	117.77	67.52	16.85	3.34	3.58	2.47
410	2	7	153.62	20.84	1.35	95.69	116.91	70.16	17.78	5.48	3.56	2.63
411	3	7	153.11	21.32	1.45	92.29	119.74	73.14	17.00	6.74	4.96	3.38
412	2	2	151.06	19.83	1.19	97.18	113.50	73.06	18.29	3.60	4.04	3.21

Columns:

(1) : ID collection number
(2) : region of origin
(3) : landrace group
(4) : days to heading (d)
(5) : flag leaf length (cm)
(6) : flag leaf width (cm)
(7) : plant height (cm)
(8) : spike length (cm)
(9) : awn length (cm)
(10) : spikelets per spike (-)
(11) : spike colour (-)
(12) : awn colour (-)
(13) : seed shrivelling (-)

Regions of origin:

1 = Lattakia
2 = Central Mountains
3 = Tartous
4 = Aleppo
5 = Idleb
6 = Hama
7 = Central Area
8 = Hassake
9 = Northeast
10 = Homs
11 = Qaryatain
12 = Damascus
13 = Quneitra
14 = Hauran

Landrace groups:

1 = Haurani
2 = Baladi
3 = Bayadi
4 = Shihani
5 = Hamari
6 = Sweidi
7 = Surieh
8 = Haririeh
9 = Nabi Jamal
10 = Mousseirieh
11 = Saglouweh
12 = Juda
13 = Sheirieh
14 = Harami
15 = Ahmar

Table 4.3. Values and coefficients of variation (in brackets) for observed traits per landrace group. Values for 1987 and 1988 collections combined (see text). Mean square experimental error is mean value of both evaluation seasons.

Landrace group	no. populations	time to heading (days)		flag leaf length (cm)		flag leaf width (cm)		plant height (cm)		awn length (mm)	
Haurani	24	149.3	(0.02)	20.2	(0.11)	1.6	(0.16)	91.5	(0.12)	98.9	(0.12)
Baladi	17	153.8	(0.03)	19.6	(0.15)	1.3	(0.17)	96.3	(0.12)	109.5	(0.16)
Bayadi	11	150.7	(0.02)	20.1	(0.12)	1.5	(0.17)	95.7	(0.12)	101.6	(0.11)
Shihani	6	151.4	(0.02)	24.6	(0.13)	1.4	(0.14)	106.2	(0.12)	126.2	(0.14)
Hamari	3	150.3	(0.02)	19.0	(0.15)	1.3	(0.17)	81.6	(0.17)	91.2	(0.19)
Suweidi	7	152.7	(0.01)	20.7	(0.16)	1.6	(0.13)	96.4	(0.11)	117.5	(0.11)
Surieh	6	153.4	(0.02)	21.8	(0.13)	1.4	(0.12)	94.5	(0.10)	117.8	(0.10)
Haririeh	2	157.7	(0.02)	21.8	(0.13)	1.6	(0.14)	96.4	(0.11)	123.2	(0.07)
Nabi Jamal	2	152.8	(0.02)	21.8	(0.19)	1.4	(0.18)	111.6	(0.15)	133.0	(0.15)
Mousseirieh	1	152.4	(0.02)	23.5	(0.11)	1.3	(0.15)	111.6	(0.14)	136.0	(0.08)
Saglouweh	1	148.3	(0.02)	19.2	(0.11)	1.6	(0.13)	71.7	(0.15)	86.0	(0.14)
Juda	1	152.3	(0.01)	22.8	(0.14)	1.3	(0.14)	90.6	(0.10)	130.3	(0.12)
Sheirieh	1	155.3	(0.02)	18.7	(0.26)	1.2	(0.19)	84.8	(0.16)	105.8	(0.19)
Harami	1	156.5	(0.02)	22.6	(0.12)	1.6	(0.10)	96.1	(0.13)	126.5	(0.07)
Ahmar	1	157.9	(0.02)	20.9	(0.09)	1.6	(0.08)	99.8	(0.08)	135.4	(0.07)
Overall mean	84	151.9	(0.03)	20.7	(0.15)	1.5	(0.17)	95.3	(0.13)	109.4	(0.17)
MS error		6.5		3.7		0.03		60.1		83.8	

*: mean value not adjusted.

Landrace group	spike length (mm)		number of spikelets per spike		awn colour		spike colour		seed shrivelling	
Haurani	53.1	(0.14)	18.8	(0.12)	1.1	(0.27)	1.5	(0.64)	2.9	(0.44)
Baladi	73.2	(0.17)	18.0	(0.13)	3.0	(0.71)	2.7	(0.56)	3.4	(0.38)
Bayadi	59.0	(0.18)	18.4	(0.12)	1.6	(0.60)	1.5	(0.61)	2.9	(0.35)
Shihani	78.8	(0.16)	15.4	(0.12)	6.4*	(0.21)	3.0*	(0.50)	2.8	(0.56)
Hamari	51.6	(0.22)	16.5	(0.13)	3.3*	(0.67)	3.7*	(0.47)	3.9	(0.32)
Suweidi	68.2	(0.14)	18.1	(0.13)	6.0	(0.33)	4.5	(0.35)	2.8	(0.43)
Surieh	72.9	(0.15)	19.0	(0.13)	4.2*	(0.64)	3.7*	(0.52)	2.9	(0.42)
Haririeh	65.9	(0.11)	20.4	(0.13)	5.7*	(0.30)	4.6*	(0.26)	2.6	(0.43)
Nabi Jamal	80.4	(0.10)	18.2	(0.11)	5.3*	(0.36)	2.0*	(0.50)	3.7	(0.39)
Mousseirieh	68.7	(0.13)	13.8	(0.14)	6.9*	(0.13)	4.7*	(0.17)	2.8	(0.34)
Saglouweh	57.0	(0.14)	15.3	(0.13)	2.7*	(0.72)	1.1*	(0.26)	1.3	(0.11)
Juda	67.3	(0.16)	13.3	(0.17)	6.7*	(0.17)	3.3*	(0.42)	2.4	(0.35)
Sheirieh	65.9	(0.17)	14.8	(0.18)	1.6*	(1.10)	1.2*	(0.72)	3.1	(0.20)
Harami	65.0	(0.10)	20.4	(0.11)	6.2*	(0.20)	4.2*	(0.30)	1.9	(0.46)
Ahmar	77.7	(0.07)	21.3	(0.12)	4.3*	(0.65)	4.0*	(0.27)	2.5	(0.23)
Ovarall mean	64.1	(0.22)	18.1	(0.14)	3.1	(0.84)	2.6	(0.70)	2.9	(0.45)
MS error	42.8		2.4		0.9		1.3		0.4	

Table 4.4. Values and coefficients of variation (in brackets) for observed traits per region of collection. Values for 1987 and 1988 collections combined (see text). Mean square experimental error is mean value of both evaluation seasons.

Region	no. populations	time to heading (days)		flag leaf length (cm)		flag leaf width (cm)		plant height (cm)		awn length (mm)	
Lattakia	10	156.6	(0.02)	20.5	(0.13)	1.4	(0.15)	97.2	(0.11)	124.2	(0.09)
Central Mountains	7	153.3	(0.02)	20.5	(0.15)	1.3	(0.13)	94.8	(0.11)	111.9	(0.17)
Tartous	10	153.3	(0.02)	20.8	(0.13)	1.3	(0.15)	94.4	(0.13)	112.9	(0.14)
Idleb	3	149.9	(0.01)	18.7	(0.19)	1.6	(0.13)	92.7	(0.14)	114.2	(0.15)
Aleppo	6	147.5	(0.02)	19.8	(0.14)	1.6	(0.16)	91.0	(0.17)	86.8	(0.15)
Hama	1	148.4	(0.02)	22.3	(0.07)	1.8	(0.10)	99.1	(0.08)	99.3	(0.09)
Central Area	13	150.2	(0.02)	21.1	(0.11)	1.5	(0.20)	99.2	(0.12)	107.8	(0.15)
Northeast	7	149.4	(0.02)	22.8	(0.15)	1.8	(0.16)	104.0	(0.12)	113.4	(0.18)
Hassake	3	149.3	(0.02)	20.7	(0.19)	1.5	(0.13)	92.6	(0.17)	107.5	(0.17)
Homs	4	150.0	(0.02)	18.9	(0.15)	1.5	(0.19)	86.1	(0.16)	97.9	(0.16)
Qaryatain	5	151.9	(0.03)	22.0	(0.12)	1.5	(0.14)	93.7	(0.10)	101.0	(0.11)
Damascus	11	149.4	(0.03)	20.2	(0.15)	1.7	(0.16)	92.8	(0.16)	101.6	(0.16)
Quneitra	1	151.6	(0.01)	21.6	(0.09)	1.7	(0.10)	90.2	(0.10)	103.8	(0.08)
Hauran	3	146.3	(0.02)	8.1	(0.10)	1.5	(0.16)	84.3	(0.11)	94.1	(0.11)
Overall mean	84	151.9	(0.03)	20.7	(0.15)	1.5	(0.17)	95.3	(0.13)	109.4	(0.17)
MS error		6.5		3.7		0.03		60.1		83.8	

*: mean value not adjusted.

Region	spike length (mm)		number of spikelets per spike		awn colour		spike colour		seed shrivelling	
Lattakia	73.3	(0.14)	17.8	(0.14)	5.0*	(0.46)	4.0*	(0.39)	2.5	(0.42)
Cental Mountains	75.8	(0.12)	17.6	(0.14)	2.8	(0.76)	2.8	(0.62)	2.9	(0.45)
Tartous	73.0	(0.16)	17.6	(0.13)	4.3	(0.61)	3.2	(0.50)	3.3	(0.32)
Idleb	66.6	(0.15)	18.7	(0.10)	6.0*	(0.41)	3.9*	(0.36)	3.1	(0.42)
Aleppo	46.3	(0.14)	18.7	(0.11)	1.6*	(0.59)	2.1*	(0.72)	3.8	(0.34)
Hama	53.6	(0.08)	18.6	(0.10)	1.0*	(0.00)	1.0*	(0.08)	3.2	(0.36)
Central Area	61.2	(0.16)	18.1	(0.14)	2.0	(0.58)	2.0	(0.69)	2.7	(0.47)
Northeast	66.4	(0.26)	17.7	(0.12)	4.4*	(0.62)	2.4*	(0.63)	3.2	(0.45)
Hassake	54.1	(0.28)	17.3	(0.11)	3.0*	(0.94)	1.9*	(0.75)	2.9	(0.52)
Homs	55.4	(0.21)	17.9	(0.15)	3.7*	(0.69)	3.6*	(0.69)	3.2	(0.34)
Qaryatain	62.2	(0.16)	19.3	(0.12)	1.3*	(0.90)	1.9*	(0.60)	3.2	(0.31)
Damascus	50.5	(0.24)	18.7	(0.14)	1.2*	(0.74)	1.1*	(0.33)	2.5	(0.61)
Quneitra	48.1	(0.13)	16.0	(0.14)	1.0*	(0.07)	1.0*	(0.12)	3.2	(0.26)
Hauran	43.9	(0.12)	17.9	(0.12)	1.0*	(0.49)	1.0*	(0.36)	2.0	(0.54)
Overall mean	64.1	(0.22)	18.1	(0.14)	3.1	(0.84)	2.6	(0.70)	2.9	(0.45)
MS error	42.8		2.4		0.9		1.3		0.4	

Table 4.5. Correlation coefficients between site and plant characteristics. Only correlation coefficients with $p \leq 0.05$ are given.

	days to heading	flag leaf length	flag leaf width	plant height	awn length	spike length	spike-lets per spike	awn colour	spike colour	seed shriv-elling
daylength amplitude (h)		0.23*		0.24*		0.27*		0.39**	0.32**	0.22*
altitude (m)				-0.25*	-0.28*	-0.28*	0.22*	-0.42**	-0.35**	
rainfall (mm $year^{-1}$)	0.38**		-0.52**		0.30**	0.49**			0.32**	
max. temperature (°C)	-0.32**	0.24*	0.35**	0.23*		-0.26*				
min. temperature (°C)	0.30**		-0.46**		0.23*	0.40**				
potential evaporation (mm)	-0.23*	0.30**	0.36**	0.28**						
stoniness (%)	0.32**		-0.37**			0.25*				
surface soil depth (cm)				0.27*						
organic matter (%)	0.31**		-0.57**			0.46**	-0.29*			
nitrogen (ppm)	0.28*		-0.57**			0.44**	-0.28*			
phosphorus (ppm)		-0.27*								
inputs	0.27*		-0.31**		0.32**	0.35**	-0.26*	0.44**	0.38**	
sowing rate (kg ha^{-1})	0.25*		-0.39**		0.27*	0.39**	-0.25*	0.37**	0.43**	
average grain yield (ton ha^{-1})			0.26*				0.31*			-0.35**
max. grain yield (ton ha^{-1})									-0.35**	-0.38**
max. straw yield (ton ha^{-1})									-0.28*	

*: $0.01 < p \leq 0.05$
**: $p \leq 0.01$

Table 4.6. Correlation coefficients between plant characteristics. Only correlation coefficients with $p < 0.05$ are given.

	days to heading	flag leaf length	flag leaf width	plant height	awn length	spike length	spikelets per spike	awn colour
flag leaf width		0.44**						
plant height		0.69**	0.31**					
awn length	0.56**	0.45**		0.38**				
spike length	0.67**	0.30**	-0.38**	0.34**	0.69**			
spikelets per spike			0.40**					
awn colour	0.31**	0.43**		0.30**	0.67**	0.47**	-0.26*	
spike colour	0.32**	0.26*			0.45**	0.32**		0.81**
seed shrivelling							0.23*	

*: $0.01 < p \leq 0.05$
**: $p \leq 0.01$

4.3 Results

Population means of observed plant characeristics are given in Table 4.2, and mean values per landrace group and per region of collection, are given in Tables 4.3 and 4.4, respectively.

Correlation coefficients between site and plant characteristics (see for characteristics and scales Chapter 3), significant at $p = 0.01$ were generally low, with values less than $|0.45|$ (Table 4.5). Highest significant correlations were found between flag leaf width and annual rainfall ($r = -0.52$), soil organic matter ($r = -0.57$), and soil nitrogen ($r = -0.57$). The results also suggest that drought and high temperature stress is negatively correlated with days to heading, but positively with flag leaf width and, although less pronounced, with flag leaf length and plant height. Rainfall and low temperatures further show positive correlation with spike and awn length. Soil fertility, use of inputs and sowing rate are negatively correlated with flag leaf width and length and spikelets per spike, but otherwise these site characteristics are positively related with plant characteristics. Separately processing of the 1987 and 1988 collection data sets gave a comparable matrix of correlation coefficients.

Among plant characteristics (Table 4.6), the highest significant correlation coefficients were between awn and spike colour ($r = 0.81$), awn length and spike length ($r = 0.69$), awn length and colour ($r = 0.67$), flag leaf length and plant height ($r = 0.69$) and days to heading and spike length ($r = 0.67$).

With PCA, possible relationships between landrace groups and between regions were elucidated. Three principal components were defined, of which the first two accounted for 51% and 29%, respectively, of the variance in the factor space (Table 4.7). The first axis was positively related to days to heading, awn and spike colour and awn and spike length, and the second axis to flag leaf width and spikelets per spike. Plant height and flag leaf length were explained about equally by both first two factors, while degree of seed shrivelling was highly related only to the third factor.

Apart from some outliers, the Haurani and Bayadi landrace groups overlapped at the negative side of the first factor, and the majority of the populations had positive values for the second factor (Figure 4.1). This implicates relatively early heading, short, light coloured awns and

Table 4.7. Unrotated factor loadings and proportion of variance in factor and data space.

	pc 1	pc 2	pc 3
days to heading	0.61	-0.28	0.48
flag leaf length	0.58	0.65	-0.20
flag leaf width	-0.12	0.86	-0.13
plant height	0.53	0.65	0.08
awn length	0.87	-0.07	-0.08
spike length	0.78	-0.27	0.29
spikelets per spike	-0.14	0.52	0.59
awn colour	0.83	-0.06	-0.31
spike colour	0.69	-0.07	-0.06
seed shrivelling	-0.02	0.09	0.73
variance in factor space	51%	29%	20%
variance in data space	46%	10%	14%

spikes, broad flag leaves and a high number of spikelets per spike. Baladi populations appeared mainly in the lower half of the diagram. The Shihani landrace group was plotted at the upper end of the first factor, neighboured at by the Sweidi landrace populations. Surieh landrace populations were found amidst Sweidis, although restricted to the negative side of the second factor. Shihani landrace populations were generally characterized by higher values for all traits. Sweidi and Surieh were late in heading, had long and dark coloured awns and spikes, were tall and had long flag leaves. Surieh landrace populations were further characterized by moderately narrow flag leaves and relatively few spikelets per spike. Hamari landrace populations carried the same last two characteristics.

For clarity, landrace groups represented by only one or two accessions were not included in the figure. The two Haririeh populations appeared close to coordinates (1.2,0.1), Nabi Jamal at (1.7,1.9), Mousseirieh at (1.9,-0.4), Saglouweh at (-1.3,-0.8), Juda at (1.2,-1.1), Sheirieh at (-0.3,-1.8), Harami at (1.2,0.5), and Ahmar at (1.4,0.4).

Grouping sites on basis of regions of collection (Figure 4.2) produced less clear differentiation, due to strong overlap of regions. Western collection regions appeared in majority in the fourth quadrant, whereas the southern collection regions were distributed generally over the second and third quadrants. Northern, central and eastern collection sites were

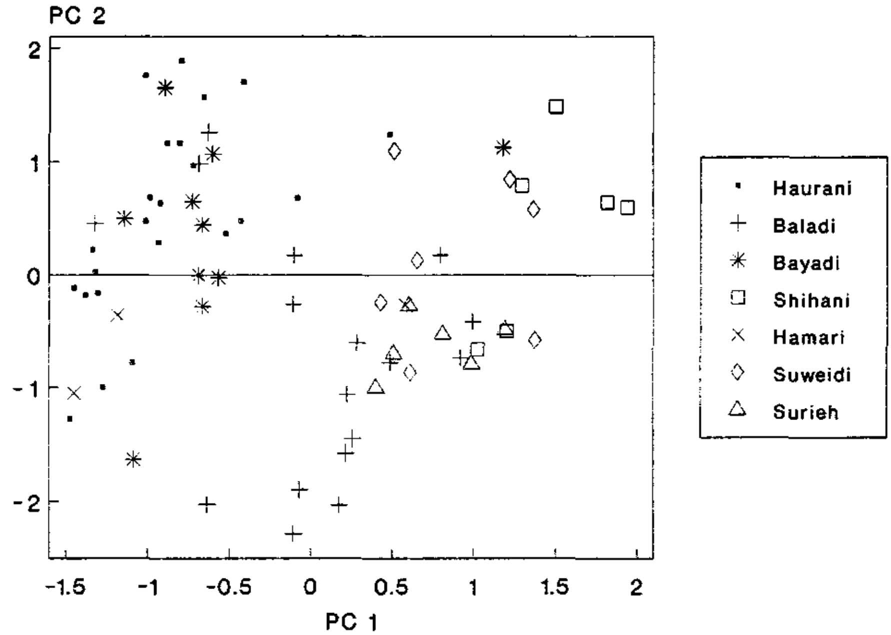


Figure 4.1. Landrace groups plotted against the first two principal components, formed in PCA.

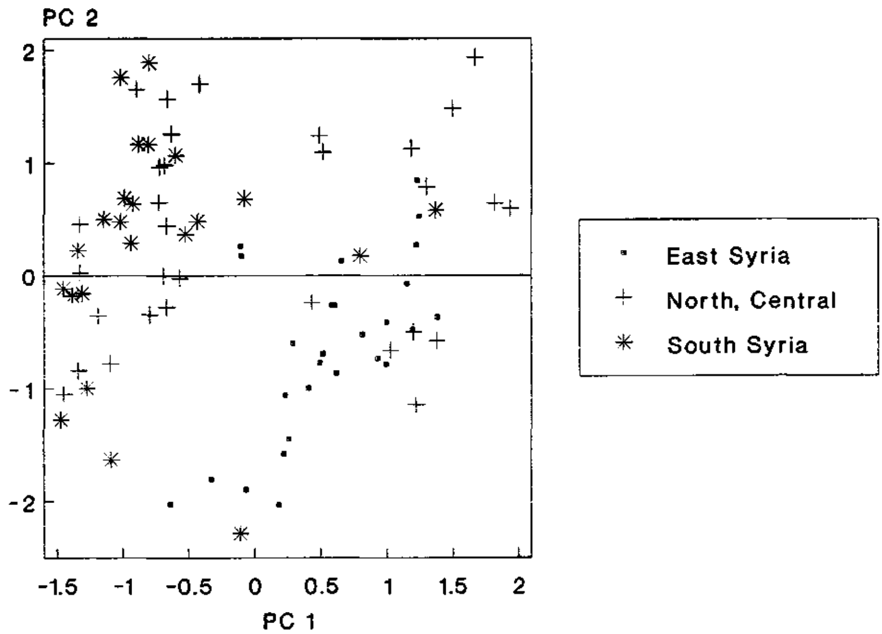


Figure 4.2. Regions of origin plotted against the first two principal components, formed in PCA.

plotted in all quadrants. Separation into subregions gave no substantial improvement, because of spatial separation of sites belonging to the same subregion.

Landrace populations from western collection sites can be characterized by late heading, long and dark coloured awns and spikes, narrow flag leaves and a few spikelets per spike; populations from southern sites by early heading and short and light coloured awns and spikes.

In Tables 4.3 and 4.4 are given the coefficients of variation by landrace group and by region. Whereas differences between plant characters were high, values per landrace group and per region were relatively stable. The highest coefficient of variation of days to heading was 0.03, in contrast to the highly variable awn and spike colour and, to a lesser extent, the degree of seed shrivelling.

The contributions of phenotypic variation components as calculated on basis of the nested ANOVA model is given in Table 4.6. The contribution of among population variation to the total variation was generally much higher than of lines within populations: 96% and 4%, respectively. Among landrace groups, contribution to total variation varied from 64% to 92%, with a mean value of 79%. Among regions, these values were 59%, 86% and 75%, respectively.

In all cases, awn colour had the highest component of variation. Days to heading ranked second for variation among populations and fifth for the other two components, but otherwise no major differences appeared in the sequences.

4.4 Discussion

All observations are phenotypic, and thus comprise an environmental component, which is however, difficult to estimate on the basis of available information. The mean square of the experimental error is given in Table 4.3 as an indication. The environmental variation consists of three elements, viz. a year effect, a field effect, and an effect caused by growing the plants in an environment different from the original one. Rescaling partially eliminated year effects, and allocation of all lines of a particular population to one block reduced within population variation at the expense of among population variation. Awn and spike colour are particularly sensitive to environmental conditions (Hervey-Murray, 1980; Zeven, 1983), and scoring on a quantitative scale can over-emphasize shades of colour. These and other field evaluations, though, suggest that under Syrian arid conditions post-anthesis drought stress induces de-colouration. In this respect, both evaluation seasons have had similar effects, moreover since drought stress has been relatively uniform within evaluation fields.

The fact that PCA formed multivariate components of variation that discriminated improperly between all landrace groups and poorly between regions of collection implies that the combination of characters into principal components has reduced the total variation, but that within group variation was reduced less, or that clusters are similar. Based on the characters evaluated, grouping of accessions on the basis of landrace groups is more promising than on the basis of regions of collection. The generally low correlations between site and plant characteristics confirms this. Although the origin of the seed was verified, there remains the possibility that farmers have traded seed between regions.

The earlier conclusion based on spike characters that the Haurani and Bayadi landrace groups are morphologically similar (Chapter 3) was confirmed by the PCA, which did not distinguish between these two landraces groups.

The Arabic word "baladi" means native or indigenous; in other words, it indicates that a population carrying this name is local, and can be a representative of any landrace group. This is not clearly shown in Figure 4.1, which displays these populations intermediately, but separately processing of the 1987 collection data (resulting plot not given) makes this more obvious. The Baladi's then overlap considerably with other groups. Figure 4.1 further suggests similarity of the Sweidi and Surieh landrace groups.

From the relations between site and plant characteristics, it was concluded that landrace populations originating from sites characterized by favourable growth conditions tend to be later in heading, to have smaller flag leaves, and to have longer spikes with longer awns but with less spikelets. Especially the tendency of smaller flag leaves seems contradictory to the normally positive relation between growth conditions and size of vegetative organs. However, as the material was evaluated at fields low in organic matter, nitrogen and phosphorus, genotypes from favourable regions may have had a comparative disadvantage, which resulted in reduced growth and smaller leaves. Such expression of genotype x environment interaction illustrates the care with which single evaluations, have to be interpreted.

Consistency in geographical patterns of variation was shown by several of the studied plant characteristics, as indicated by the matrix of correlation coefficients (Table 4.6).

Table 4.8. Estimates of phenotypic variation components, as percentage of total variation. Mean values for 1987 and 1988 collections.

character	among populations	among landrace groups	among regions
awn colour	99.2	92.8	86.1
days to heading	98.9	77.7	76.6
spike length	98.8	91.9	84.8
spike colour	98.8	89.6	81.6
awn length	98.1	91.6	83.7
flag leaf width	95.0	72.0	74.8
flag leaf length	94.4	72.8	68.6
seed shrivelling	94.4	63.9	71.8
spikelets per spike	93.6	69.9	59.3
plant height	88.7	65.1	58.1
mean	96.0	78.7	74.5

Phenotypic variation could be allocated almost entirely to differences among populations (Table 4.8), whereas within population variation was low. Especially populations collected in non-mountainous regions are morphologically relatively homogeneous; also, the experimental design has influenced the distribution of variation. Variation among landrace groups and among regions contributed about equally to the total variation, although for some characteristics classification on basis of landrace groups seemed more discriminative. Landrace groups showed little within variation, and the magnitude of the c.v. was not related to the number of populations forming the landrace group, as it did not increase with the populations number.

This is in agreement with other estimates of variation components, although results tend to depend on the character studied, the statistics that expresses variation, and the number of components included in the nested ANOVA. Measures of variation that assume additive decomposition of total genetic variation suffer from conceptual inconsistency, according to Gregorius (1988). He recommends to characterize demes by the number of individuals by which they differ from the remainder of the population. However, if mean square is used as estimate, variation among groups of countries (Jain et al., 1975) or countries (Porceddu, 1976; Spagnoletti Zeuli et al., 1984; Spagnoletti Zeuli & Qualset, 1987) dominates, just as variation among regions (Bogyo et al., 1980; Damania & Porceddu, 1983; van Leur et al., 1989). In some cases, variation among regions is lower than variation within regions (Weltzien, 1989) or lower than variation among populations and among lines (Bekele, 1984). Comparisons with landrace groups were not given in these studies. Whereas Harlan (1986) argues that greatest diversity occurs at the local level, other distribution patterns seem to exist as well.

A collection of Syrian and Jordanian barley landraces has been studied by Weltzien (1988, 1989) for agronomic and morphological characters, Ceccarelli et al. (1987a) for agronomic characters and van Leur et al. (1989) for disease reactions. Weltzien reported 37% and 15% variation among regions (mean values of eight characters), when total variance was split into among and within region components, and into among regions, within regions and within populations, respectively. Ceccarelli et al. observed 83% among population variation (mean value of 12 characters), and van Leur et al. showed that effects for regions and sites within regions were not significant for all studied diseases. The regions used in this study were partly located in other parts of the country and were smaller than the ones defined by Weltzien and van Leur et al. The smaller within region variation for durum wheat in comparison to barley could be explained by this difference in region size, and by the more intensive seed exchange between farmers in the case of durum wheat (J. van Leur, ICARDA, personal communication). Within population variation, determined by Ceccarelli et al. as mean squares, was also low in the case of barley.

Chapter 5

AGRONOMIC PERFORMANCE

Abstract

It is demonstrated that sub-classification in landrace groups, followed by evaluation of a representative part of the collection, may be an effective approach to germplasm evaluation. The application of single-evaluation results has potential for forecasting crop behaviour in other years and at other locations, taking into account genotype x environment interaction.

Syrian durum wheat landrace populations were evaluated. Only in the case of the highest yielding experiment the best check variety yielded higher than the best landrace, which demonstrates the breeding value of locally domesticated germplasm.

Grain yield was stable between years within sites. Population effect was significant for grain yield, but not for total yield. In many cases, fertilizer application resulted in a decrease in kernel density and grain yield.

Correlations among plant characters were consistent among experiments. Annual rainfall, summer maximum and winter minimum temperatures, potential annual evapotranspiration, and soil organic matter and nitrogen content were collection site characteristics most correlated to plant characters.

Relating grain yield to landrace groups resulted in more pronounced clusters than relating to regions of origin. Landrace groups may have been domesticated within relatively small areas with specific climatic conditions, followed by recent dispersion of some groups without losing characteristics.

5.1 Introduction

The task of plant genetic resources centres is to collect or otherwise acquire, evaluate, maintain and disseminate germplasm with characteristics that now or in future may contribute to improvement and stabilization of yields, in either specific or diverse environments. Evaluation results, which form the basis for selection, are often of limited applicability, due to the considerable genotype x environment interaction. Therefore, extrapolation of single-evaluation results is difficult (Ceccarelli, 1989), or even impossible when location x year interaction is significant (Lin & Binns, 1988). To overcome that problem, extensive multi-locational or multi-seasonal evaluation would be needed, but that is normally not possible because of financial constraints. Hence, an efficient evaluation methodology is required, in which the properties of large numbers of accessions in various climatic conditions can be investigated.

Assuming that collected plants have evolved in the environment of collection, the agro-ecological characteristics of the environment of origin will greatly determine their genotypic constitution. At other locations, interaction of the genotype with different environments will determine plant growth and development. It may thus be expected that the environmental characteristics of the region of origin can be related to plant characters at locations with other environmental conditions (Burt et al, 1979; Frankel, 1989). Information on the location and environmental characteristics of collecting sites is routinely recorded (IBPGR, 1985). Although this so-called passport and collection information is as valuable as the seeds themselves in view of assessment of their properties, it is seldomly considered in interpretation of field trials.

Constraints to wheat production in arid regions are the year-to-year fluctuations in the amount and distribution of rain; low soil fertility; low winter temperatures and high temperatures during the grain filling period; and occurrence of pests and diseases (Ceccarelli et al., 1987b; Miller, 1987). Germplasm domesticated in the Fertile Crescent (Vavilov, 1951) and adapted to the erratic exposure to growth-limiting factors may contribute to the improvement of yield level and yield stability in Middle Eastern countries, which in many cases face a growing food gap (Adamowicz, 1988).

This paper relates evaluation results to the agro-ecology of collection regions. The study's overall objective is to develop a method that enables the application of results of a single evaluation for forecasting crop behaviour in other years and at locations with by different climatic conditions.

Table 5.1. International Cereal Durum Wheat (ICDW) accession numbers of the evaluated durum wheat landrace populations and environmental information on the respective collection sites.

ICDW accession number	ID collection number	Landrace group	Environmental characteristics of collection sites[a]							
			1	2	3	4	5	6	7	8
19489	1	Haurani	730	150	34.0	1.5	1950	0.87	584	5.2
19491	4	Haurani	990	290	32.0	2.5	1600	0.83	526	1.9
19500	25	Haurani	780	235	34.0	2.5	1750	0.96	713	17.6
19506	32	Haurani	800	215	36.0	2.0	2050	0.89	716	4.0
19511	40	Haurani	1060	800	28.0	1.5	1200	1.71	889	27.3
19521	54	Haurani	1220	270	32.0	1.0	1750	0.87	556	4.5
19523	56	Haurani	860	165	34.0	1.0	2000	1.44	889	11.1
19524	58	Baldadi	840	165	34.0	0.5	2000	1.03	682	10.4
19529	70	Haurani	700	215	35.5	2.0	2000	0.86	518	8.2
19530	72	Haurani	750	215	35.0	2.0	2000	0.83	526	3.4
19555	127	Shihani	490	380	39.5	2.0	2350	1.03	599	3.7
19558[b]	135	Shihani	500	440	40.0	2.0	2400	1.32	831	9.4
19559[b]	136	Haurani	500	440	40.0	2.0	2400	1.32	831	9.4
19574	163	Haurani	570	430	39.5	2.5	2350	1.29	824	5.6
19576	167	Shihani	540	425	39.5	2.0	2350	1.45	975	4.5
19578	172	Haurani	410	290	39.0	1.5	2200	1.22	797	6.0
19583	203	Bayadi	440	300	36.5	2.0	1850	2.30	1374	14.9
19584	205	Baladi	540	300	36.5	2.0	1900	1.01	712	4.0
19586	208	Sweidi	440	455	35.0	3.0	1650	0.96	584	2.8
19587	209	Sweidi	610	495	35.0	3.0	1650	2.02	1346	16.5
19594	218	Baladi	490	420	35.0	1.5	1650	0.94	583	4.0
19596	220	Hamari	600	495	35.0	1.5	1600	1.72	1019	18.2
19598	222	Hamari	590	450	35.0	1.5	1650	1.73	1025	28.4
19599	224	Baladi	490	355	36.0	1.5	1750	1.33	756	11.4
19600	225	Haurani	470	315	36.5	2.0	1900	2.19	1197	10.0
19609	236	Sweidi	350	665	35.0	4.0	1650	3.17	1776	11.4
19617	245	Haurani	450	480	34.0	3.5	1600	2.37	1390	22.9
19618	246	Sweidi	410	545	34.0	4.0	1600	1.43	774	58.6
19622[c]	250	Hamari	670	645	31.0	5.0	1300	1.67	900	6.3
19623[c]	251	Sheirieh	670	645	31.0	5.0	1300	1.67	900	6.3
19626	255	Bayadi	350	325	37.0	3.0	1900	1.85	1165	13.6
19636	272	Baladi	520	1305	28.0	5.0	1200	5.11	2505	33.8
19638	274	Baladi	970	1385	26.0	4.0	1200	3.20	1429	6.3
19639	275	Baladi	680	1310	26.0	4.0	1200	6.23	3174	7.4
19640	276	Baladi	610	1160	27.0	5.0	1200	3.78	2130	5.2
19641	277	Baladi	50	920	30.0	8.0	1400	2.62	1438	16.7
19648	287	Baladi	570	1200	30.0	7.0	1200	3.34	1651	2.3
19651	290	Baladi	160	915	30.0	8.0	1400	3.68	2016	69.8

a : see legend on next page
b,c : same collection sites

Table 5.1. Continued.

1: Altitude (m)
2: Rainfall (mm $year^{-1}$)
3: Mean maximum August temperature (°C)
4: Mean minimum January temperature (°C)
5: Potential evapotranspiration (mm $year^{-1}$)
6: Soil organic matter (%), Walkley and Black method
7: Total soil N content (ppm), Kjeldahl, Bremner method
8: Total soil P content (ppm), Olsen

5.2 Materials and methods

Collecting missions for durum wheat landraces [Triticum turgidum L. var. durum (Desf.) MK] in various parts of the Syrian Arab Republic in 1987 yielded a total of 185 populations (Chapter 3; van Slageren et al., 1989). Fifty-nine of these presumably originated at or in the vicinity of their collection sites, and were considered representative for the respective environments. Table 5.1 provides a list of thirty-eight evaluated landrace populations and agro-ecological information on their collection sites.

Since rainfall amount and distribution is a dominant factor in dry matter production in arid environments (Entz & Fowler, 1989), four locations in Syria, characterized by different long-term rainfall averages, were selected for agronomic evaluation: Tel Hadya, site of ICARDA's main experimental farm; Breda, an ICARDA sub-station; and the towns of Homs and Izra'a, with long-term annual rainfall means of 330, 271, 425 and 300 mm, respectively. Table 5.2 gives their geographical coordinates. Temperature regime in Breda is more extreme than at other sites.

Per location and year, the thirty-eight landrace populations and three check varieties were sown at two levels of nutrient availability in two replicates. A randomized complete block design with two replicates was used for each experiment.

Natural fertility represented one level of nutrient availability, whereas the other level was created through additional nitrogen and phosphorus application. Nitrogen (ammonium nitrate 33.5%) at a rate of total 40 kg ha^{-1} for Tel Hadya, Breda and Izra'a, and 60 kg ha^{-1} for Homs, was split-dressed in equal amounts at sowing and at end of tillering. These arbitrary application levels were used to eliminate nitrogen deficiency and achieve comparable production levels, which is higher for the

Table 5.2. Geographical coordinates of the four evaluation sites and soil characteristics in 1988 and 1989, before fertilizer application at sowing; and dates of sowing and harvest for the two seasons.

Site	Longitude	Latitude	Season	Total K^+ (meq 100 g^{-1})[1]	Total N (ppm)[2]	Extactable P (ppm)[3]	Organic matter (%)[4]	C/N ratio	Date of sowing	Date of harvest
Tel Hadya	36°56'E	36°01'N	89-90	1.34	466	4.3	0.82	10.30	28/11	4/6
Breda	37°10'E	35°56'N	88-89	1.28	661	3.6	1.12	9.83	12/12	29/5
			89-90	0.42	600	5.2	0.97	9.33	21/11	6/6
Homs	36°43'E	34°45'N	88-89	0.86	851	10.5	1.46	9.99	11/12	11/6
			89-90	0.81	861	9.3	1.24	8.36	17/12	24/6
Izra'a	36°14'E	32°52'N	88-89	1.24	521	1.7	0.93	10.36	10/12	2/6
			89-90	1.44	535	8.4	0.73	7.85	6/12	21/6

1: extracted by 1 normal ammonium acetate solution pH=7, measured by flame photo meter
2: Kjeldahl, Bremner method
3: Olsen
4: Walkley and Black method

high-rainfall site Homs. At all locations, 40 kg ha^{-1} phosporus (triple superphosphate 46%) was applied at sowing. Soil characteristics determined just before sowing are presented in Table 5.2. The use of different fields in the second season may be the cause of high variability in soil characteristics for Breda and Izra'a.

The three durum wheat check varieties included in the experiment were: Haurani-27, a landrace originating from Lebanon and generally used as local check; Cham 1, a variety suitable for high input conditions; and Cham 3, a variety with better stress tolerances than Cham 1. Checks were sown in double the number of plots of the landrace populations.

Before sowing, seeds were treated with Vitavax 200 (2.5 g carboxine and thiram per kg seed) against common bunt (Tilletia caries and T. foetida). During the growing season, plants were sprayed at regular intervals with Bayfidan (0.5 l ha^{-1}, 250 g l^{-1} Triadimenol), a broad spectrum fungicide. Pest and disease incidense was low in all situations.

Plants were sown in plots of 2.5 x 1.6 m, in eight rows 20 cm apart. To avoid border effects, no space was left between plots. Dates of sowing and harvest are given in Table 5.2.

As a precaution against possible grain mixture and interplot competition at plot borders, only inner plants were considered. At all locations plant height, spike density, total aboveground dry weight, grain yield and thousand kernel weight were recorded. Spike density was recorded in all trials except at Homs in 1989. Plant height was measured between flowering and maturity; spike density was determined in duplicate using a metal frame of 0.5 m^2; total dry weight and grain yield were determined at harvest on the central 2 m of the inner six rows; straw yield, harvest index and number of kernels per spike were calculated. At Tel Hadya, date of anthesis was also observed.

The significance of factors was tested through combined analysis of variance (ANOVA) per plant character. Location and year were considered main factors, and population and fertilizer level sub-factors. This design yields more accurate information on population and fertilizer effects, at the expense of information on location and year effects (Sokal & Rohlf, 1981). Also, per year and location, the effects of population and fertilizer application on plant characters were determined by means of two-way ANOVA.

Correlation coefficients among plant characters, and between plant

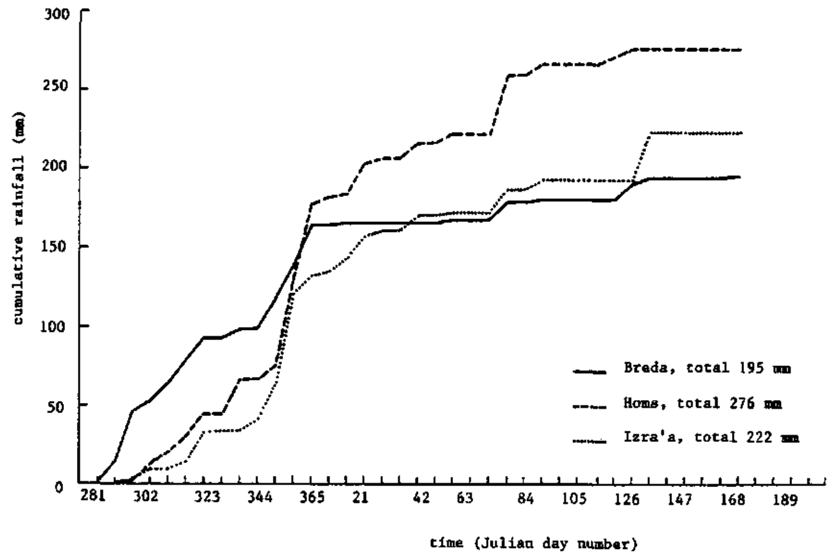


Figure 5.1. Cumulative rainfall during the 1988-89 season at Breda, Homs and Izra'a.

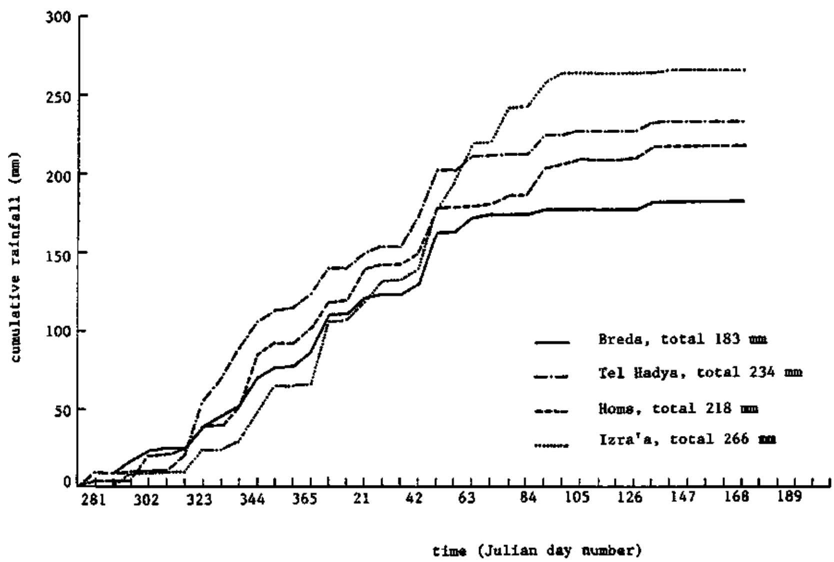


Figure 5.2. Cumulative rainfall during the 1989-90 season at Tel Hadya, Breda, Homs and Izra'a.

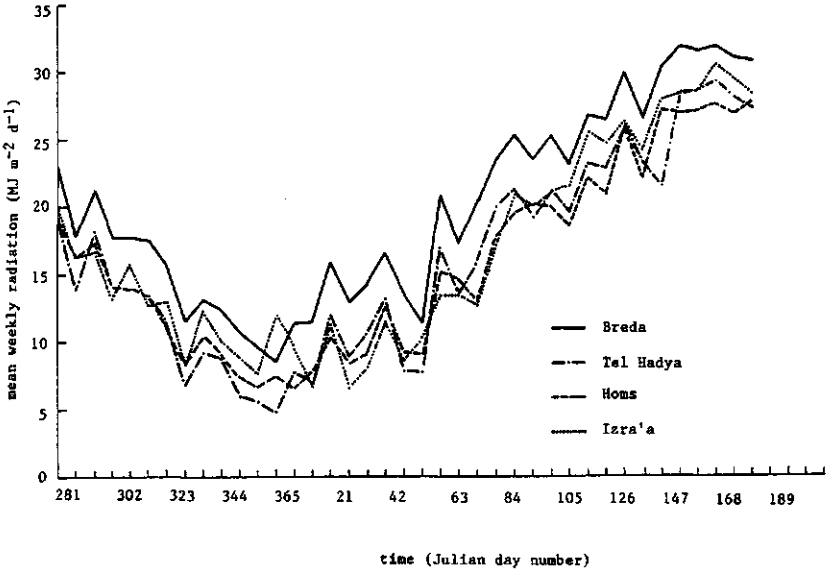


Figure 5.3. Mean weekly radiation during the 1989-90 season at Tel Hadya, Breda, Homs and Izra'a.

characters and collection site characteristics were calculated per location and fertilizer level.

Grain yield was related to the classification of regions of collection based on minimization of variation in climatic characteristics, and to the taxonomic classification of populations into landrace groups on the basis of information supplied by farmers (Chapter 3).

5.3 Results

Rainfall, graphically presented in Figures 5.1 and 5.2, was below average in both seasons. Homs did not receive particularly more precipitation than the other sites, but the soil contained residual moisture from rainfall or irrigation in the previous season. Mean weekly radiation for 1989-90, which were similar to those for 1988-89, is given in Figure 5.3. Radiation was highest at Breda, whereas radiation levels at the other sites were comparable. Highest maximum May temperatures were recorded at Breda (39.0 and 43.1°C in 1989 and 1990, respectively); lowest at Homs (36.2 and 40.9°C). During the coldest week of the growing season, highest absolute minimum temperatures were recorded at Homs and Izra'a, both with -8.0°C in 1989 and 1990, respectively; and lowest at Breda (-9.4°C) and Tel Hadya

(-8.7°C), in 1989 and 1990, respectively. Coldest sites also experienced more frost days.

Results of Tel Hadya 1988-89 were considered not reliable because of leaf yellowing as early as March, possibly due to a residual herbicide effect. These data were eliminated, and therefore, Tel Hadya 1990 was also excluded from the four-way ANOVA. However, comparison with three-way ANOVA including Tel Hadya 1990 did not show major differences in effects of main and sub-factors: significant location or year effects combined into significant location-year effects. Since at Homs 1989 spike density was not established, analysis of this trait and number of kernels per spike excluded both Homs seasons.

Evaluation results as mean values over all landrace populations per location, year and fertilizer level are given in Table 5.3. Considerable differences were observed among locations. Homs showed satisfactory performance in both seasons, and to a lesser extent Izra'a in 1990, whereas the other locations and years showed very low yields.

Mean grain yield of landraces is lower than that of one or more of the checks, however, maximum grain yield is achieved by landraces (Figure 5.4). Only in the highest yielding experiment (Homs 1989+; + and - indicate with and without additional fertilizer, respectively), was Cham 3 the highest yielding. Under lowest yielding conditions, grain yield of check varieties sometimes was lower than the landrace population mean.

Main effects were significant, except the year effects for grain yield and harvest index; the location effect for number of kernels per spike; the population effect for total dry matter; and the fertilizer effects for spike density, number of kernels per spike and plant height (Table 5.4). Interaction effects of the two main factors, location and year, were significant, except for spike density and number of kernels per spike. Interaction effects of both sub-factors, population and fertilizer application, were not significant. For yield levels, significance was shown for the interaction effects of location and fertilizer application on grain and straw yield and total biomass production; and for the interaction effect of location and population for grain yield. Among populations, total dry matter was more stable than either grain and straw yield.

Two-way ANOVA's per location and year are summarized in Table 5.5. Generally, significant population and fertilizer effects for grain yield were demonstrated, whereas effects for straw and total dry matter were

Table 5.3. Mean values of evaluation results per location, year and fertilizer level. Standard deviations per experiment are given in brackets.

Location	Year	Fertilizer	Plant height (cm)	Grain yield (kg ha^{-1})	Straw yield (kg ha^{-1})	Total dry weight (kg ha^{-1})	Harvest index	Spike density (m^{-2})	Kernels per spike	Thousand kernel weight (g)	Kernel density (m^{-2})
Tel Hayda	1990	-	50.6	376	1774	2150	0.173	187.4	6.88	29.0	1229
		+	47.2	297	1895	2162	0.135	192.6	5.24	28.4	1080
			(7.2)	(199)	(421)	(552)	(0.059)	(30.1)	(2.57)	(3.3)	(163)
Breda	1989	-	43.1	172	987	1163	0.150	87.3	6.45	31.2	407
		+	44.0	178	1017	1195	0.154	85.9	6.78	31.1	358
			(5.0)	(78)	(297)	(351)	(0.045)	(29.8)	(2.63)	(2.2)	(93)
	1990	-	58.6	434	1400	1834	0.237	151.9	9.27	31.2	1570
		+	58.0	431	1438	1869	0.232	156.3	9.06	31.1	1507
			(5.0)	(90)	(242)	(295)	(0.036)	(24.5)	(2.14)	(2.6)	(64)
Homs	1989	-	107.3	2020	5161	7181	0.292	-	-	40.6	3988
		+	109.2	2279	5541	7820	0.294	-	-	41.6	4434
			(10.9)	(457)	(1604)	(1886)	(0.382)			(4.5)	(713)
	1990	-	101.6	1284	5547	6831	0.191	304.8	10.03	42.5	3736
		+	101.7	1418	5756	7174	0.199	329.7	10.59	40.8	3132
			(10.7)	(377)	(1566)	(1724)	(0.050)	(50.2)	(2.20)	(3.4)	(776)
Izra'a	1989	-	49.4	200	1102	1302	0.158	136.3	6.10	24.9	904
		+	48.5	163	1233	1396	0.118	131.3	5.08	24.7	472
			(4.5)	(57)	(320)	(346)	(0.033)	(22.6)	(1.59)	(2.4)	(254)
	1990	-	82.1	765	3833	4598	0.175	247.2	9.07	34.8	2442
		+	81.1	754	4948	5702	0.136	267.7	8.85	32.2	2271
			(5.0)	(113)	(1122)	(1122)	(0.042)	(36.4)	(1.52)	(2.3)	(578)

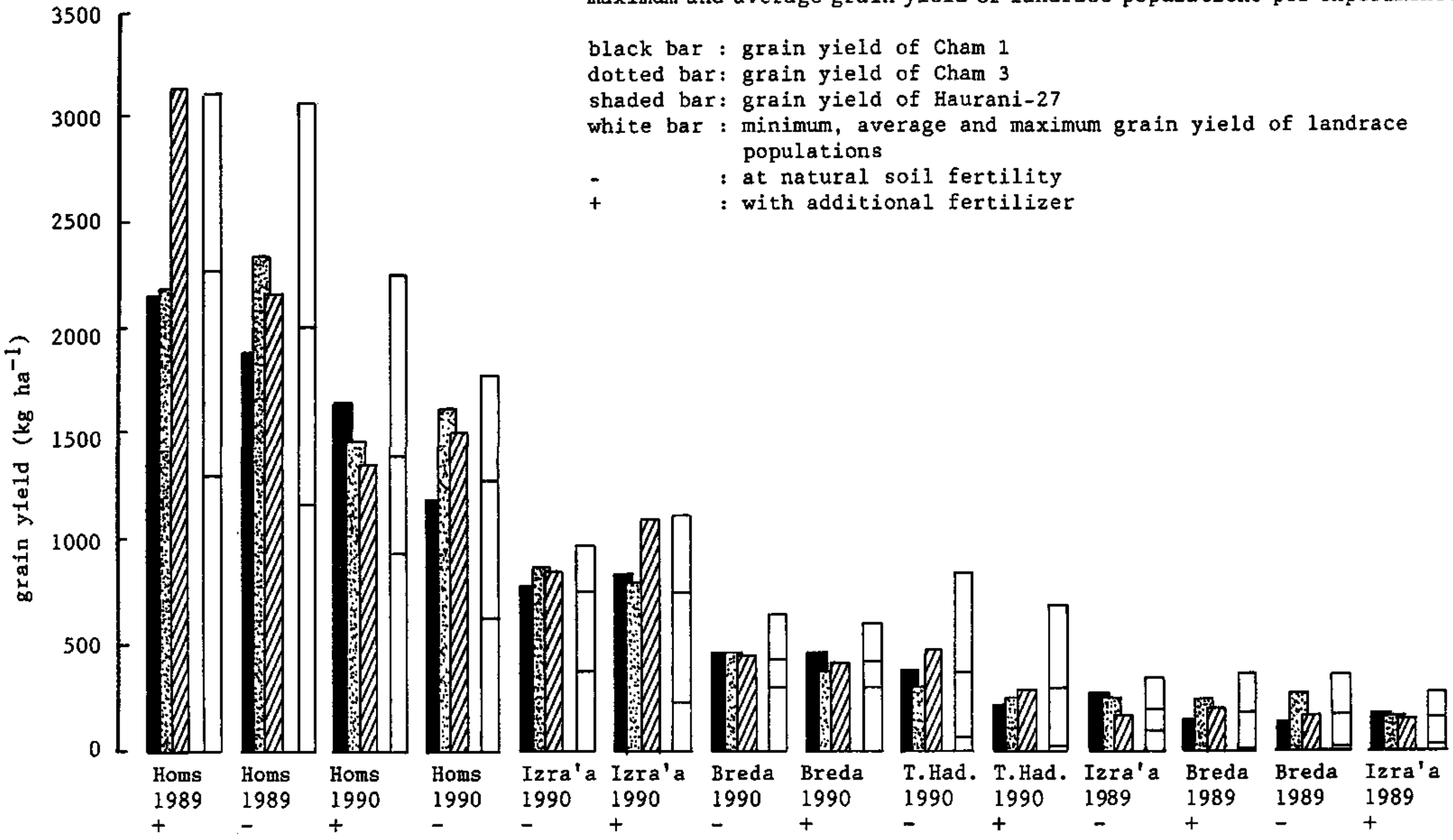


Figure 5.4. Grain yield of check varieties, and overall minimum, maximum and average grain yield of landrace populations per experiment.

black bar : grain yield of Cham 1
dotted bar: grain yield of Cham 3
shaded bar: grain yield of Haurani-27
white bar : minimum, average and maximum grain yield of landrace populations
- : at natural soil fertility
+ : with additional fertilizer

Table 5.4. Mean squares and significance of year, location, landrace population and fertilizer application effects.

Effect	d.f.	Spike density	Kernels per spike	d.f.	Plant height	Grain yield	Straw yield	Total dry weight	Harvest index	Thousand kernel weight
Year	1	$1.4x10^{6}$**	$1.4x10^{4}$**	1	$4.2x10^{4}$**	346	$3.9x10^{6}$**	$4.0x10^{6}$**	0.031	$2.2x10^{3}$*
Location	1	$8.6x10^{5}$**	87.0	2	$2.4x10^{5}$**	$1.9x10^{6}$**	$1.4x10^{7}$**	$2.6x10^{7}$**	1.079*	$1.3x10^{4}$**
YxL	1	$1.2x10^{5}$	24.4	2	$2.9x10^{4}$**	$3.9x10^{5}$**	$2.1x10^{6}$**	$3.8x10^{6}$**	0.991*	$1.8x10^{3}$*
Rest 1	4	$1.0x10^{4}$	13.2	6	544	585	$1.5x10^{5}$	$1.6x10^{5}$	0.107	180.6
Population	37	$2.0x10^{3}$**	27.7**	37	92.7*	$1.5x10^{3}$**	$2.0x10^{4}$**	$2.3x10^{4}$	0.043*	30.9**
Fertilizer	1	$3.2x10^{3}$	14.4	1	0.3	$7.7x10^{3}$**	$2.3x10^{5}$**	$3.2x10^{5}$**	0.147*	83.5**
PxF	37	733	5.1	37	62.5	537	$8.9x10^{3}$	$1.1x10^{4}$	0.023	6.1
YxP	37	$1.3x10^{3}$*	11.3*	37	54.4	$1.0x10^{3}$	$9.6x10^{3}$	$1.3x10^{4}$	0.030	12.9
YxF	1	$9.4x10^{3}$**	2.9	1	75.8	702	$4.3x10^{4}$	$3.3x10^{4}$	0.029	166.0**
LxP	37	$1.3x10^{3}$*	9.6**	74	73.9	$1.4x10^{3}$**	$1.3x10^{4}$	$1.6x10^{4}$	0.026	12.0*
LxF	1	$1.5x10^{3}$	18.3	2	70.3	$1.1x10^{4}$**	$6.7x10^{4}$**	$6.8x10^{4}$*	0.034	37.3*
Rest 2	449	844	4.9	711	56.3	723	$1.2x10^{4}$	$1.5x10^{4}$	0.026	8.8
Total	607		911							

** = significant at $p = 0.01$
* = significant at $p = 0.05$

Table 5.5. Significant effects for two-way ANOVA's per combination of location and year. No significant effects for Breda 1990 were found.

Location and year	Plant height	Grain yield	Straw yield	Total dry weight	Harvest index	Spike density	Kernels per spike	Thousand kernel weight
Tel Hadya 1990	F***	F*	-	-	F***	-	F***	-
Breda 1989	-	P***	-	-	P***	-	P***	P***
Homs 1989	-	P*** F***	-	-	-	n.o.	n.o.	-
Homs 1990	-	F***	-	-	-	F**	-	F***
Izra'a 1989	-	P*** F***	P* F**	-	P*** F***	P***	P*** F***	P***
Izra'a 1990	P*	P*** PxF***	P*** F***	P* F***	P*** F***	F***	P*** PxF***	P*** F***

P = Population effect
F = Fertilizer effect
PxF = Population x fertilizer effect
*** = significant at p = 0.01
** = significant at p = 0.02
* = significant at p = 0.05
n.o. = not observed.

Table 5.6. Experiments showing significant correlations ($p \leq 0.1$) between collection sites and plant characteristics. The sign of the correlation is given first in brackets, followed by the relevant experiments.

Site characteristic	Plant character							
	Plant height	Grain yield	Straw yield	Total dry weight	Harvest index	Spike density	Kernels per spike	Thousand kernel weight
Latitude	(+) Iz90+	-	-	-	-	(-) Iz90-	-	(+) Iz90+
Longitude	(+) Iz89- Iz90+ Ho90-	(+) Br90- Iz90+	(-) Iz89+	(+) Br90+	(+) Br89+ Iz90+	-	(+) Ho90-	(-) Iz89- Ho89-
	(-) Ho89-	-	(+) Br90+	(-) Iz89+	-	-	-	-
Altitude	-	(+) Ho90-	(-) Iz90+	(-) Iz90+	(+) Ho90-	(-) Iz89+ TH90+	(+) Iz89-,+ Ho90-	(+) Br89+
	-	(-) Iz90+	-	-	-	-	-	-
Rainfall	-	(-) Br89- Iz90+	(+) Iz89-,+ Iz90-,+ TH90-	(+) Iz89-,+ Iz90-,+	(-) Br89+ Iz89-,+ Iz90-,+	(+) Br89-,+ Iz89-,+ Iz90+ Ho90-,+ TH90-	(-) Br89-,+ Iz89-,+ Iz90+ Ho90-,+	(+) Iz89-,+ Ho89-
	-	-	(-) Br90+	(-) Br90+	(+) Br89-	(-) Br90+	-	(+) Br90-
Max. temp.	(+) Iz90+	(+) Br89-,+ Iz90+ TH90+	(-) Iz89-,+ Iz90-,+	(-) Iz89-,+ Iz90-,+	(+) Br89-,+ Iz89- Iz90-,+ TH90+	(-) Iz89+ Ho90-,+	(+) Br89-,+ Iz89-,+ Ho90- TH90+	(-) Iz89-,+ Ho89-
	-	-	(+) Br90+	(+) Br90+	-	-	-	-
Min. temp.	-	(-) Br89-,+ Iz89-	(+) Iz89+ Iz90-,+	(+) Iz89+ Iz90-,+	(-) Br89-,+ Iz89-,+ Iz90-,+ Ho90-	(+) Iz89-,+ Ho90-	(-) Br89-,+ Iz89-,+ Ho90-	(+) Iz89-,+

Eva- poration	(+) Iz90+ Ho90-	(+) Br89-,+ Iz89- Iz90+	(-) Iz89+ Iz90-,+	(-) Iz89+ Iz90-,+	(+) Br89-,+ Iz89- Iz90-,+ TH90+	(-) Iz89+ Ho90-	(+) Br89-,+ Iz89-,+ Ho90-	(-) Iz89-,+ Ho89- TH90-
	-	-	(+) Br90+	(+) Br90+	-	-	-	-
Soil org. matter	-	(-) Br89-,+ Iz89- Iz90- Ho90-	(+) Iz89-,+ Iz90-,+	(+) Iz89+ Iz90-,+	(-) Br89-,+ Iz89- Iz90-,+ TH90-	(+) Br89- Iz89-,+ Iz90+ Ho90+ TH90-	(-) Br89-,+ Iz89-,+ Iz90+ Ho90- TH90-	(+) Iz89-,+
	-	(+) Br90-	(-) Br90+	(-) Br90+	-	(-) Br90+	-	-
Soil N	-	(-) Br89-,+ Iz89-,+ Iz90- Ho90- TH90-	(+) Iz90-,+	(+) Iz89+ Iz90-,+	(-) Br89-,+ Iz89- Iz90-,+ Ho90- TH90-	(+) Iz89-,+ Iz90+ Ho90+	(-) Br89-,+ Iz89-,+ Iz90+ Ho90- TH90-	(+) Iz89-,+
	-	-	(-) Br90+	(-) Br90+	-	(-) Br90+	-	-
Soil P	(-) Ho90-	-	(+) Iz90-,+	(+) Iz90-,+	(-) Br89+ Iz89+ Iz90-	(-) Iz90+	-	(+) Ho89-
	-	-	-	(-) Br90+	-	-	-	-

(+) = significant positive correlation
(-) = significant negative correlation
Br = Breda
Ho = Homs
Iz = Izra'a
TH = Tel Hadya
89 = 1989
90 = 1990
- = natural soil fertility
+ = with fertilizer application.

only significant at Izra'a. For Breda 1990, no significant effect was found. Fertilizer application significantly postponed anthesis at Tel Hadya 1990 by one day from 144 to 145 days after sowing.

The pattern of interrelationships among plant characters in different experiments was comparable. Correlation coefficients per location and fertilizer level among plant characters did not indicate significant negative correlations among grain and straw yield and total dry matter. Plant height was not significantly correlated with other plant characters, with the exception of spike density for Breda 1990+ and Izra'a 1990-. Total dry matter and grain yield were not or positively, but never negatively, correlated with number of kernels per spike and with spike density. Only in the case of Tel Hadya 1990+ was the number of kernels per spike significantly positively correlated with spike density.

Grain yield was strongly linearly correlated with calculated kernel density (Table 5.3):
grain yield m^{-2} = -12.3 + 0.43 x number of kernels m^{-2} (r = 0.989, $p \leq$ 0.001).
This relationship was independent of the fertilizer application level.

Latitude and altitude of the collection sites were rarely significantly correlated to any of the plant characters (Table 5.6), and longitude and soil P only in few cases; however, annual rainfall, summer maximum temperature, winter minimum temperature, potential annual evapotraspiration, soil organic matter content and total soil N content were significantly correlated to plant characters in higher frequencies. Harvest index and number of kernels per spike and, to a lesser extent, grain yield and spike density were the plant characters most frequently significantly correlated to site characteristics. The Izra'a experiments, Breda 1989 and Homs 1990- gave the highest numbers of significant correlations. Breda 1990+ is exceptional because of the inverse correlations compared to the majority of correlations.

Relating grain yield to regions of origin was difficult. At best, weak tendencies could be identified, indicating that landrace populations originating from mountainous areas performed relatively well in high yielding experiments. Regions with intermediate climatic conditions, e.g. Idleb, northeastern Syria, Homs and Hauran (Chapter 3), provided populations that yielded relatively moderate to good in all experiments.

Although variation was high, differentiation with respect to grain

Table 5.7. Grain yield (kg ha^{-1}) per experiment for evaluated landrace groups and checks.

Experiment	Landrace group							Check		
	Haurani	Baladi	Bayadi	Shihani	Hamari	Sweidi	Sheirieh	Haurani	Cham 1	Cham 3
Homs 1989 +	2267	2124	1754	2646	1989	2706	3033	2180	2203	3145
Homs 1989 -	2031	1841	1834	2030	2040	2401	1927	1910	2367	2183
Homs 1990 +	1495	1402	1051	1426	1565	1278	1336	1675	1483	1371
Homs 1990 -	1364	1272	1064	1175	1180	1310	1179	1209	1616	1514
Izra'a 1990 -	802	718	794	710	783	752	938	800	888	863
Izra'a 1990 +	807	652	856	811	574	865	727	844	800	1099
Breda 1990 -	464	429	362	447	412	413	420	473	471	466
Breda 1990 +	433	389	543	485	423	470	432	478	381	442
Tel Hadya 1990 -	401	327	282	346	439	424	395	400	309	504
Tel Hadya 1990 +	318	221	232	379	305	295	505	228	265	294
Izra'a 1989 -	228	171	226	203	192	171	221	279	266	173
Breda 1989 +	209	125	212	169	264	151	142	155	251	204
Breda 1989 -	214	146	242	123	154	133	122	157	289	184
Izra'a 1989 +	186	130	219	128	131	166	183	195	185	160

- = at natural soil fertility
+ = with additional fertilizer

yield on the basis of landrace groups proved more successful (Tables 5.1 and 5.7). Haurani, the most widespread landrace within Syria, performed relatively well to very well in all experiments; in contrast to Baladi, which generally performed relatively poorly. The Bayadi, Sweidi and Shihani landrace groups had their comparative tops in the lowest, medium and highest yielding experiments, respectively. Sheirieh performed well, except in the lowest yielding experiment, and Hamari was variable.

5.4 Discussion

Under Syrian arid conditions, yield levels are closely related to available water and soil fertility. Residual soil moisture from the previous season in Homs was reflected in higher yields. Higher radiation at Breda than at other locations may have intensified the water stress. Although high temperatures during grain filling can reduce the thousand kernel weight (Ehdaie & Waines, 1988; Wardlaw et al., 1989), water stress at Breda, Izra'a and Tel Hadya seems to have dominated. At Homs, where more water was available, thousand kernel weight was higher.

Yields of landraces under sub-optimal conditions demonstrate that selection of locally adapted plants can contribute to achieve breeding goals. Previously, Nachit et al. (1988) found that certain landraces possessed desirable traits lacking in other germplasm, such as resistance to drought and cold, early plant vigour and long peduncle. However, these traits are not common to all landraces. Furthermore, landrace populations showing superior performance under all conditions could not be identified (cf. significant population effect in Table 5.4). And at more favourable locations grain yield of varieties was higher than mean grain yield of landraces (cf. Ehdaie et al., 1988). The high variability in grain yield of landrace populations reflects different response to environmental variation. This may be related to the fact that traditional Syrian agriculture has developed into a situation of geographical diversification of populations (Chapter 3) with buffer capacity based on their genotypically heterogeneous nature to account for seasonal environmental variation.

Grain filling rate may be source limited, i.e. determined by the supply of assimilates, or sink limited, i.e. determined by the temperature-dependent potential rate of dry matter accumulation in the kernels (van Keulen & Seligman, 1987; Sofield et al., 1977). Relations between spike density, number of kernels per spike and grain yield are well described by the strong linear correlation between kernel density and grain yield. However, since this is not proven to be a causal relation, it can not be deducted that grain filling duration (which under conditions of drought stress after flowering corresponds with post-anthesis green area duration) and kernel density were the only major yield determining factors. Water stress may have resulted in reduced source capacity.

Drought in itself may have affected the ear-bearing tiller number, by affecting by the tiller survival rate (Blum & Pnuel, 1990), and post-anthesis green area duration, whose limited length may have exhausted more rapidly stem reserves. Landrace populations and check varieties showed comparable yield reduction with decreasing water availability, hence neither seems capable of maintaining grain yield level under severe drought stress.

Fertilizer application positively influenced total biomass production, though not significantly (see Table 5.5), but only at Homs and Breda 1989 did grain yield increase. The generally negative effect on kernel density reflected in lower grain yields. This effect is different from the normally positive effect of increased nitrogen availability on the kernel number (van Keulen & Seligman, 1987). The one-day delay of anthesis, as observed at Tel Hadya 1990, shortened the already limited grain filling period.

The significant population effect for grain yield contrasts with the stability for total biomass production among populations (Table 5.4). On the other hand, a year effect was found for total biomass production, and not for grain yield. Harvest index is affected differently over populations, years, locations and fertilizer levels.

The number of significant correlations between collection site characteristics and plant characters at evaluation is limited, but the majority of relations has equal sign (Table 5.6). In combination with the generally consistent interrelationships among plant characters, this facilitates interpretation of a specific experiment in terms of forecasting crop behaviour under different growth conditions.

Surprisingly, relating grain yield to landrace groups resulted in more pronounced clusters than relating to regions of origin. Although variation within groups was wide, this observation suggests that genotypes within the landrace groups of the T. turgidum var. durum sub-species are relatively uniform. Nevertheless, it remains probable that plant characters are largely determined by the environment in the domestication area. If so, then it must be concluded that durum wheat landrace groups have been domesticated within relatively small areas with specific climatic conditions, followed by dispersion of some groups without losing characteristics. This probably has occured only recently, since otherwise dispersed landrace groups would have been less uniform in agronomic characteristics due to different environmental pressure.

Regions with moderate climatic conditions provided landraces with relatively stable yields. This observation supports the practice of utilization of germplasm from such regions. Only for regions where specific stress factors are prevailing, germplasm from regions with more extreme environmental conditions may be more useful.

An effective first step in evaluation of landrace germplasm seems to be taxonomic sub-classification, followed by agronomic evaluation of a representative part of the collection. Prediction of best performing accessions seems unlikely, but the fact that a number of correlations between collection site characteristics and evaluation results appear to have wider validity, suggests that experimental establishment of such relations may lead to identification of groups from which successful selections or crosses most likely are made.

Chapter 6

SIMULATION OF GROWTH AND DEVELOPMENT

Abstract

A crop growth simulation model, developed for spring wheat, was adapted to durum wheat and applied for analysis of the results of durum landrace evaluations. Thirty-eight landrace populations of durum wheat were evaluated for agronomic performance over two growing seasons at four locations in Syria, characterized by different rainfall patterns, at two levels of nutrient availability.

Under favourable environmental conditions, weather variability is reflected in the amount of reserve carbohydrates at the end of grain fill, and variation in grain yield among populations within a given experiment is mainly the result of differences in net flow of assimilates. Under low-yielding conditions, when early complete senescence leads to cessation of grain fill, higher grain yields are the result of more efficient remobilization of reserve carbohydrates, mainly due to higher kernel densities. Factors that influence grain filling duration are reflected in grain yield.

Total dry matter production was higher under higher total, and higher spring rainfall. At higher levels of moisture availability, more aboveground dry matter was produced per kg rainfall. Moisture and nitrogen availability interacted. At very low rainfall, moisture availability was the dominant growth limiting factor, whereas at higher levels of moisture availability, nitrogen recovery and total dry matter production increased, and nitrogen availability became an additional growth-limiting factor.

The low observed minimum straw nitrogen content of 0.0019 kg kg^{-1} appears to be partly a species characteristic, and partly a landrace characteristic.

Despite shortcomings, the model simulated a recognizable durum wheat crop and reproduced in a consistent way genotype x environment interactions and their effects on yields. Application of modelling in evaluation of extensive germplasm collections, through forecasting growth and development in diverse environments, would reduce quantitative and

qualitative limitations to evaluation programmes.

6.1 Introduction

Potential dry matter production of wheat in arid regions is limited by amount and distribution of rainfall (Buresh et al., 1990; Entz & Fowler, 1989). Stapper and Harris (1989) concluded on the basis of the results of a validated crop growth model and historical weather data, that with respect to weather variables, grain yields were most sensitive to rainfall and that timely sowing is important, as early canopy development restricts moisture losses by soil surface evaporation. In addition, nutrient deficiencies are widespread in the Mediterranean region and are a yield-limiting factor in many instances (Buresh et al., 1990; van Keulen, 1975; Matar & Brown, 1989).

In such environments, evaluation results of yield trials are strongly influenced by genotype x environment interactions, and extensive multilocational or multiseasonal evaluations are needed to assess plant characters. Such a costly procedure can often not be applied to entire germplasm collections, which may consist of many thousands of accessions. For example, the Genetic Resources Unit of ICARDA comprises about 17,500 accessions of durum wheat (ICARDA, 1992). Initial selections are made on the basis of preliminary characterization and evaluation (IBPGR, 1985), carried out during one or a few seasons. The consequence is that part of the useful germplasm may not be recognized, and hence not utilized. An efficient evaluation method is therefore required, that allows investigation of large numbers of accessions under various climatic conditions.

Crop growth simulation models dynamically simulate dry matter production and phenological development, incorporate plant and site characteristics, and account for their interactions, within defined system boundaries (de Wit, 1982), and excluding processes of supposedly minor importance. Crop models facilitate extrapolation of effects at the level of single plant organs to the growth of a canopy in a continuously changing field environment (Spitters & Schapendonk, 1990). A well-calibrated simulation model offers a comprehensive tool to analyze genotype x environment interactions, and can assist in germplasm evaluation and selection for specific environmental conditions.

Simulated growth and development will mostly to some degree deviate from reality. However, in preliminary evaluation, some error is acceptable, as curators are interested in a general overview of an entire collection, rather than in performance of individual populations under specific conditions. Subsequent detailed evaluations may provide additional information on plant properties.

This paper reports on application of an adapted crop growth simulation model for spring wheat in analyzing multilocational, multiseasonal evaluation data for durum wheat landraces in an arid Mediterranean environment.

6.2 Materials and methods

6.2.1 Field evaluations

Collection missions for durum wheat landraces [*Triticum turgidum* L. var. *durum* (Desf.) MK] in the Syrian Arab Republic in 1987 and 1988 yielded a collection of germplasm representative for various agro-ecological regions (van Slageren et al., 1989). Thirty-eight populations, whose putative origin was at or in the vicinity of their collection sites, were evaluated for agronomic performance over two growing seasons, viz. 1988-89 and 1989-90, at four locations in Syria, viz. Tel Hadya, Breda, Homs, and Izra'a (Table 5.2), characterized by different climatic conditions. Details on experimental design, weather conditions, observed data, and establishment of relations between plant and collection site characteristics have been reported in Chapter 5. Natural fertility represented one level of nutrient availability, while a second level was created through application of nitrogen at a rate of 40 kg ha^{-1} at Tel Hadya, Breda and Izra'a, and 60 kg ha^{-1} at Homs, and phosphorus at a rate of 40 kg ha^{-1}. Three check varieties were included in the experiment: Haurani-27, a local landrace; Cham 1, a variety suitable for high input conditions; and Cham 3, a more stress tolerant variety than Cham 1.

Previously reported observations included grain and straw yield, tiller density, grain density (Chapter 5), and late season frost damage (Chapter 7). Additionally, phenological development stages (Zadoks et al., 1974), death of flag leaves, stems and spikes, and grain dry matter content were determined at about weekly intervals at ICARDA's principal experimental farm at Tel Hadya, during 1989-90. Results of Tel Hadya 1988-89 were omitted because of premature leaf yellowing in early March.

As flag leaves, stems and spikes remained completely green until anthesis, their relative green area at that moment was defined as 100%,

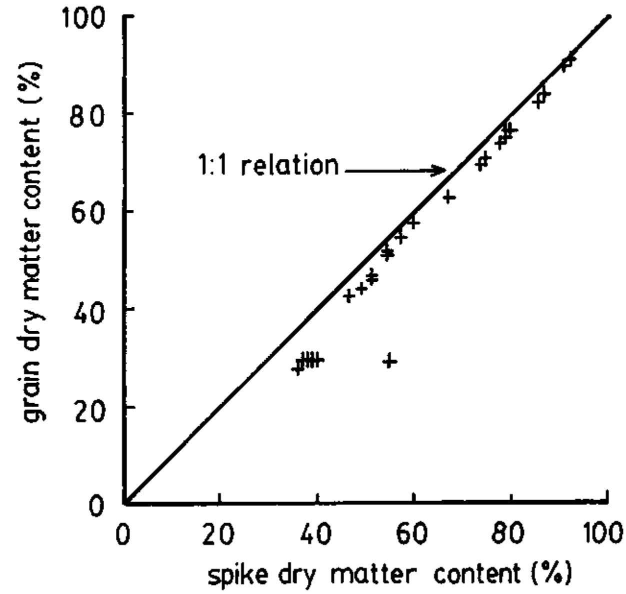


Figure 6.1. The observed relation between grain dry matter content and total spike dry matter content. Crosses and the solid line represent observations and the theoretical 1:1 relation, respectively.

and subsequent death was estimated from their relative discolouration.

End of grain filling can be established from grain dry matter content, since, after cessation of transport of water to the grains, water loss continues and grain dry matter content sharply increases (van Keulen and Seligman, 1987). As a nearly 1:1 relation was observed between complete spike and grain dry matter content (Figure 6.1), the former was used as indicator. Four randomly selected spikes per plot were harvested and transferred to a refrigerator; total fresh weight was determined the same day, and total dry weight after drying for 48 hours at 120 °C in a ventilated oven.

Seed and straw nitrogen contents were determined at maturity by near-infrared reflectance and microkjeldahl analysis, respectively (Williams et al., 1988). Nitrogen use efficiency was calculated as total aboveground dry matter production (kg ha^{-1}) divided by total nitrogen uptake (kg ha^{-1}), and three-quadrant graphs (van Keulen, 1986) for population averages were constructed per year and site. The initial slope of the yield-nitrogen uptake curve is called initial efficiency, and was calculated as:

1/(0.01 + 0.004 x straw weight/grain weight) (van Keulen, 1986).

The proportion of applied nitrogen taken up by the aboveground plant material is defined as the nitrogen recovery fraction.

6.2.2 Model description

The simulation model applied to study the effects of genotype and environment on growth and development was adapted from the spring wheat model described by van Keulen and Seligman (1987). A FORTRAN-version runs in the FORTRAN Simulation Environment (van Kraalingen, 1991). Daily values of rainfall, maximum and minimum air temperature, total global radiation, air humidity and wind run are required weather inputs. Sets of soil and plant parameters characterize the soil environment and plant genotype, respectively. The soil moisture balance is described on the basis of 10 soil layers, for each of which daily changes in soil moisture content are tracked. Crop transpiration is dependent on live canopy leaf area, rooted depth and soil moisture status. The soil nitrogen balance includes organic nitrogen in stable organic matter, in labile fresh organic matter, and in microbial biomass, and mineral nitrogen. The model includes descriptions of the effects of soil moisture and nitrogen availability on growth.

Dry matter accumulation is based upon daily gross CO_2-assimilation, calculated as a function of daily radiation, total green canopy area and the photosynthesis-light response curve of individual leaves, characterized by its initial light use efficiency and maximum assimilation rate (Goudriaan, 1986; Spitters, 1986; Spitters et al., 1986). Daytime air temperature below 10 ^{o}C, soil moisture status and nitrogen status of the crop affect gross assimilation. Maintenance and growth respiration are accounted for. Phenological development is a function of average temperature only, neglecting photoperiod sensitivity and vernalization requirements. Partitioning of assimilates to roots, leaf blades, stems and leaf sheaths, and a reserve pool is governed by crop phenological development and modified by moisture and nitrogen availability. Assimilates from the reserve pool may be remobilized, before anthesis for growth of vegetative organs, after anthesis for grain growth. Organ formation includes tillers, spikes, spikelets, fertile florets and finally grains. The rate of organ initiation is proportional to the rate of carbohydrate supply to the meristematic sites during the successive development phases and inversely proportional to the rate of development. It is influenced by temperature through development rate and assimilation, and by moisture and nitrogen availability through assimilate availability. Nitrogen availability only affects tiller formation directly.

6.2.3 Model modifications

The model, that was calibrated for modern bread wheat varieties, had to be modified for durum wheat landraces (Table 6.1). In comparison to modern wheat varieties, landraces are generally characterized by more and longer roots, lower harvest indices, less kernels per m^2 and per spike, more leaves, higher tiller production, but lower tiller survival, which results in lower assimilate utilization efficiency, restricted response to nitrogen application, and higher tolerance to environmental stresses. These characteristics are reflected in relatively stable yields, viz. low potential grain yields under favourable growth conditions, but restricted reductions in dry matter production and grain yield under environmental stress (Ehdaie & Waines, 1989; Hawkes, 1983).

Durum wheat belongs to the tetraploid wheats, an intermediate stage between diploid and hexaploid wheats with respect to average photosynthetic and transpiration rates (Araus et al., 1989; Kaminski et al., 1990). However, as within-species variation is high (cf. Ecochard et al., 1988), and own observations at different levels of soil moisture and nitrogen availability (Heitholt et al., 1991) were not available, calibration for photosynthesis was not performed.

Simulations started well before sowing, since early season rains appeared to affect final dry matter production. Initial moisture contents of soil compartments were selected such, that early-season root growth was just not hampered. Only for Homs residual soil moisture was assumed because of high rainfall and supplementary irrigation in the preceding seasons. Since information on soil mineral N was not available, its distribution over soil compartments was derived iteratively from simulated nitrogen uptake by the crop.

Table 6.1. Added and modified model input, exclusive site specific weather and soil data.

Acronym	Description	Unit	Value**
AGEFT	Relative green area of spikes as function of development stage	-	0 , 0 0.47, 0 0.49, 1 0.8 , 1 0.85, 0 1.1 , 0
CROHTB	Crop height as function of development stage	m	0 , 0 0.3, 0.2 0.5, obs. 1.1, obs.
CULTM	Parameter to modify post-anthesis development rate	unitless	1.2
DIV*	Balance of dry matter distribution between main shoot and tillers	unitless	2
FACT1*	Parameter to modify pre-anthesis development rate	unitless	obs.
FNEXT	Fraction of labile nitrogen exported from vegetative tissue to the grain, as a function of average nitrogen concentration in the vegetative tissue	-	0 , 0 0.0025, 0 0.007 , 0.3 0.012 , 0.5 0.016 , 0.44 0.02 , 0.4 0.025 , 0.36 0.0375, 0.24 0.07 , 0.16
FROSTL*	Relative death rate of leaves due to late frost damage	d^{-1}	obs.
PGRIGT	Potential growth rate of individual grains as function of air temperature	-	0, 0 8, 0 10, $7.5x10^{-7}$ 16, $2.025x10^{-6}$ 20, $2.475x10^{-6}$ 25, $2.775x10^{-6}$ 30, $3x10^{-6}$ 35, $3x10^{-6}$
RED1*	Empirical parameter in relative death rate of leaf blades due to water shortage	unitless	0.4
RED2*	Empirical parameter in relative death rate of stems due to water shortage	unitless	0.7
RGRL	Relative growth rate of leaf area in exponential leaf area growth phase	unitless	0.014
TLNFIN*	Final main stem and tiller number	unitless	obs.
TLNSEC*	Number of tillers per plant	unitless	2.5

* : new input
**: obs. = observation

Table 6.2. Timing of average phenological development stages (Zadoks et al., 1974) for durum wheat landraces during the 1989-90 growth cycle at Tel Hadya, Syria.

Julian calendar day (1990)	Phenological development stage		
	without fertilizer	with fertilizer	description
3	13	13	3 leaves unfolded
24	22	22	main shoot and two tillers
31	22.5	22.5	2.5 tillers
42	30	30	pseudo stem elongation
80	31	31	first node detectable
96	41	41	flag leaf sheath extending
102	49	49	first awns visible
110*	65		anthesis halfway
111**		65	anthesis halfway

* : equals 991 d°C
**: equals 1008 d°C

Pre-anthesis development rates were derived from observed flowering dates and temperature sums at Tel Hadya 1989-90 (Table 6.2).

Early drought may cause premature senescence of tillers or plants. To more accurately describe this process, a distinction was made between main shoots and tillers. A tiller was assumed to receive half the assimilates of the main shoot, and temperature sums were tracked separately. Pre-anthesis loss of biomass due to drought was reflected in reduced tiller weight, while main shoots were assumed unaffected until death of all tillers. As plant organ dynamics appeared difficult to simulate accurately, tiller density was introduced as a forcing function, characterized by sowing density, formation of 2.5 tillers per main shoot (Table 6.2), and observed final tiller density. Spike density was set equal to tiller density at anthesis, and grain density was based on field observations.

Sink-limited, temperature-dependent, exponential growth of the green leaf area, as described by Spitters et al. (1989), was introduced. Following their suggestions, the development stage (DVS) for the switch from sink-determined to source-determined growth rate was set at 0.15 and the relative growth rate at 0.014 per unit degree-day.

The effects of late season frosts were derived from experimental data (Chapter 7) and described by a fractional decline in green leaf weight and area, for each day after floret initiation with daily minimum air temperature below -4 °C.

Since anthesis generally followed heading within 2-4 days, the function relating development stage to relative green area of the ears was adapted to spike appearance at DVS = 0.47. Calculation of stem green area, based on total plant height, was subsequently adjusted to a maximum spike length of 10 cm.

As grain yield was initially underestimated due to sink limitations, the potential grain filling rate at 30 °C was set to 3×10^{-6} kg $grain^{-1}$ d^{-1} (Pinthus, 1963).

In the original version of the model, death due to water shortage was underestimated, and post-anthesis green area duration and length of the grain filling period were overestimated. Therefore, relative death rate of leaf blades after anthesis due to water shortage was defined as the maximum of the potential death rate due to dehydration, and the relative transpiration deficit, multiplied by an empirical factor. Death of stems and spikes after anthesis followed that of leaf blades with an observed delay of eight days, with a relative death rate derived from that of the leaves by multiplying by an empirical factor.

Nitrogen translocation from the vegetative material to the grains is determined by either the demand of the grains or the supply from the vegetative parts. Simulation results showed that initially the potential rate of nitrogen accumulation in the grain was limiting, and only at later stages the supply rate. Initial results showed insufficient nitrogen translocation and consequently underestimation of grain nitrogen accumulation. Export from the vegetative tissue in the model was therefore enhanced by increasing the relative rate of nitrogen turnover in the vegetative biomass, and doubling the potential fraction of labile nitrogen exported to the grains.

6.2.4 Water use

Water use efficiency (WUE) was defined as total aboveground biomass (kg dry matter ha^{-1}) divided by total rainfall (kg ha^{-1}), the water use coefficient (WUC) as total transpiration (kg ha^{-1}) divided by total gross photosynthesis (kg CO_2 ha^{-1}), and the transpiration coefficient (TC) as total transpiration (kg ha^{-1}) divided by total aboveground biomass (kg dry matter ha^{-1}) (de Wit, 1958).

6.3 Results

6.3.1 Field evaluations

Soil characteristics at sowing, as presented in Table 5.2, show that at Izra'a and Homs soils at the beginning of the 1989-90 season were characterized by relatively low carbon/nitrogen ratios.

Phenological development of fertilized and unfertilized crops was similar throughout most of the growing season prior to anthesis (Table 6.2), which was significantly delayed by one day in the fertilized treatment (Chapter 5). This could be an indirect effect of nitrogen shortage through increased canopy temperature (van Keulen & Stol, 1991).

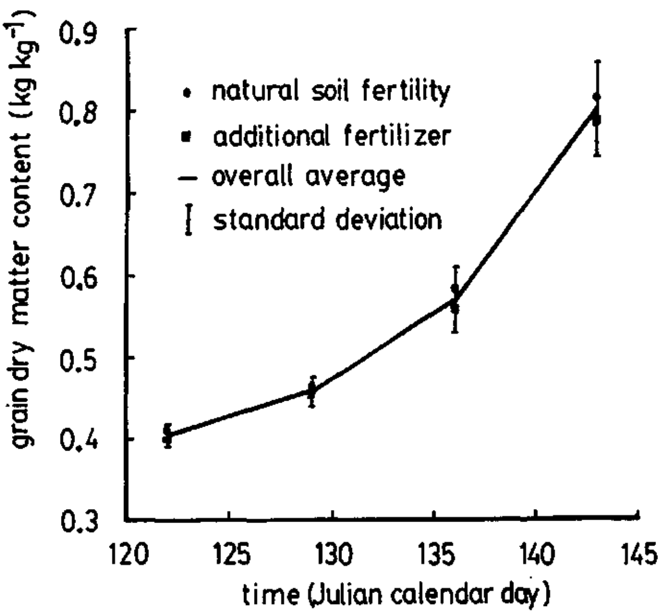


Figure 6.2. Grain dry matter content as a function of time, at natural soil fertility and additional fertilizer application. The standard deviation refers to the overall average.

Grain dry matter content was not significantly influenced by fertilizer application (Figure 6.2). Combined data for all populations showed increasing variation in time. At complete senescence, grain dry matter content was about 0.45 kg kg^{-1}, i.e. below the value of 0.65 kg kg^{-1} that generally characterizes physiological maturity (van Keulen & Seligman, 1987), and was reached about 10 days later.

Average grain and straw yields, grain and straw nitrogen contents and uptake, nitrogen harvest index and nitrogen use efficiency per experiment are presented in Table 6.3. Variation among years and locations in nitrogen uptake, in combination with highly variable dry matter production and harvest index, resulted in wide variation in nitrogen contents in both grain and straw. Dry matter production and grain yield were positively correlated with nitrogen harvest index (NHI), with the exception of Breda 1989-90. Total dry matter production was also positively correlated with NUE.

Fertilizer application had variable effects (Figures 6.3a to d). At Breda, neither nitrogen uptake nor grain yield were affected. At Izra'a, grain yield was not affected in either season, but in the more favourable 1989-90 season nitrogen uptake increased. However, late season moisture stress then caused early senescence and cessation of grain filling. Therefore, at Breda and Izra'a, moisture availability appeared the dominant growth-limiting factor. At Homs 1988-89, natural soil fertility was high, and as grain yield was higher under fertilizer application without higher nitrogen uptake, nitrogen availability appears non-limiting. In the 1989-90 season however, at substantially lower natural soil fertility, nitrogen application (recovery fraction 0.15) resulted in increased total dry matter production and grain yield, hence nitrogen availability was growth-limiting. At Tel Hadya 1989-90, moisture availability allowed an intermediate level of total dry matter production (2.2 ton ha^{-1}), and at low natural soil fertility, fertilizer application with a recovery fraction of 0.16 resulted in a slight increase in total dry matter. However, grain yield was lower, as a direct consequence of lower kernel density (Chapter 5). A significant nitrogen recovery fraction, even though very low in most cases, was always associated with an increase in total dry matter or grain yield.

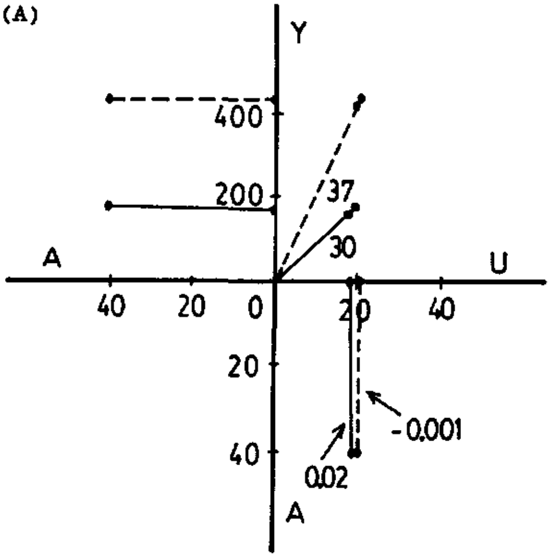
Data from individual experiments showed that minimum straw nitrogen concentrations below 0.004 kg kg^{-1} were reached at Izra'a 1989-90 and in

Table 6.3. Observed (o) and simulated (s) grain and straw yield (assuming 10% moisture content), grain and straw nitrogen (N) content, grain and straw nitrogen uptake, nitrogen harvest index (NHI), and nitrogen use efficiency. Values are averages over 38 landrace populations, hence the difference between the sum of average grain and straw nitrogen and actual average total nitrogen uptake.

Location and season	o,s	N dressing (kg ha^{-1})	Yield (kg ha^{-1})		N content (%)		N uptake (kg ha^{-1})				NHI	N use efficiency (kg kg^{-1})
			grain	straw	grain	straw	grain	straw	total	calculated total		
Tel Hadya	o	0	376	1774	2.30	0.76	8.31	13.24	24.99	21.55	0.38	84.1
1989-90	o	40	297	1895	2.74	1.09	7.76	20.31	31.92	28.07	0.27	68.7
	s	0	376	2254	1.68	0.72	6.05	16.33	22.31	22.38	0.27	85.6
	s	40	290	2367	1.76	0.70	4.87	16.77	21.48	21.64	0.22	85.9
Breda	o	0	172	987	3.18	1.27	5.47	12.78	20.24	18.26	0.31	55.8
1988-89	o	40	178	1017	3.22	1.31	5.72	13.50	21.39	19.21	0.31	53.3
	s	0	162	827	1.68	1.93	2.76	15.73	18.57	18.49	0.14	40.6
	s	40	164	847	1.68	1.85	2.74	15.72	18.59	18.46	0.15	41.5
Breda	o	0	434	1400	2.70	0.64	11.68	8.99	23.46	20.67	0.57	68.3
1989-90	o	40	431	1438	2.67	0.63	11.47	9.15	23.28	20.62	0.56	70.1
	s	0	316	1584	1.76	1.08	5.49	17.34	22.67	22.83	0.24	59.0
	s	40	291	1621	1.82	1.06	5.25	17.31	22.38	22.56	0.23	59.1

Homs	o	0	2020	5161	2.14	0.51	44.28	30.08	79.85	73.92	0.64	80.8
1988-89	o	60	2279	5541	2.07	0.48	46.93	27.99	84.71	74.71	0.65	80.2
	s	0	2350	4402	1.57	0.80	36.25	36.52	72.88	72.77	0.51	84.6
	s	60	2487	4472	1.55	0.77	38.37	34.52	72.95	72.89	0.53	86.2
Homs	o	0	1284	5547	2.00	0.36	25.71	20.30	50.27	46.01	0.59	131.3
1989-90	o	60	1418	5756	2.17	0.42	30.28	24.50	60.90	54.78	0.58	111.6
	s	0	1494	3472	1.54	0.74	22.21	26.29	47.62	48.50	0.46	84.5
	s	60	1640	3273	1.49	0.77	23.66	25.90	48.50	49.56	0.48	84.5
Izra'a	o	0	200	1102	3.21	0.88	6.36	9.79	17.88	16.15	0.40	67.9
1988-89	o	40	163	1233	3.36	1.08	5.45	13.30	20.55	18.75	0.29	66.2
	s	0	282	1262	1.68	0.90	4.69	11.25	16.03	15.94	0.29	71.9
	s	40	232	1350	1.72	0.84	3.94	11.34	15.41	15.28	0.25	72.9
Izra'a	o	0	765	3833	2.16	0.32	16.32	12.76	31.24	29.08	0.59	132.0
1989-90	o	40	754	4948	2.63	0.48	19.59	24.60	47.20	44.19	0.47	113.9
	s	0	438	1576	1.13	1.57	4.91	24.69	29.74	29.60	0.17	57.4
	s	40	473	1639	1.06	1.53	4.91	25.01	30.06	29.92	0.16	60.0

(A)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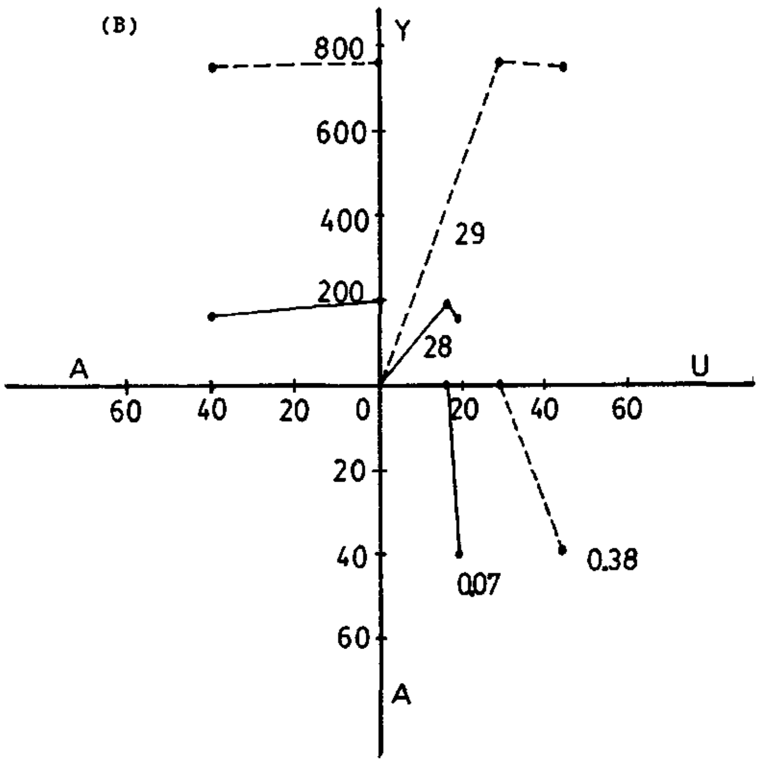
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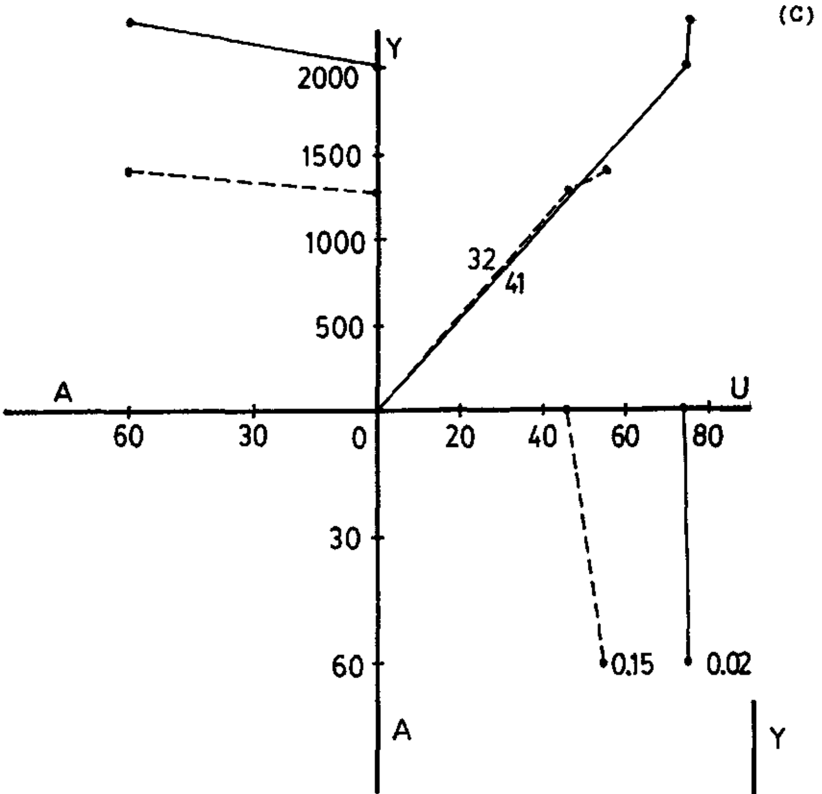

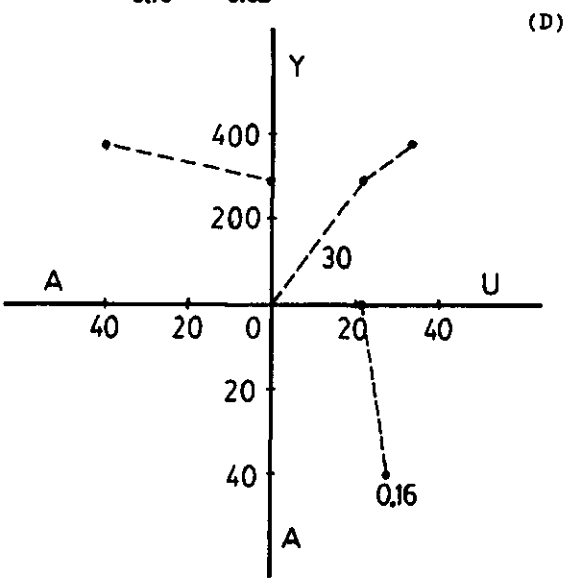

Figure 6.3. The average relations between nitrogen uptake and grain yield, between application and nitrogen uptake, and between nitrogen application and grain yield for durum wheat landraces at Breda (a), Izra'a (b), Homs (c), and Tel Hadya (d), respectively. Solid lines and dashed lines represent the 1988-89 and 1989-90 seasons, respectively. Initial efficiency and nitrogen recovery fraction are given by the figures in the first and fourth quadrant, respectively. A = nitrogen application (kg ha^{-1}), U = nitrogen uptake (kg ha^{-1}), Y = grain yield (kg ha^{-1}).

both seasons at Homs, with an absolute minimum of 0.0019 kg kg^{-1}. Lowest straw nitrogen concentration in the check varieties was 0.0025 kg kg^{-1}, and lowest grain nitrogen concentration in landrace populations 0.0151 kg kg^{-1}. Initial efficiencies ranged from 27 to 30 kg kg^{-1} (Figures 6.3a to d), with the exception of Breda 1989-90 and Homs 1988-89, with values of 37 and 41 kg kg^{-1}, respectively.

6.3.2 Simulation of growth and development

Differences in sowing dates and temperature regimes among locations and years resulted in different development patterns in the vegetative stage. However, development stages (DVS) converged towards anthesis. Grain filling generally ceased before physiological maturity.

Green area index (GRAI, Figure 6.4) varied little among populations at a given location. Higher values of maximum GRAI generally coincided with higher values for total dry matter production and grain yield. At Homs, simulated senescence was completed 1-2 weeks later than at the other locations, which matches unrecorded observations during irregular field visits. Sharp increases in GRAI followed the end of the exponential leaf area growth phase and the onset of stem elongation (DVS=0.175).

Populations in a given experiment showing different yields, generally differed not significantly in simulated weight of other plant organs. Higher grain yields were the result of increased remobilization of reserve carbohydrates, which was also the main cause of variation in straw yield. Under favourable growing conditions, as at Homs, reserve carbohydrates were fully depleted, whereas under unfavourable conditions, as at Breda, complete senescence caused termination of grain filling before physiological maturity was reached, and the reserve pool was not depleted.

Observed dry matter production per population was very variable among locations and years, and an overall best performing landrace was not identified (Chapter 5). Average simulated grain and straw yields per evaluation site and fertilizer regime are given in Table 6.3. Observed and estimated grain yields lower than 1000 kg ha^{-1} mostly corresponded with a maximum error of 140 kg ha^{-1}, but under more favourable conditions, grain yields were overestimated and straw yields underestimated. Total dry matter production was strongly underestimated for Izra'a 1989-90, and

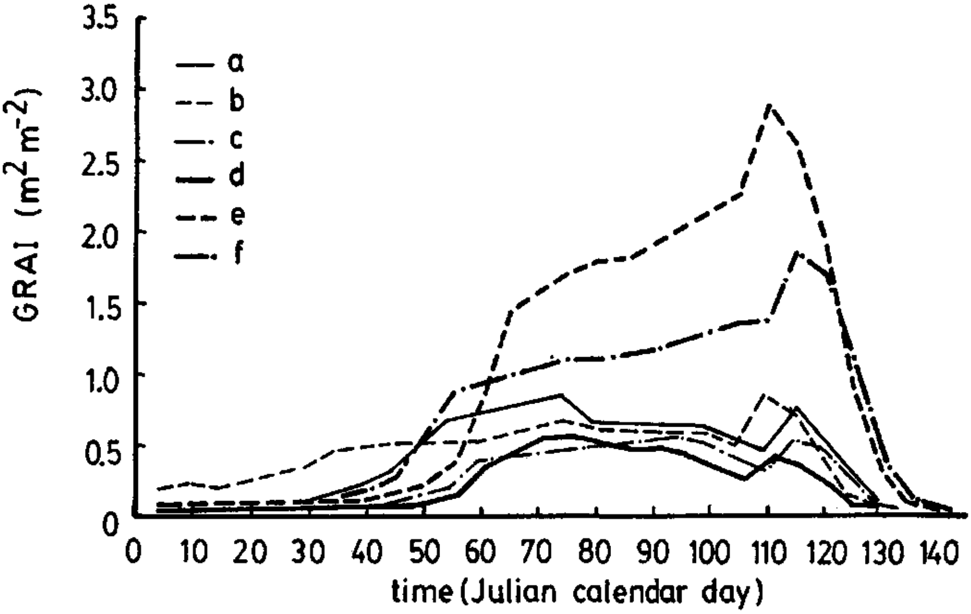

Figure 6.4. Simulated green area index (GRAI) of population ICDW 19521 grown at natural soil fertility, at various locations and years. a = Breda 1989-90, b = Tel Hadya 1989-90, c = Izra'a 1988-89, d = Breda 1988-89, e = Homs 1988-89, f = Homs 1989-90.

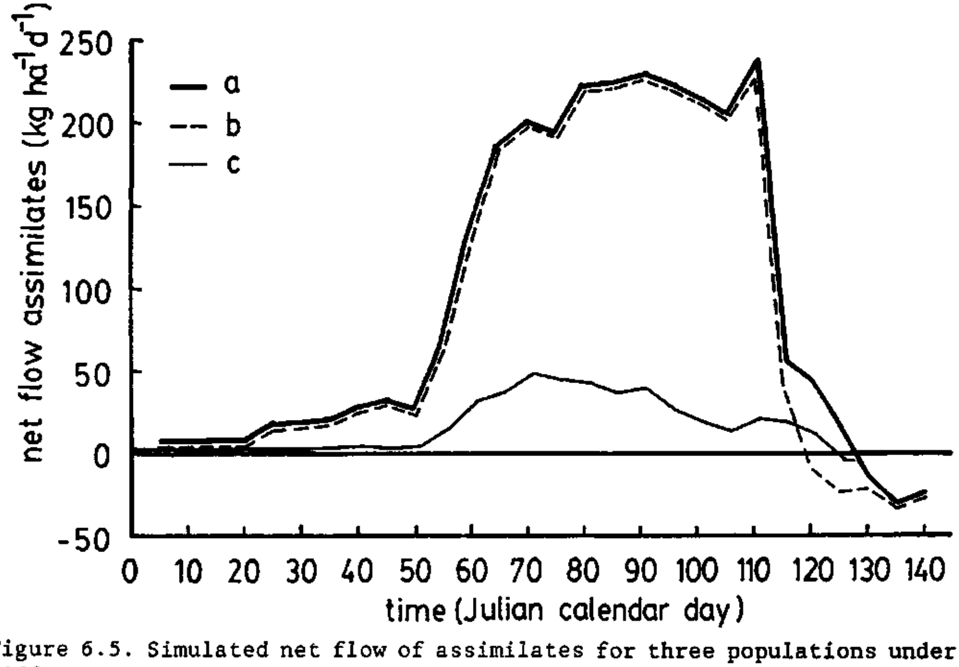

Figure 6.5. Simulated net flow of assimilates for three populations under different growing conditions. a = ICDW 19521 at Homs 1988-89, b = ICDW 19574 at Homs 1988-89, c = ICDW 19558 at Breda 1988-89.

could only be corrected by assuming a higher soil nitrogen content, which, however, resulted in strong overestimation of nitrogen uptake. Assuming additional soil moisture supply at various moments during the growing season did not improve the simulation results.

Examples of the net flow of assimilates, i.e. the difference between gross assimilation rate and maintenance respiration rate, are given in Figure 6.5. At Homs 1988-89 maintenance requirements for ICDW 19521 and ICDW 19574 were about similar, but assimilation rates for the former were higher after day 115, resulting in higher grain yield, viz. 2.8 and 1.8 ton ha^{-1}. Also in low-yielding environments, net flow of assimilates became negative towards the end of the growth cycle, but without consequences for yield, since the reserve pool was not depleted.

Grain growth rate at Homs 1988-89 was constant for 18 days at about 130 kg ha^{-1} d^{-1}, after which it slowly decreased, reaching zero when the reserve carbohydrates were exhausted, well before physiological maturity. Grain filling in lower-yielding environments followed similar patterns, but at lower rates (e.g. about 10 kg ha^{-1} d^{-1} at Breda 1988-89).

6.3.3 Nitrogen balance

Validation of the nitrogen balance (Table 6.3) was aimed at achieving a realistic balance of grain and straw yield, and grain and straw nitrogen contents at harvest.

Despite model modifications, simulated nitrogen translocation to the grains was consistently underestimated, so that the final nitrogen harvest index was too low in all cases (Table 6.3). Simulated nitrogen contents in the vegetative tissue at maturity available for translocation (AVN) were at most five kg ha^{-1}, except for Breda, where higher values were found. Translocation is thus limited by this low value of AVN, and also associated with the low weight of live vegetative tissue. In principle, AVN can be increased by assuming a lower level of residual non-remobilizable nitrogen in the vegetative tissue, which would be supported by the observed low straw nitrogen contents. However, that hardly affected the simulated translocation rates because of the low weight of live vegetative tissue. Accelerating translocation by increasing the temperature-dependent potential rate of nitrogen accumulation in the grains, resulted in higher grain nitrogen contents. However, experimental data to support this modification were not available.

Simulated grain nitrogen uptake for the highest yielding population (ICDW 19521) at Homs 1988-89 under additional fertilizer (Figure 6.6), shows that potential rate of nitrogen accumulation in the grains was limiting for about one week after the onset of grain fill, and subsequently potential rate of nitrogen export from the vegetative tissue. In lower-yielding environments, where grain filling duration was shorter, potential rate of nitrogen accumulation was the predominant limiting factor.

6.3.4 Water use

Simulated WUE, WUC and TC are given in Table 6.4, calculated on the basis of average plant characteristics per experiment. At higher levels of moisture availability, more aboveground dry matter is produced per unit rainfall, and less water is transpired per kg aboveground dry matter. Assimilation in terms of water use was most efficient at Breda 1989-90, and least efficient at Homs 1988-89. On the whole, there seems to be no relation with total dry matter production.

Rainfall distribution strongly influences all three variables. Seasonal rainfall was comparable in both seasons at Breda, however total dry matter production in 1989-90 was about 1.5 times that in 1988-89, when a larger proportion of precipitation fell early in the growing season, and was lost by soil surface evaporation resulting in lower seasonal crop transpiration. Also Izra'a 1988-89 and Tel Hadya 1989-90 received comparable amounts of precipitation, but as rainfall distribution was more favourable at Tel Hadya, seasonal transpiration and total dry matter production were higher here.

A strong positive correlation exists between total seasonal crop transpiration and total dry matter production (Tables 6.3 and 6.4). In general, differences in total crop transpiration between experiments increased after the onset of stem elongation. With the exception of both seasons at Homs, and to a less extent Izra'a 1988-89, in all environments high relative transpiration deficits were simulated during the major part of the growing season (e.g. ICDW 19521, see Figure 6.7).

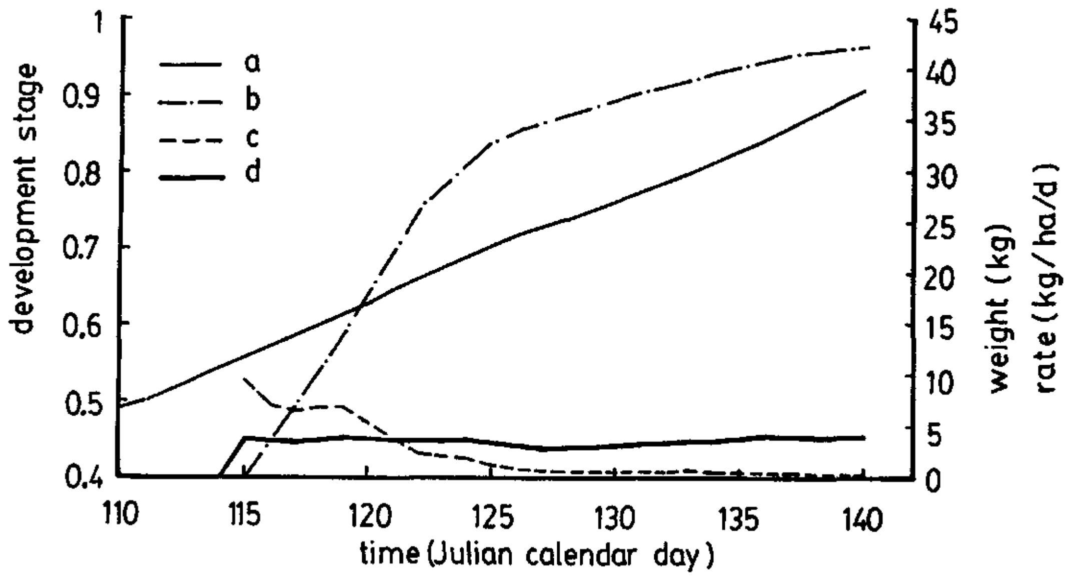

Figure 6.6. Simulated development stage, potential rates of nitrogen export and uptake, and grain nitrogen content of population ICDW 19521 grown at Homs 1988-89 with additional fertilizer. a = development stage, b = grain nitrogen weight, c = potential rate of nitrogen export, d = potential rate of nitrogen uptake.

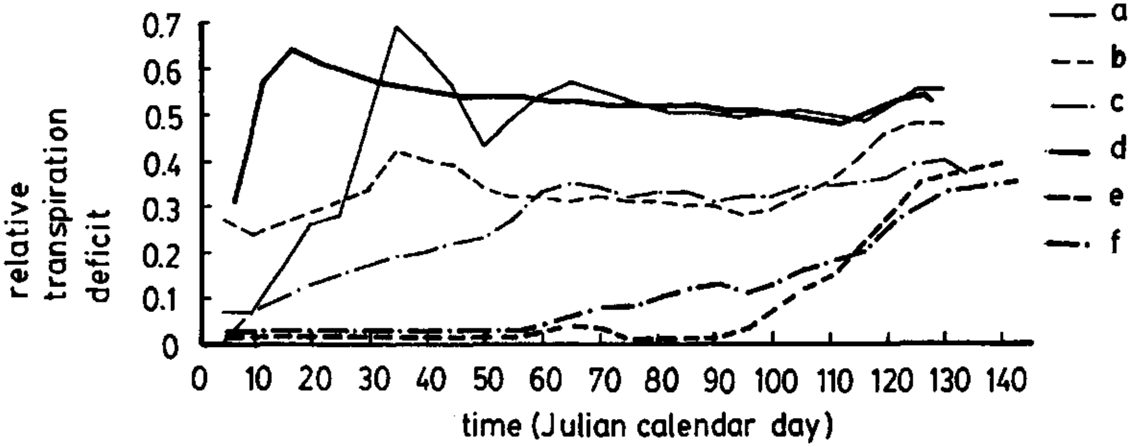

Figure 6.7. Simulated relative transpiration deficit of population ICDW 19521 grown at natural soil fertility, at various locations and years. For key, see legend of Figure 6.4.

Table 6.4. Total seasonal precipitation, and simulated total seasonal transpiration, water use efficiency, water use coefficient, and transpiration coefficient, using average plant characteristics at four evaluation sites during two growing seasons at two levels of nutrient availability.

Location	Season	Seasonal precipitation (mm)	Seasonal transpiration (mm)		Water use efficiency (10^{-3} kg kg^{-1})		Water use coefficient (kg kg^{-1})		Transpiration coefficient (kg kg^{-1})	
			-	+	-	+	-	+	-	+
Tel Hadya	1989-90	227	89	89	0.85	0.83	68	67	458	476
Breda	1988-89	190	58	61	0.40	0.41	82	83	764	786
	1989-90	178	67	70	0.70	0.77	50	50	536	512
Homs	1988-89	273*	211	213	2.22	2.31	87	87	348	338
	1989-90	218*	153	153	1.93	2.02	72	71	372	354
Izra'a	1988-89	222	69	69	0.52	0.51	85	81	593	611
	1989-90	264	77	82	0.66	0.69	80	80	440	453

* : residual soil moisture assumed
\- : natural soil fertility
\+ : additional fertilizer application

Table 6.5. Relative change (%) in simulated grain and straw yields, as a result of relative changes in input values, for Tel Hadya 1989-90 and Homs 1988-89, without fertilizer application. Each first and second datum represents the relative change in grain and straw yield, respectively.

Input	Relative change in input			
	Tel Hadya		Homs	
	-10%	+10%	-10%	+10%
Sowing density	0/ +2	0/ 0	+1/ +1	-1/ -1
Sowing date[1]	+4/+15	-40/+13	+14/ -4	+2/ -6
Tiller density	0/ -2	0/ +1	-1/ -1	+1/ 0
Tillers per plant	0/ +1	0/ -1	+1/ 0	-1/ 0
Dry matter distribution between main shoot and tillers	0/ -1	0/ +1	-1/ 0	+1/ 0
Plant height	0/ -1	0/ 0	+1/ -1	0/ +1
Pre-anthesis development rate	-55/+15	+9/ 0	+4/ -3	-3/ -1
Post-anthesis development rate	-10/ +1	0/ 0	0/ 0	+6/ 0
Initial light use efficiency	0/ -3	0/ +2	-4/ -2	+4/ +2
Threshold concentration of reserves beyond which assimilation is affected	0/ -9	0/ +7	-5/ -3	+10/ +1
Time constant for dehydration of tissue[2]	0/ 0	0/ 0	0/ 0	0/ 0
Average life span leaves	0/ -2	0/ +3	+5/ -2	+4/ +1
Maximum rate of root extension	0/ -7	0/ +3	-2/ -1	+1/ +2
Ratio of stem to leaf death, due to senescence	0/ +1	0/ -1	0/ 0	0/ 0
Proportionality factor between relative death rates of stem and sheaths and leaf blades	0/ 0	0/ 0	0/ 0	0/ 0
Proportionality factor between relative death rates of roots and stem and sheaths	0/ +1	0/ -1	+2/ 0	-1/ 0
Empirical parameter in relative death rate of leaves	0/ 0	0/ 0	0/ 0	0/ 0
Empirical parameter in relative death rate of stems and spikes	+8/ -2	-7/ -2	+4/ 0	-1/ 0
Reduction factor for leaf blade growth as function of relative transpiration deficit	0/ -3	0/ +1	0/ 0	0/ 0
Delay in death of spike and stem[3]	-13/ +2	+8/ +1	-9/ 0	+10/ 0
Potential grain filling rate	-10/ +2	+10/ -2	-3/ 0	+6/ 0
Floret density	-10/ +2	+10/ -2	-3/ 0	+6/ 0
Relative growth rate leaves in exponential leaf area growth phase	0/ +3	0/ +4	-2/ 0	+2/ -1
Development stage at end of growth exponential leaf area growth phase	0/ 0	0/ +6	0/ 0	0/ +6

Relative leaf death rate due to late frost	0/ 0	0/ 0	0/ 0	0/ 0
Basic relative rate of nitrogen turnover in vegetative biomass	0/ 0	0/ 0	0/ 0	0/ 0
Fraction labile nitrogen exported from vegetative tissue to grains	0/ 0	0/ 0	0/ 0	0/ 0
Level of residual non-remobilizable nitrogen in leaves	0/ +1	0/ -1	0/ 0	0/ -1
Level of residual non-remobilizable nitrogen in stems	0/ 0	0/ 0	0/ 0	0/ 0
Initial weight of fresh organic material in soil	0/ -1	0/ +2	0/ 0	0/ +2
Initial weight of stable organic material in soil	0/ 0	0/ 0	0/ 0	0/ 0
Initial weight of nitrogen in stable organic material in soil	0/ -1	0/ +1	0/ -2	0/ +2
Initial mineral nitrogen in soil	0/ -4	0/ +4	0/ -4	+1/ +5
Nitrogen application	0/ 0	0/ 0	0/ 0	0/ 0

1: changes in sowing date have intervals of one week
2: changes in time constant for dehydration of vegetative tissue have intervals of one day
3: changes in delay of death of spike and stem have intervals of one day

6.3.4 Sensitivity analysis

Table 6.5 summarizes the relative changes in simulated grain and straw yields resulting from 10% variation in both directions in the values of a series of initial conditions and parameters, for the low-yielding environment at Tel Hadya 1989-90, and the high-yielding environment of Homs 1988-89, under natural soil fertility, using average values for plant characters. *Unless indicated otherwise, responses for the fertilized* treatment were similar.

Advancing sowing date at Tel Hadya results in a shorter sink-limited growth phase due to higher temperatures in the early growth stages, and a longer source-limited growth phase, since anthesis is less advanced than DVS=0.15. This results in more vegetative tissue, and a slightly higher grain yield. Delayed sowing results in lengthening, respectively shortening of the vegetative and reproductive growth phases, and reduced grain yield. Advancing sowing date at Homs results in earlier anthesis, a longer grain filling period, and higher grain yield.

Lower pre-anthesis development rate at Tel Hadya delays the onset of grain filling and reduces the length of the grain filling period and grain yield. Straw yield increases due to a longer vegetative period, and more residual reserve carbohydrates. Lower post-anthesis development rate also delays the onset of grain filling, which, in combination with fixed senescence, results in lower grain yield. With fertilizer application, the onset of grain filling is not delayed, and grain yield remains constant. At Homs, the consequences of variations in pre-anthesis development rate for grain and straw yield are determined by the balance between the opposite effects on dry matter production and the associated accumulation of reserve carbohydrates on one hand, and maintenance requirements on the other. Variations in post-anthesis development rate influence the timing of the onset of grain fill. With additional fertilizer, lower development rates cause grain yield reductions.

Variations in the initial light use efficiency, and in the threshold concentration of reserves beyond which assimilation is affected, influence total dry matter production and reserve carbohydrate accumulation. At Tel Hadya, this affects straw yield, but not grain yield, as the pool of reserve carbohydrates is not depleted, whereas at Homs, also grain yield is affected.

In the fertilized treatment at Tel Hadya, a 10% decrease in average leaf life span causes a reduction in vegetative biomass, one day earlier complete senescence, and 8% lower grain yield. At Homs it results in lower maintenance requirement and a reduction in reserve carbohydrates. Hence, more carbohydrates are available for translocation to the grains. A longer average life span also results in a higher level of carbohydrate reserves at the onset of grain fill, and higher grain yields.

A lower maximum rate of root extension at Tel Hadya leads to a slight reduction in rooting depth and seasonal transpiration, with consequences for dry matter production and straw yield.

At Tel Hadya, the empirical parameter governing the relative death rate of stems and spikes, and the delay in the onset of stem and spike death following death of leaves influence the date of complete senescence, and thus grain filling duration, which is reflected in grain yield. At Homs, variations in the former parameter have less effect than at Tel Hadya, since the relative change in grain filling duration is smaller. Limited variations in the relative death rate of leaf blades due to water shortage do not affect the overall death rate after anthesis, which is dominated by the relative transpiration deficit.

At Tel Hadya, variations in potential rate of grain filling and floret density are fully reflected in grain yield, indicating that sink capacity is a dominant yield-determining factor. At Homs, variations in these plant characteristics are only partly reflected in grain yield, as reserve carbohydrate availability also plays a role.

At Tel Hadya, the relative growth rate of leaves in the exponential growth phase only influences straw yield. At Homs, however, higher values lead to higher dry matter production, more reserve carbohydrates, and higher grain yields.

The development stage marking the end of the exponential growth phase, and initial soil nitrogen levels only influence straw yield. Variations in initial soil nitrogen content affect available nitrogen in the wet rooted zone, nitrogen uptake by the vegetation, and total dry matter production, but not remobilization of reserve carbohydrates to the grains and grain nitrogen content.

6.4 Discussion

At all locations except Homs, moisture availability was low in both seasons, and crop performance was characterized by low transpiration and assimilation rates, high relative transpiration deficits, rapid senescence after anthesis, and low values for GRAI, total dry matter production and straw and grain yields. Early senescence prevented complete translocation of pre-anthesis reserve carbohydrates to the grains.

Under arid conditions, variation in amount and distribution of rainfall is the major cause of variation in dry matter production (Chaves, 1991). Higher moisture availability stimulates dry matter production (Homs), and, provided autumn rainfall is sufficient for emergence and early growth, higher spring rainfall leads to increased dry matter production and water use efficiency (Breda). Moreover, post-anthesis senescence rates will be lower and grain filling duration longer.

The Breda experiments show that at very low rainfall (<200 mm), nitrogen application is not effective. At higher rainfall, total dry matter production, and nitrogen uptake and recovery are higher, but late season moisture stress may limit grain yields (Tel Hadya, Izra'a 1989-90). At still higher moisture availability, grain yields increase with increasing nutrient availability (Homs, both seasons). At high nitrogen supply from natural sources, nitrogen uptake hardly responds to fertilizer application (Homs 1988-89), and the increased yield must therefore have been due to other nutrients applied. These results are in agreement with the general observation that under arid conditions, in the absence of growth-limiting nutrient shortages, available water explains most of the variation in dry matter production (Blum & Pnuel, 1990; Buresh et al., 1990; Stapper & Harris, 1989), and that at higher moisture availability, recovery of fertilizer nitrogen increases (Buresh et al., 1990).

Under favourable environmental conditions, i.e. sustaining yields of 1-2.5 ton ha^{-1}, differences in weather conditions among locations and years are reflected in the residual reserve carbohydrates at the end of grain fill. Among populations within a given experiment, the balance between maintenance requirements and assimilation after anthesis determines to what extent the reserves are used by vegetative tissue at the expense of grain yield. Severe drought stress after anthesis results in rapid senescence and cessation of grain fill, so that the reserve pool is not depleted. Under those conditions, grain filling is initially sink-limited, as determined by grain density and potential grain filling rate, and subsequently source-limited by length of the grain filling period. Therefore, factors influencing post-anthesis green area duration, e.g. sowing date, development rates, average life span of leaves, relative death rate of stems and spikes, and the delay in death of stems and spikes, are reflected in grain yield. Additionally, higher grain densities will allow more rapid translocation of reserve carbohydrates (Mac Key, 1988).

Blum et al. (1983a, 1983b) observed continued, although reduced, translocation and kernel growth after chemical desiccation of photosynthetic active organs after anthesis, without any effect on grain fill duration. Including that process in the simulation model, consistently resulted in overestimation of grain yields. This would suggest that accelerated senescence due to abiotic stress is associated with cessation of grain fill.

For a given experiment, the model simulates similar total dry matter production and fraction reserve carbohydrates at anthesis for different populations. Under high-yielding conditions, variation among populations in grain yield is mainly the result of differences in net flow of assimilates, and as reserve carbohydrates are fully depleted, straw yields are similar. Under low-yielding conditions, higher grain yields are the result of increased translocation of reserve carbohydrates, which is the main cause of variation in straw yield. However, under all conditions, actual straw yields show variation (Chapter 5). As under high-yielding conditions reserve carbohydrates, which also may vary, are depleted, actual total dry matter production at anthesis is most probably variable as well. Also under low-yielding conditions, it seems unlikely that populations originating from very different environments (Chapter 3), have similar total dry matter production.

The fact that the model could not reproduce these differences in total dry matter production limits its analytical capacity. Genotypic parameters would have to be identified to account for that variation, especially photosynthetic characteristics, duration of the sink-limited leaf growth phase, and the relative growth rate in that phase (Table 6.5). Variation in physiological characteristics in durum wheat germplasm has been reported (Gummuluru et al., 1989), but as detailed information at that level was lacking, the model could not be calibrated per population.

The slight overestimate of grain yield at Homs could be associated with underestimation of the death rate of vegetative tissue and overestimation of the assimilation rate, whereas the underestimate of straw yield may have been the result of incorrect initialization of soil moisture or nitrogen content. The serious underestimate of dry matter production at Izra'a 1989-90 may have been caused by incorrect weather and soil input data (de Wit & van Keulen, 1987). For instance, rainfall data seemed to exclude values below 0.3 mm. This seems more likely than attributing the aberrant behaviour to model structure, considering its performance under other conditions.

Without resorting to statistical analysis on the basis of individual populations, Table 6.3 indicates that grain nitrogen concentrations are inversely related to harvest index and grain yield, in agreement with observations in bread wheat (Dalling, 1985; Kramer, 1979), and that grain and straw nitrogen concentration are positively related. Lowest minimum straw nitrogen concentrations were found in experiments with highest total dry matter production and NHI, which corresponds with Dalling's (1985) estimate that under conditions where post-anthesis supply of soil nitrogen is low, for example due to water shortage, nitrogen redistribution from vegetative organs can contribute more than 80% to grain nitrogen yield. These very low minimum straw nitrogen concentrations seem to be characteristic for durum wheat landraces. The higher values for the check varieties were confirmed by unpublished results from non-fertilized durum wheat breeding material (M. Nachit, ICARDA, personal communication, 1991). These values, however, are still lower than the generally accepted value of 0.004 kg kg^{-1} (van Keulen & van Heemst, 1982).

Nitrogen translocation from vegetative tissue to the grains was in general underestimated, which could not be corrected by adjusting the rate of translocation, because of the small amounts of vegetative tissue during grain fill. Moreover, if grain filling duration was short because of early senescence, the potential rate of nitrogen accumulation in the grains (PRNAGR) was mostly the limiting factor. Introducing higher values of PRNAGR indeed resulted in higher translocation rates and more correct NHIs. Genotypic variation in efficiency of nitrogen redistribution in bread wheat has been demonstrated (Dalling, 1985; Dalling et al., 1975), which may be related to the activity levels of proteolytic enzymes in the senescing organs (Bewley & Black, 1985), but higher rates of nitrogen accumulation would require higher rates of protein synthesis. It is questionable therefore, whether a value for PRNAGR that accounts for the large difference between observed and simulated values is realistic.

Two features of the modified model limit its applicability: Firstly, tiller and grain density were introduced as forcing functions. Grain density is a dominant yield-determining factor especially under low-yielding conditions, and it is important therefore to include an explanatory description in the model. Secondly, post-anthesis death was treated descriptively, and although at lower yield levels grain yield was estimated satisfactorily, it showed sensitivity to the parameter describing death of stems and spikes. Also here, an explanatory description is required.

The quantitative and qualitative limitations to evaluation of large germplasm collections can be reduced by pursueing an explanatory approach. It is shown in this study that under variable growing conditions where genotype x environment interactions are significant, a crop growth simulation model presents a comprehensive tool to increase insight in plant growth processes. Despite shortcomings, the model simulated a recognizable durum wheat crop and reproduced in a consistent way genotype x environment interactions and their effects on yields. Preliminary evaluations of plant genetic resources are primarily aimed at establishing a general overview of the properties of an entire collection, and the relative values of individual accessions, which relaxes the demands on accuracy in evaluation results, if it provides broad knowledge over diverse environments. Subsequent specific selections in promising material may effectively result in the desired germplasm.

Data on plant characters for which model performance is sensitive are required. Partly, they can easily be recorded in common preliminary evaluations, such as date of anthesis and the associated temperature sum. Additionally, basic information on for instance relative leaf growth rate as a function of ambient temperature, dry matter distribution and assimilation characteristics of individual leaves is required, characteristics that in landraces may be different from modern varieties, as can be deduced from their different growth performance. These may be determined experimentally on a limited number of selected genotypes, and then applied more broadly. Environmental input may consist of long-term weather averages and preferably detailed soil characterization, if necessary complemented by specific weather or soil data representing more favourable or adverse growing conditions. Such an approach would provide adequate information on agronomic potentials of a given population.

Chapter 7

FROST TOLERANCE

Abstract

Syrian durum wheat landraces were evaluated for early and late season frost tolerance. Populations appear to be tolerant to early frosts in January, but late frosts in March can severely damage foliage. Locally evolved germplasm presumably is well adapted to usual environmental conditions such as limited early frosts. Late frost tolerance of foliage appears to be related to minimum winter temperatures in the regions of origin, with populations from coastal regions showing highest sensitivity. In simulation studies, foliar damage within the range of observed rates, did not reduce final grain yield, whereas additional floret damage caused reduced grain yields, in combination with a similar increase in straw yield. Therefore, it appears important to give the effects of late frosts on the apex priority over the customary scoring for foliar damage.

7.1 Introduction

Low temperature is an environmental factor that may limit dry matter production of plants. Although there appears to exist a wide temperature range for optimum photosynthetic performance, van Keulen & Seligman (1987) hypothesize that average daytime temperatures below 10 °C reduce maximum gross assimilation rate. Below 0 °C, plant growth ceases (Kirby & Appleyard, 1987). The rate of leaf initiation and appearance on the main culm are linearly related to the temperature of the shoot meristem (White et al., 1990), and therefore low temperatures will result in lower development rates and delay future development stages. Temperatures below zero may have a detrimental effect on cell structures, if morphological, physiological and biochemical adaptation is insufficient (Levitt, 1980).

Low temperature tolerance is a desirable plant characteristic for autumn-sown cereals in continental and mountainous areas of the Mediterranean region, which are characterized by winter and unpredictable late

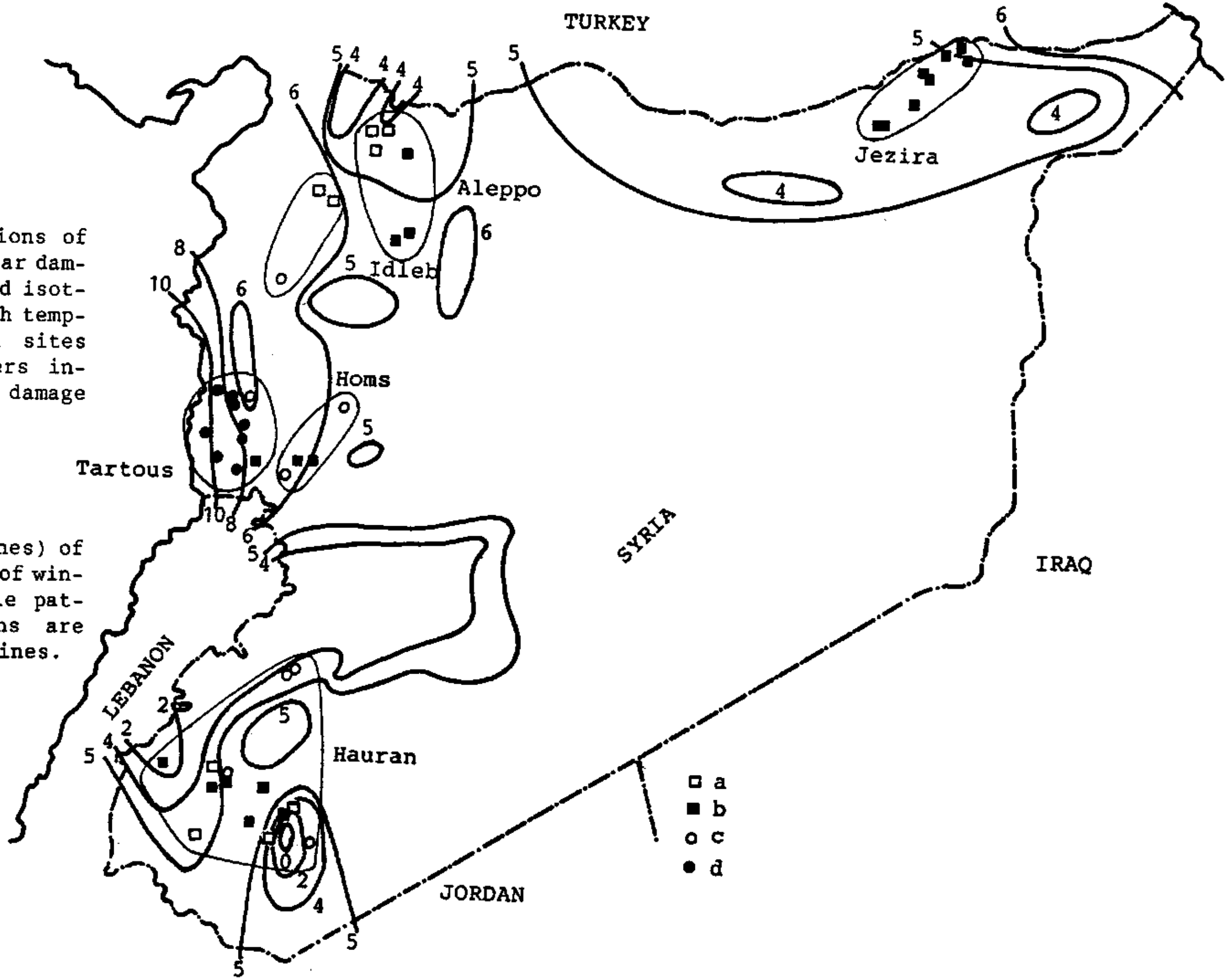

Figure 7.1 Sites and regions of collection, degree of foliar damage due to March frost, and isotherms of mean minimum March temperature (°C). Collection sites are represented by letters indicating different frost damage scores:

a = score 0 - 1.0
b = score 1.1 - 2.0
c = score 2.1 - 4.0
d = score 4.0

Isotherms (thick solid lines) of mean minimum temperatures of winter months show comparable patterns. Collection regions are indicated by thin solid lines.

frosts in spring. Stapper and Harris (1989) call the occurrence of frost the main uncertainty in the thermal regime in Syria. Landraces are a source for cold tolerance in cereal breeding, since some possess a wide genetic variation for this character.

In this paper, results are reported of an evaluation for frost tolerance of durum wheat landraces from Syria, with regard to their geographical origin. On the basis of simulation of plant growth and development at two locations characterized by different moisture availability, effects of late frosts on final grain and straw yield are discussed.

7.2 Materials and methods

Collection missions in the Syrian Arab Republic in 1987 and 1988, conducted in collaboration between the ICARDA Genetic Resources Unit and the Genetic Resources Unit of the Agricultural Research Centre, Douma, resulted in a collection of durum wheat [Triticum turgidum L. var. durum (Desf.) MK] landraces (van Slageren et al., 1989). Forty-nine populations, whose putative origin was at their 45 collection sites or in their vicinity (Figure 7.1), were considered representative for their respective environments (Chapter 3). These were subjected to agronomic evaluation at ICARDA's principal experimental station, located at Tel Hadya, Syria (36°01'N, 36°56'E), during the 1989-90 crop cycle. The experimental design included two levels of nutrient availability in two replicates. Natural fertility represented one level of nutrient availability, while a second level was created through additional nitrogen and phosphorus (both 40 kg ha^{-1}) application.

A two-week period of below-zero daily minimum temperatures was recorded at the beginning of 1990 (Figure 7.2). During the remainder of January and February a number of shorter periods with night-frosts of decreasing severity occurred. In March a one-week period of frosts occurred with a minimum of -8.9 °C. Whereas early season frosts are characteristic for the climate at Tel Hadya, the probability of such severe frosts after mid-March may be as low as once in a century (W. Göbel, ICARDA, personal communication).

This temperature pattern provided an opportunity to evaluate tolerance in locally evolved landrace germplasm to both early and late season frosts. The January frost period coincided with early tillering (phenolog

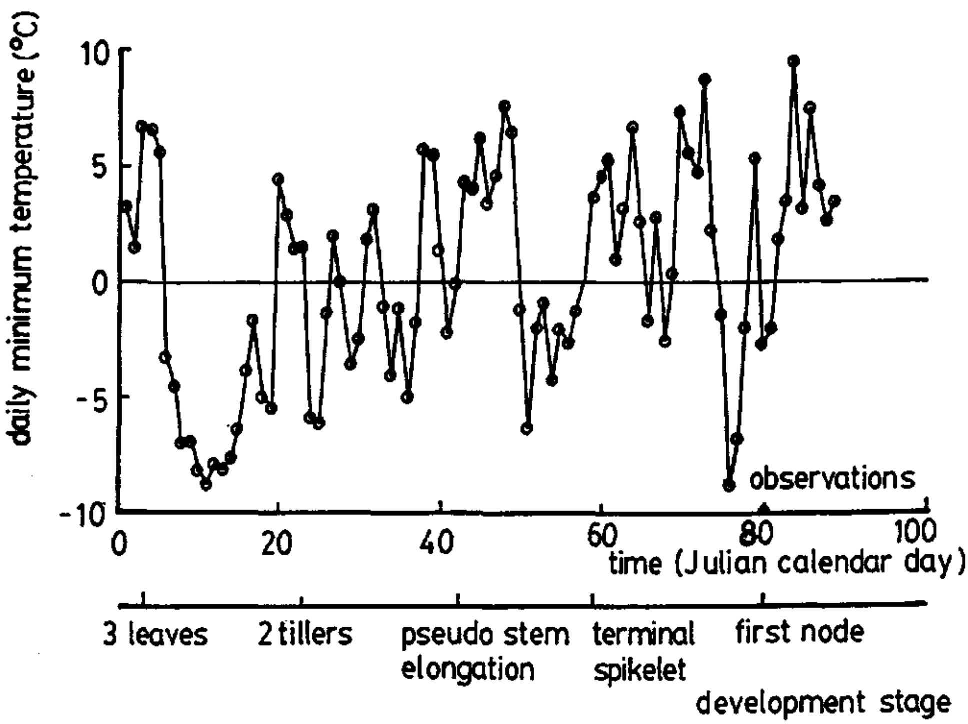

Figure 7.2. Daily minimum temperature at Tel Hadya, Syria, for January, February and March 1990, with average phenological development stages of durum wheat landrace populations.

ical stages 21 and 22; Zadoks et al., 1974). The March frosts occurred just before plants reached first node stage (phenological stage 31). Start of floral initiation, start of spikelet differentiation and terminal spikelet stage were estimated at Julian days 4, 15 and 59, respectively, on the basis of a crop growth and development model for spring wheat (van Keulen & Seligman, 1987).

The January frosts caused little apparent foliar damage, and the effect was not observed. Only severity of the stronger late season frost damage to the foliage was visually scored on March 21 (Julian day 80).

Frost damage was related to minimum winter temperatures in the regions of collection (Figure 7.1), and to a classification in landrace groups (Chapter 3). A landrace group is a subgroup within the Syrian durum wheats, as identified by farmers. Each group is characterized by some morphological traits, and by a specific geographical distribution pattern.

Reduction of grain and straw yield due to late frost damage could not be determined experimentally, because of absence of a control not subjected to frost. Instead, yield reduction was estimated using a crop growth and development model for spring wheat (van Keulen & Seligman, 1987) that was modified to take into account dry matter distribution between main shoot and tillers, and with respect to post-anthesis senescence as a consequence of water shortage. The effect of late frost damage was described by a fractional decline in green leaf weight and area (relative frost damage rate, FDR), every day after floret initiation the daily minimum temperature dropped below an arbitrary value of -4 °C. Although decreasing temperature presumably increases frost damage, because of lack of experimental data and absence of temperatures below -9 °C, FDR was left uninfluenced by frost severity.

Growth and development were simulated for two locations in Syria, viz. Tel Hadya and Homs (36°43'N, 34°45'E), which represent a low and a high yielding environment, respectively. Plant growth at Tel Hadya during 1989-90 was limited by a low seasonal precipitation of 234 mm, whereas a similar amount of 218 mm at Homs was compensated by residual soil moisture of the previous season. For both locations, late frost damage was simulated at Julian days 76 and 77. For each location, final grain and straw yield were estimated for both levels of nutrient availability, and for increasing values of FDR. Consequences of only foliar damage, and of both foliar and floret damage, which was assumed equal to foliar damage, were simulated.

7.3 Results and discussion

Germplasm evolved in Syria presumably is well adapted to local environmental conditions. Durum wheat, since it evolved in the fifth millennium B.C. in the Fertile Crescent from cultivated emmer (Zohary & Hopf, 1988), has yearly been exposed to local temperature regimes, such as early season frosts. The low damage caused by the early frosts in January, which were not particularly severe, suggests that prefrost acclimatation was sufficient, and that tolerance has evolved naturally.

Populations without and with additional fertilizer scored on average 2.0 and 2.5 (see Table 7.1 for scale), respectively. This response is opposite to reported increase of resistance to early frost in Syrian barley by fertilizer application (Salahieh & Abd, 1990). However, the negative fertilizer effect for late frost damage was not significant at $p = 0.01$, and therefore all four observations on frost damage were averaged to one population mean.

Severe foliar damage due to late frosts occurred to landrace populations originating from the coastal region of Tartous and the western littoral mountains (Table 7.1 and Figure 7.1; mean score 4.9, mean score other regions 1.1-2.1). Although the probability of severe frosts in March

Table 7.1. Damage to check varieties and landraces, classified per region of collection and landrace group, due to March frost.

	number of populations	frost damage+	
		mean	range
Checks			
Haurani		1.5	
Cham 1		4.9	
Cham 3		3.5	
Regions of collection			
Tartous	10	4.9	2.0-6.5
Homs	6	2.1	1.3-4.3
Hauran	14	1.8	1.0-3.0
Jezira	10	1.4	0.8-1.8
Aleppo	6	1.1	0.3-1.8
Idleb	3	1.1	0.3-1.8
Landrace groups			
Baladi	14	4.0	1.0-6.5
Sheirieh	1	2.0	-
Hamari	3	1.8	1.3-2.3
Nab el Jamal	3	1.7	0.3-4.3
Haurani	18	1.6	0.8-3.0
Bayadi	5	1.5	1.3-1.8
Sweidi	4	1.5	1.0-2.3
Shihani	1	1.5	-
Overall mean	49	2.3	

+ : measured on a 0-9 scale; 0, no damage, 9, 90% or more damaged.

is very low, and this specific environmental condition has had minor evolutionary influence, observations indicate that tolerance to late season frosts is determined by more probable low temperatures during earlier winter months. During the months November - March, mean minimum temperatures inland are lower than in coastal regions, which is reflected in higher cold tolerance of germplasm originating from inland regions. Cocks & Ehrman (1987) found similar results when evaluating frost tolerance of annual legumes of Syrian origin.

Classification of landrace population into landrace groups (Chapter 3) gave a bimodal distribution: the Baladi landrace group showed a mean damage score of 4.0, whereas other groups scored an average of 1.5-2.0 (Table 7.1). This corresponds with the geographical distribution pattern of the Baladi landrace group, which was collected mainly from the coastal region of Tartous, whereas other landrace groups originated from other parts of the country.

At Tel Hadya, late frosts daily caused 12% foliar damage on average, and a maximum of 41% was scored. Observed grain and straw yields are given in Table 7.2.

Table 7.2. Observed average grain and straw yield (kg dry matter ha^{-1}) at Tel Hadya and Homs, for the season 1989-90, at two levels of nutrient availability.

Location	Fertilizer application	Grain yield	Straw yield	Total dry matter production
Tel Hadya	-	338	1597	1935
	+	267	1706	1973
Homs	-	1156	4992	6148
	+	1276	5180	6456

- : natural soil fertility
+ : additional fertilizer application

Late frost damage to florets was not observed. Whereas early in the season the apex is below the soil and protected against low temperatures, damage may occur later on. Syrian barley landraces show variation in rate

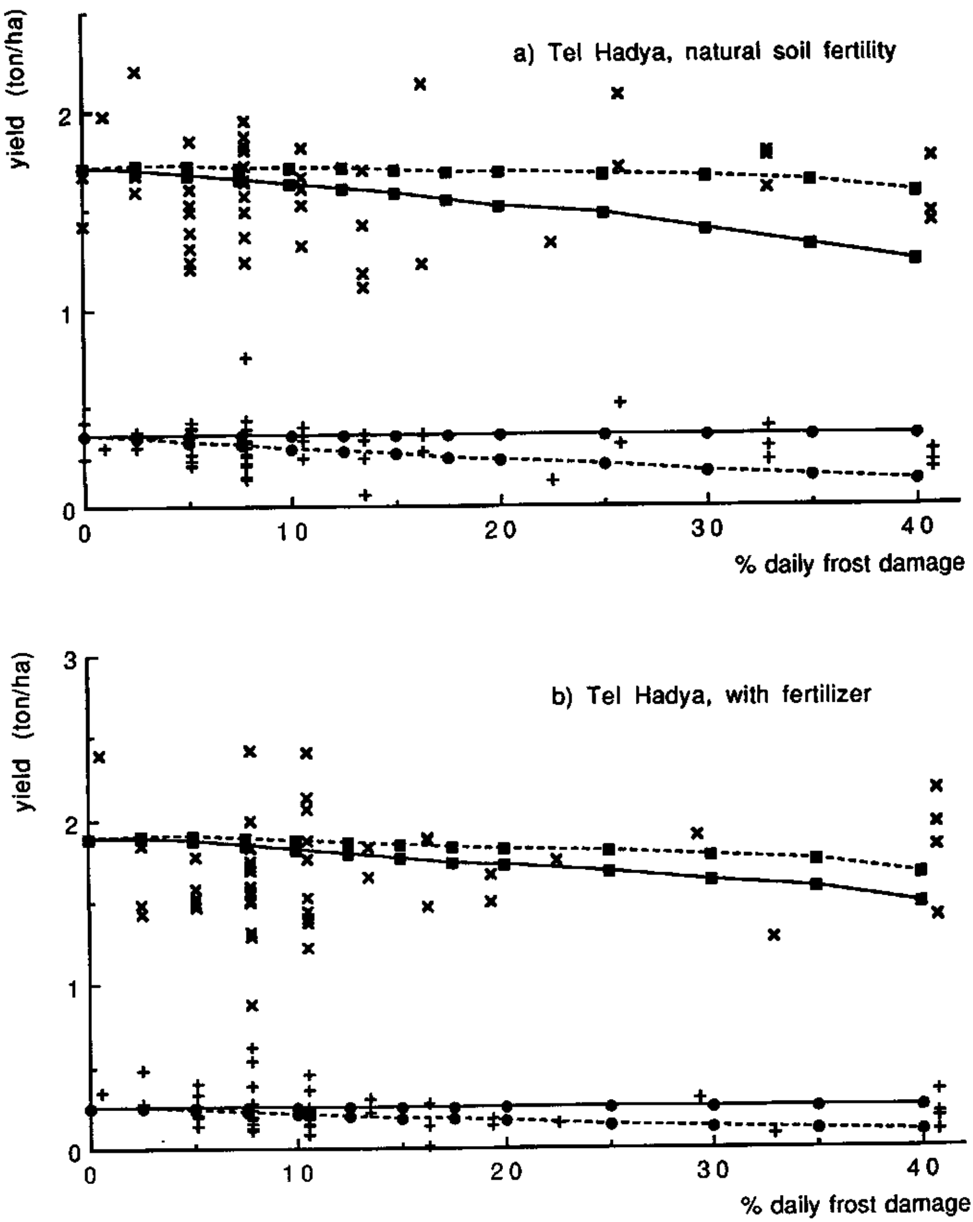

Figure 7.3. Observed and simulated grain and straw yields at Tel Hayda for the 1989-90 crop cycle, for different levels of daily frost damage, at natural soil fertility (a) and with fertilizer application (b). Simulations assuming only foliar damage, and both foliar and floret damage are presented.

Legend: + = observed grain yield
× = observed straw yield
● = simulated grain yield
■ = simulated straw yield
—— = only foliar damage simulated
---- = both foliar and floret damage simulated

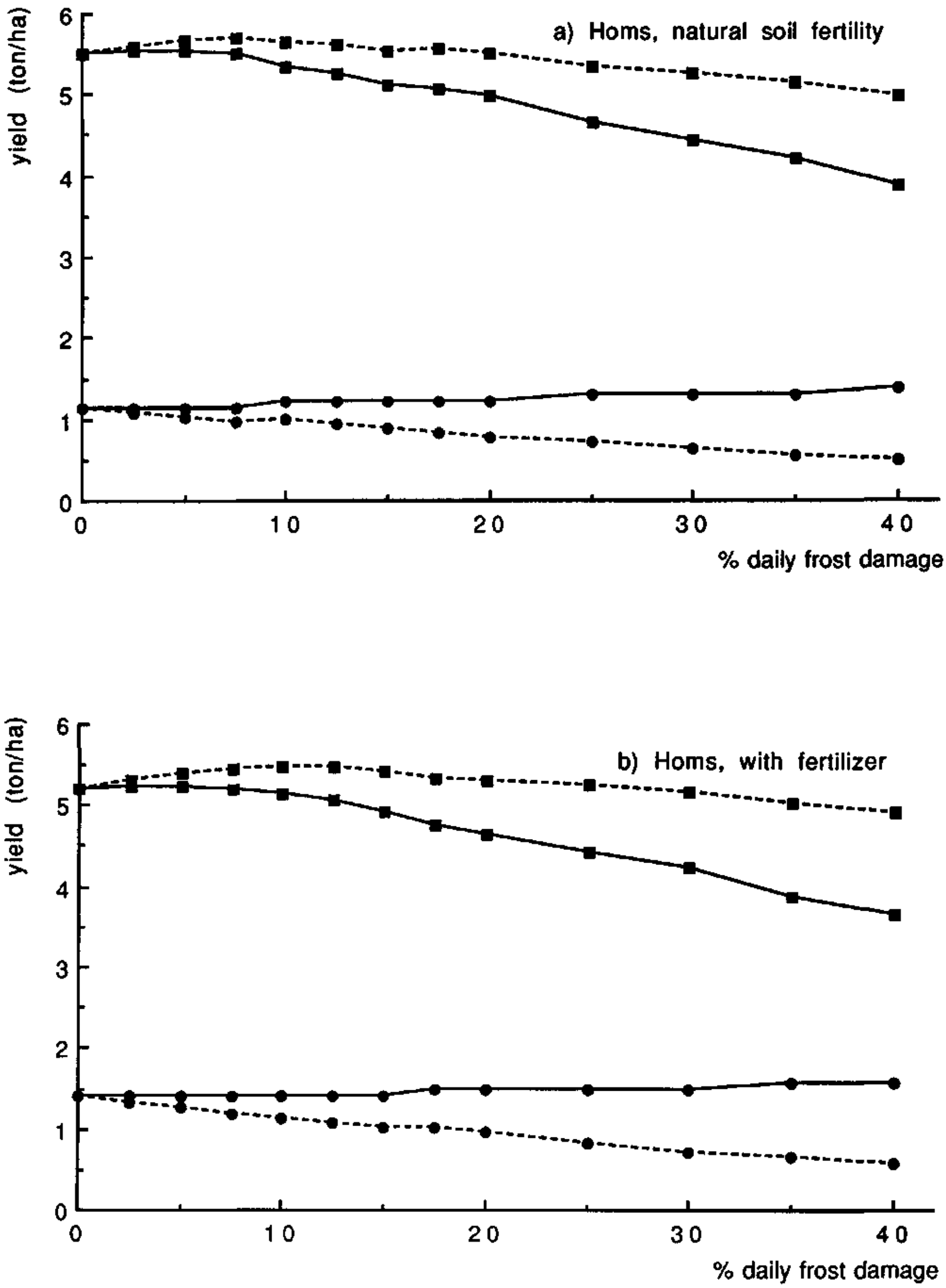

Figure 7.4. Simulated grain and straw yields at Homs for the 1989-90 crop cycle, for different levels of frost damage to foliage, at natural soil fertility (a) and with fertilizer application (b). Simulations assuming only foliar damage, and both foliar and floret damage are presented. See Figure 7.3 for legend.

of apex development; a vernalization requirement results in slow initial apex development, which leads to high levels of cold tolerance through low temperature avoidance (E. van Oosterom, ICARDA, personal communication). The same mechanism may be found in Syrian durum wheat landraces.

Observed and simulated grain and straw yield for Tel Hadya assuming foliar damage only, and simulated yields assuming both foliar and floret damage, are presented in Figures 7.3a and b. Observed yields, however, represent different populations and thus comprise a genotype and a genotype x environment interaction component. This caused variation and absence of an apparent trend in yield decrease. Simulated values correspond on the average with observed values. Simulated grain yield is in the case of only foliar damage, within the range of observed rates of frost damage, not affected, unlike straw yield. Additional floret damage causes grain yield reduction, and an increase in straw yield with a similar amount in comparison with only foliar damage.

For the high yielding location Homs (Figures 7.4a and b), no observed data on frost damage were available. Simulation of only foliar damage resulted in a small grain yield increase, and a decline in straw yield. Grain yield increase was due to a slightly longer grain filling period as a consequence of a longer green area duration. Additional floret damage caused grain yield reduction, and for both nutrient conditions a slight initial increase in final straw yield, caused by reserve carbohydrates not translocated to the grains in combination with only a slight decrease in total dry matter production. Final straw yield decreased at higher frost damage rates.

Nutrient availability has only limited influence on the relative changes in straw yield, although grain yield may be affected considerably. In the case of only foliar damage and FDR = 0.12 (the observed average), grain yield remained stable, and straw yield decreased with 3% to 6%. Only in the case of Homs with additional fertilizer, grain yield increased with 6%. In the case of both foliar and floret damage, grain and straw yield changes of -18% to -24% and -2% to +5%, respectively, were observed.

Simulation of the effects of late frosts under both low and high yielding conditions, resulted in grain yields not affected by damage to foliage only, whereas already low levels of additional floret damage resulted in grain yield reduction. This decrease in final grain weight is about equal to the increase in weight of reserve carbohydrates at the end of the growth cycle, which causes the increase in straw yield in comparison with only foliar damage. It appears that the number of florets per m^2 influences final grain yield, and therefore, it is important to observe the effects of late frosts on the apex, in addition to the customary scoring of foliar damage.

Chapter 8

FUNGAL DISEASE RESISTANCES

Abstract

As a consequence of the large size of many germplasm collections, preliminary evaluation can often not be carried out in great detail. To optimize collection and evaluation, knowledge on the relation between distribution of disease incidence and presence of host resistance, can be utilized.

Fourty-nine Syrian durum wheat landrace populations, whose putative origin was in the vicinity of the collection sites, were evaluated for response to the fungal diseases common bunt, yellow rust, and septoria tritici blotch. Results were interpreted on the basis of collection regions and landrace groups.

Host resistance to common bunt and septoria tritici blotch was highest in germplasm originating from regions with environmental characteristics favourable for development and incidence of the concerned disease. However, host resistance to yellow rust was lowest in germplasm from 'favourable' regions. Landrace groups were also characterized by different levels of disease resistances, and were generally slightly more homogeneous than collection regions with respect to infection percentage.

With respect to fungal disease resistances, collection of landrace germplasm may best be organized according to collection regions established on the basis of agro-ecological information, whereas evaluation for disease resistance could make use of classification in landrace groups.

8.1 Introduction

Indigenous landrace germplasm often possesses well functioning resistance against locally prevalent diseases (Hussey, 1990), since natural selection is likely to be successful in creating stable complexes of resistance genes and genotypes (Allard, 1990). Therefore, landraces are an important source of resistance in plant breeding. Although a small selection pressure exists against susceptibility to diseases, certain balance mechanisms in landrace populations maintain their susceptible components (van Leur et al., 1989), and therefore, absolute resistance of all plants within a population is unlikely.

Evaluation of plant germplasm at genebanks is normally of preliminary nature, as a consequence of the large size of germplasm collections. Promising material is subsequently evaluated in more detail. In the case of genetically heterogeneous landraces, this may imply that response to diseases is evaluated at plant population level, using inoculums consisting of several races, and that thus responses of individual genotypes to specific races is not known. However, it is important that understanding is obtained with respect to geographical distribution of disease incidence, as determinded by agro-ecological characteristics of cultivation areas affecting disease development, and that relations are established between this distribution and the presence of disease resistance in plants. Such information is, for instance, helpful in planning germplasm collection missions (Marshall & Brown, 1983; Vavilov, 1951), and effectively selecting for disease resistances.

The fungal diseases common bunt [Tilletia foetida (Wall.) Liro and T. caries (DC) Tull], yellow rust [Puccinia striiformis Westend. f. sp. tritici], and septoria tritici blotch [Mycosphaerella graminicola (Funkel) Sand.] are distributed over large parts of Asia, Europe, the Americas, Africa and Australia (Commonwealth Agricultural Bureaux, 1970, 1977, 1978, 1984). Mamluk et al. (1990), in a four season field survey in Syria, reported common bunt, yellow rust and septoria tritici blotch as the most frequently encountered wheat diseases in all areas of the country.

Durum wheat [Triticum turgidum L. var. durum (Desf.) MK] originates from the so-called Fertile Crescent, of which Syria forms a part (Vavilov, 1951; Zeven & de Wet, 1982). It has been cultivated in its region of origin since the fifth millennium B.C. (Zohary & Hopf, 1988). Durum wheat landrace populations were collected in 1987 and 1988 from various regions of Syria (van Slageren et al., 1989). Populations whose putative origin was at the collection sites or in their vicinity, were considered representative for their respective environments (Chapter 3). Of this part of the collection, 49 populations were selected and used to examine the geographical distribution of resistance to the diseases common bunt, yellow rust and septoria tritici blotch, in relation to environmental

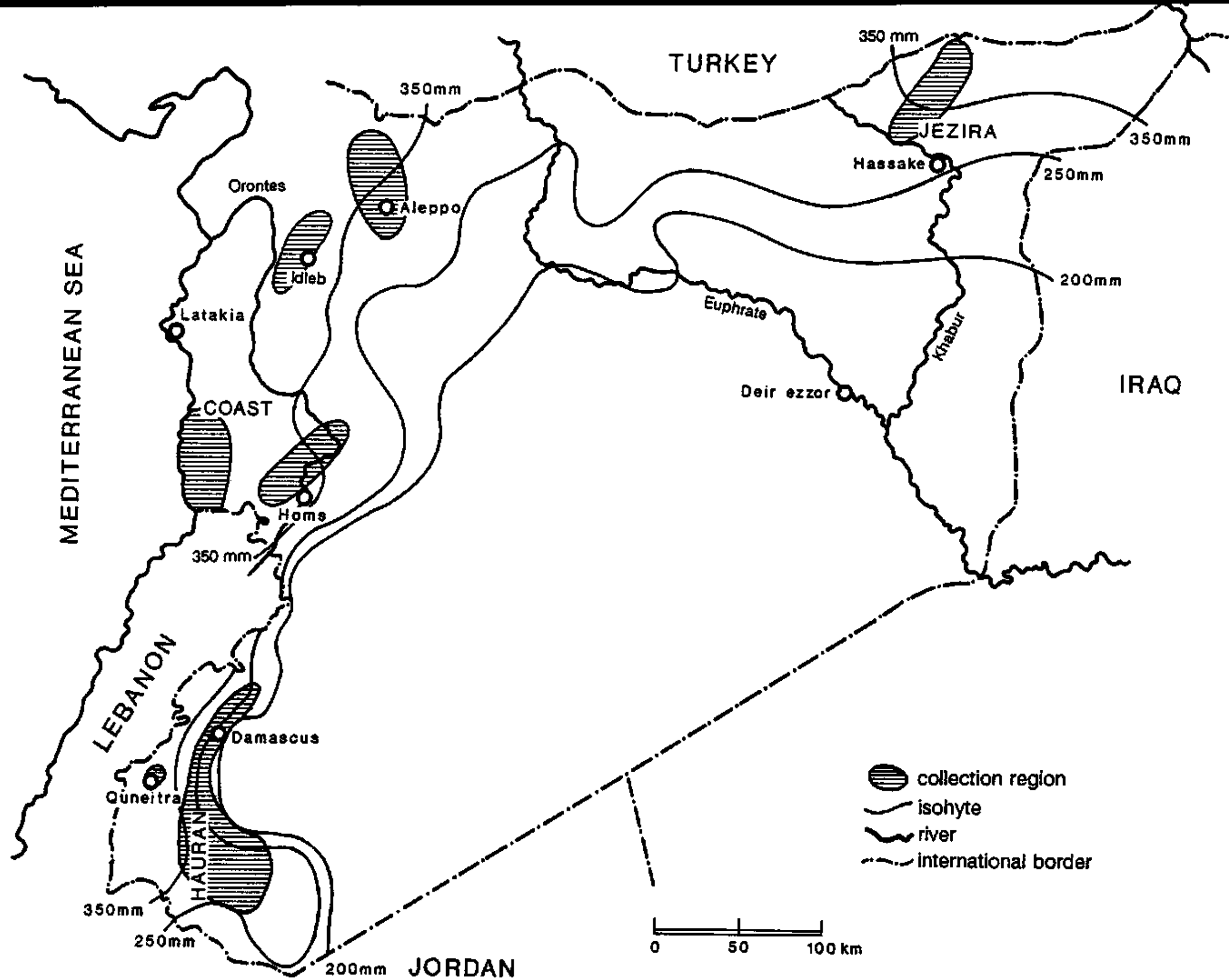

Figure 8.1. Collection regions in Syria from where durum wheat landraces were collected and evaluated for resistance to common bunt, yellow rust and septoria tritici blotch.

characteristics of the collection regions, and to formulate germplasm collection and evaluation strategies.

8.2 Materials and methods

The 49 landrace populations, originating from 45 sites, were evaluated under field conditions. The populations represented eight landrace groups, i.e. taxonomical groups as distinguished by farmers, each group with specific morphological characteristics and a geographical distribution pattern, and referred to by a local name (Chapter 3). The collection sites were grouped in seven regions (Figure 8.1), that were combined with the agro-ecological zoning (Anonymous, 1977), used by Mamluk et al. (1990), restricted to the rainfed zones.

The populations were sown in two separately randomized replications for two seasons, viz. 1988/1989 and 1989/1990. Resistance to common bunt and yellow rust was field evaluated at ICARDA's principal station at Tel Hadya, near Aleppo, Syria, where the climate is characterized by hot and dry summers, a rainfall peak from December through February (mean annual precipitation 330 mm), and low relative atmospheric humidity. Screening for septoria tritici blotch was carried out in fields at the coastal ICARDA sub-station near Lattakia, where the climate is strongly influenced by the Mediterranean and is characterized by a longer rainy season with higher annual precipitation (annual mean 887 mm), higher relative atmospheric humidity, higher winter and lower summer temperatures.

Plants were artificially inoculated. The common bunt inoculum used was a composite bulk of teliospores, in which the presence of races L-9 and T-11 had been identified (Ismail, 1992), and which was prepared from bunted wheat spikes collected at various sites in Syria and adjusted to a _T_. _foetida_ : _T_. _caries_ spore ratio of approximately 1:1. Inoculum density was 0.006 gram spores per gram seed, resulting in about 80,000 spores per seed.

Yellow rust was inoculated three times between early tillering and early booting stage, in the late evening when dew formation was expected, or after slight rain. The inoculum was a bulk of viable uredospores preserved from the previous season, comprising the two predominant races in Syria and neighbouring countries, viz. 6E16 and 82E16. This was mixed with talcum powder and dusted over the plants. About 5 gram of uredospores per hectare was used.

Septoria tritici blotch inoculum consisted of a bulk of blastospores produced from pycnidiospores grown on artificial yeast-malt-saccharose-agar medium (YMSA, 4-4-4-18 gram l^{-1} water) and multiplied on liquid medium (YMS) for five days. Pycnidia originated from leaf samples collected from all septoria-infected areas of the country. Between tillering and heading, plants were mist irrigated six times, and subsequently sprayed with an inoculum suspension of 2×10^6 spores ml^{-1}. About 1.5 ml suspension per plant was applied.

Common bunt was evaluated on plots of a single, 1-meter-long row. At maturity, when symptoms were clearly visible, spikes of a randomly chosen half meter per row were harvested. Numbers of bunted and healthy spikes were counted, and infection percentages determined.

Yellow rust evaluation was conducted in plots of four, 1-meter-long rows. When symptoms were clearly visible after anthesis, percentage severity and reaction type were recorded. Severity of yellow rust was scored according to the modified Cobb scale (Peterson et al., 1948). The reaction type was classified in five classes: resistant (R), moderately resistant (MR), intermediate (M), moderately susceptible (MS), and suscep-

Table 8.1. Disease severity and vertical disease development of septoria tritici blotch, quantified based upon the 0-9 scale of Saari and Prescott (1975). Not presented scores are defined by intermediate severity and development.

Score	Severity	Vertical development
0	Free from infection	
1, very resistant	Few isolated lesions	Lowest leaves only
5, intermediate	Severe infection on lower leaves; moderate to light infection to the mid-point of the plant with upper leaves free	Infections do not extend beyond the mid-point of the plant
9, very susceptible	Severe infection; spikes infected to some degree	All leaves

Table 8.2. The response of Syrian durum wheat landraces, per collection region and landrace group, to the diseases common bunt, yellow rust and septoria tritici blotch.

	common bunt			yellow rust					septoria tritici blotch			
	no. pop.	% infected spikes		no. pop.	% severity		reaction type, range	ACI[1]	no. pop.	score[2]		
		mean	range		mean	range				mean[3]	range	
											v.d.	sev.
Collection region												
Hauran	12	9	0-25	13	32	22-50	R-S	24	13	7/5	6-8	4-7
Quneitra	1	11	-	1	30	-	M-MS	23	1	7/6	-	-
Homs	6	10	4-18	6	39	13-60	MR-S	33	6	5/5	3-7	3-8
Coast	10	13	4-22	10	45	18-65	R-S	37	10	6/4	4-7	2-5
Idleb	3	21	10-30	3	27	15-48	R-S	20	3	6/4	6	4
Aleppo	6	7	4-17	6	22	8-38	R-S	15	6	7/5	7	4-6
Jezira	8	6	1-14	10	45	21-80	MR-S	38	10	6/4	4-8	2-6

Landrace group												
Haurani	16	9	0-25	18	31	21-50	R-S	23	18	7/5	7-8	5-7
Baladi	14	11	4-22	14	40	14-65	R-S	32	14	6/4	4-7	2-5
Bayadi	3	5	4- 6	3	28	13-38	MR-S	24	3	7/6	7	6
Shihani	4	4	1-11	5	50	21-75	MR-S	47	5	6/4	4-8	2-6
Hamari	3	10	4-16	3	23	8-48	R-MS	13	3	6/6	3-7	4-8
Sweidi	4	20	10-30	4	33	15-53	R-S	28	4	6/4	5-6	4
Nab el Jamal	1	2	-	1	80	-	MS	64	1	5/4	-	-
Sheirieh	1	17	-	1	60	-	MS-S	52	1	5/3	-	-
overall mean	46	10		49	37			29	49	6/5		
s.d.		7			17			16		1/1		

1: average coefficient of infection
2: measured on a scale 0-9
3: 1st digit = vertical disease development (v.d.), 2nd digit = disease severity (sev.)

tible (S). Scores on disease severity and reaction type were converted to coefficients of infection (Stubbs et al., 1986).

Septoria tritici blotch was evaluated on plots of one row of 35 cm length, and observations were made after anthesis. Vertical disease development and disease severity were quantified based upon the 0-9 scale of Saari and Prescott (1975, Table 8.1).

Populations were heterogeneous with respect to the durum wheat genotype, and sometimes consisted of mixtures of durum and bread wheat (Chapter 3). In the case of common bunt, harvested bread wheat spikes were discarded; in the case of yellow rust and septoria tritici blotch, observations were made on the durum wheat plants only, and one datum per plot was established by estimating the average score after inspection of 10-20 plants. Data of the four replicates were averaged to one value per population, with the exception of yellow rust reaction type, which was transformed to a range per population.

Mean values for observed resistance characteristics, per collection region and landrace group were calculated. Variation for infection among regions and landrace groups was studied by analysis of variance (ANOVA) of untransformed data.

8.3 Results

Mean values and ranges of the response to the three diseases, per collection region and landrace group are presented in Table 8.2. Common bunt infection varied strongly, with extremes of 0% in a Haurani population from the Hauran region, and 30% in a Sweidi population from the Idleb region. Average infection levels for populations from the Jezira region was 6%, whereas the highest average infection levels were found in those originating from the western regions of Syria, particularly from the Idleb region (21%). In general, resistance levels of the populations collected more inland, i.e. the Hauran, Aleppo and Jezira regions were highest. Among landrace groups, Nab el Jamal, Shihani, Bayadi and Haurani possessed on average highest resistance to common bunt.

Yellow rust severity varied from 8% in a Hamari population from the Aleppo region, to 80% in the Nab el Jamal population from the Jezira region. Highest average severity was observed in populations originating from Coastal sites and the Jezira region (both 45%). Regions and landrace groups with low average severity were not identified. Yellow rust reaction type varied widely for most regions and landrace groups, although the majority of individual population scores fell in the categories M and MS. Lowest average coefficient of infection (ACI) was 15, recorded for the Aleppo region, whereas the Homs, the Coastal and the Jezira regions showed ACIs of 33 and higher. The Hamari landrace group appeared most resistant (ACI = 13). Septoria tritici blotch score for vertical disease development varied from 3 in a Hamari population from the Homs region, to 8 in a Haurani population from the Hauran region and in a Shihani population from the Jezira region. For severity, the septoria score ranged from 2 in a Shihani population from the Jezira and a Baladi population from the Coastal region, to 8 in a Hamari population from the Homs region (the same population as with lowest score for vertical disease development). No regions or landrace groups were characterized by low mean scores, and on average, susceptibility to septoria tritici blotch in durum wheat landraces appears common all over Syria. Vertical development and severity of septoria infection were significantly positively related: severity = 1.33 + 0.52 x vertical development ($r = 0.52$; $p \leq 0.001$; for vertical development ≥ 1), although the explained variation was low (27%), probably due to the relative imprecise scale of observation.

One-way ANOVA (Table 8.3) showed that generally, variation in infection among landrace groups was slightly higher than among regions for all three diseases. Only variation in vertical development of septoria tritici blotch was higher among regions. Variation in infection within regions and within landrace groups was in all cases lower than among regions and among landrace groups, respectively.

8.4 Discussion

Highest average resistance to common bunt was found in populations originating from the Jezira, the Aleppo and the Hauran regions, whereas populations from the Idleb and the Coastal regions showed low resistance levels. Although common bunt is spread over all collection regions, it is endemic to, and most severely affects the durum wheats in the Jezira region (Mamluk et al., 1990). This region is characterized by relatively low rainfall and dry soil, and low daily minimum temperatures in winter and spring. Such conditions favour common bunt development (Hoffmann &

Table 8.3. Summarized analyses of variance for infection rates of common bunt, yellow rust and septoria tritici blotch.

Effect	Disease							
	Common bunt		Yellow rust			Septoria tritici blotch		
	d.f.	M.S. infection	d.f.	M.S. severity	M.S. CI	d.f.	M.S. vertical development	M.S. severity
Among regions	6	104	6	542	549	6	4.13	3.49
Within regions	39	37	42	257	205	42	0.90	0.99
Among landrace groups	7	112	7	709	712	7	3.67	3.93
Within landrace groups	38	34	41	222	169	41	0.89	0.86

d.f. = degrees of freedom
M.S. = Mean Square
CI = coefficient of infection

Schmutterer, 1983). The high disease pressure in the Jezira region may explain the development of high resistance levels in locally evolved germplasm. Environmental conditions in the Aleppo and the Hauran regions are also relatively favourable for common bunt development, which may have resulted in higher resistance levels. Analogously, although common bunt is spread in the Coastal and the Idleb regions, the less favourable environmental conditions there (higher rainfall, higher temperatures in winter and spring) may have led to lowering the selection pressure resulting in lower resistance levels found in these two regions.

Yellow rust incidence, both in terms of average severity and ACI, was highest in populations from the Coastal, the Homs and the Jezira regions. In Syria, yellow rust epidemics occur every three to four years. The disease commonly occurs in regions with high rainfall, but in years of epidemics it may also spread in areas with lower rainfall combined with a prolonged wet spring (Mamluk et al., 1990), e.g. the Jezira region, where lower rainfall is more evenly distributed over winter and spring. Additionally, disease development is favoured in the Coastal and the Homs regions by high soil fertility, and in the Jezira region by low night temperatures (Wiese, 1977). However, although the irregularity of disease occurrence may have interrupted the build-up of host resistance in favourable regions, this is no obvious reason for lower resistance in regions with high disease incidence.

In Syria, septoria tritici blotch is spread moderately extensive in areas with more than 350 mm annual rainfall, but may spread into areas with lower rainfall, if low temperatures and high rainfall prevail during the critical months of February and March (Mamluk et al., 1990; Wiese, 1977). Although on average susceptibility to the disease appeared common all over Syria, somewhat lower susceptibility scores were recorded for germplasm originating from the Idleb, the Homs and the Coastal regions, where annual rainfall is relatively high, and from the Jezira region, where the rainfall season may be extended.

Statistical evidence for these relations can not be given, as this would require extensive quantitative knowledge of the relations between environmental characteristics and disease development in Syria.

Our results on common bunt agree with those of Pecetti et al. (1989) for 118 other Syrian durum wheat accessions, who found a peak in the range of 11%-20% infection, although the mean value estimated from their graph is lower. For yellow rust, a peak was observed in the same range, with an estimated mean between 21%-30%, which is below the mean value reported here (49%). It is difficult to disentangle plant genetic, race and environmental effects in explaining this difference. However, as both our evaluation seasons were characterized by below average seasonal rainfall, which is disadvantageous to yellow rust development, and a similar inoculum was used, Pecetti et al. appear to have evaluated more resistant germplasm.

More information on race specificity, intrapopulation variation, multiline effects, etcetera, would have been obtained with evaluation of individual genotypes, multiple readings in time, and other detailed observations. However, this is not the scope of preliminary evaluations of germplasm collections. In Syrian and Jordanian barley landraces, van Leur et al. (1989) found large intrapopulation diversity for disease resistance. If a similar diversity would be present in durum wheat landrace populations, highly resistant plants may be found, even though on average the relevant populations may not be resistant.

It may not always be possible to relate disease resistance to environmental conditions, however, establishment of such relations would make future collection missions more efficient and would contribute to development of improved germplasm with adequate disease resistance for certain agro-ecological zones (van Leur et al., 1989). For example, identification of resistance to common bunt and septoria tritici blotch is most likely in germplasm originating from regions with environmental characteristics favourable to development of these diseases, and to disease incidence.

The generally slightly higher variation among landrace groups than among regions of collection, was also observed for phenotypic variation patterns of a number of plant characters of the same material (Chapter 4). In other words, landrace groups are slightly more homogeneous than regions of collection for several plant characteristics, including disease resistances. Although variation may be distributed differently for other crops and countries, the concept of landrace groups may be useful in germplasm evaluation. It appears efficient to evaluate a limited number of populations per landrace group, provided all environmental regions are incorporated, instead of evaluating all accessions for disease resistance. Most promising landrace groups, possibly from certain regions, can subsequently be evaluated in more detail.

Chapter 9

GENERAL DISCUSSION

9.1 Evaluation of large germplasm collections

Agronomic evaluation gave considerable differences in average yield among experiments. Performance per landrace population varied strongly among locations, and populations showing superior performance under all conditions could not be identified. This typifies the complications caused by genotype x environment interaction in the evaluation of plant germplasm. It is difficult or impossible to extrapolate crop behaviour to different environmental conditions, and as large collections can not be evaluated at many locations over a sufficient number of seasons, an efficient evaluation method is required.

9.2 Analysis of genotype x environment interaction

Phenotypic plant charcateristics have genotypic and environmental components, which both have to be investigated.

It is difficult to determine a plant genotype, as there is always a surrounding environment, and observations are in all cases phenotypic. Particulary plant characteristics that are the result of many underlying processes, e.g. grain yield, are difficult to determine genotypically. Unequivocal quantification of fundamental plant characteristics, e.g. temperature sum to anthesis (Chapter 6) and characteristics of the light response curve, may be easier.

In contrast, macro-environmental characteristics can be determined with suitable equipment.

9.2.1 Analysis of variance

Although determining a genotype itself is difficult, it is possible to assess the contribution of genotypic and environmental factors to the phenotypic variation. There are two methods for this: an analysis of variance (ANOVA), and a sensitivity analysis with a crop growth simulation model.

With ANOVA, sources of variation can be identified. For example, in Chapter 5 it is shown that the population, year, location and fertilizer effects were generally significant, as were interactions between year and location. Interactions between population and fertilizer application, however, were generally not significant.

This technique is useful in preliminary, qualitative, analyses of evaluation trials. It is of little value, however, in forecasting crop performance. For example, the generally significant genotypic and environmental effects indicate that under environmental conditions different from the conditions at evaluation, yield levels may be different. However, as the absence of significant effects between years indicated yield stability, one could also speculate that grain yield does not rise substatially under higher rainfall conditions. ANOVA can not solve this contradiction.

9.2.2 Sensitivity analysis

Through sensitivity analysis using a crop growth simulation model, the consequences of different values for plant genetic and environmental characteristics for plant growth and development can be assessed. This technique provides a quantitative tool, and allows the investigation of plant of environmental characteristics that are difficult to vary under experimental conditions. In paragraph 6.3.4, this is illustrated. This technique can be used to further explore and quantify sources of variation indicated by an ANOVA.

9.2.3 Growth analysis

With a crop simulation model, growth and development can be analyzed quantitatively, and therefore understanding can be obtained of processes that cause variation.

For instance, the consequences and interaction of rainfall distribution and nutrient availability with respect to dry matter production were investigated. Also, the process of grain filling was analyzed for different environmental conditions and yield levels (Chapter 6).

Under variable growing conditions where genotype x environment interactions were significant, the crop growth simulation model presented a comprehensive tool to increase insight in plant growth processes. Despite some shortcomings, the model simulated a recognizable durum wheat crop and reproduced in a consistent way genotype x environment interactions and their effects on yields. The model may be used in exploring crop behaviour under different environmental conditions, and replace extensive multilocational and multiseasonal evaluations. By pursueing an explanatory approach, the quantitative and qualitative limitations to evaluation of large germplasm collections by trial and error, may be eliminated.

9.2.4 Environmental characterization

Interpretation of evaluation results on the basis of environmental characterization of the regions of origin, may provide further understanding of crop behaviour. As this approach provides only general understanding, it is useful in preliminary evaluations that are aimed at identification of groups of accessions.

The relations between some collection site and plant characteristics at evaluation (Chapter 5), could be used to select germplasm on the basis of knowledge on the environment in the region of provenance. Application of such relations, however, is restricted to the tested environments. All evaluations were carried out at low to moderate soil moisture availability, i.e. unfavourable conditions for crop production, and a negative correlation between annual precipitation at the collection site and grain yield at evaluation was found. Inclusion of evaluation sites with higher rainfall would possibly have caused a positive correlation at higher yield levels.

Tolerance to late season frosts, which is uncharacteristic for the Syrian climate, was highest in populations from the inland, where minimum winter temperatures are lowest (Chapter 7). Application of this relation is straightforward: in the search for late season frost tolerance, breeding material can best be selected from inland populations, where chances of success are highest.

For fungal disease resistances, however, relations were not always clear (Chapter 8). Only in the case of two of the three evaluated diseases, host resistance was highest in germplasm originating from regions with environmental characteristics favourable for development and incidence of these diseases. An efficient selection method is therefore difficult to formulate. Moreover, as the frequency of plants with specific vertical resistance can be very low, it may remain necessary to evaluate an entire collection.

Regions with moderate climatic conditions provided landraces with relatively stable yields (Chapter 7). This observation supports the practice of utilization of germplasm from such regions. Germplasm from regions with extreme environmental conditions, however, may be useful for specific stress factors, e.g. late season frost tolerance.

9.2.4 Evaluation methods

Irrespective the further evaluation strategy, part of a germplasm collection should be evaluated at several locations over a number of seasons. This will provide data to analyze the variation patterns with ANOVA, validate a crop growth model, and determine possible relations between plant and collection site characteristics.

For example, yields were more stable within landrace groups than within regions of origin (Chapter 5). Therefore, a pre-selection of germplasm on the basis of landrace groups, possibly taking into account representation of regions of origin, could be made to restrict the number of accessions. Evaluation of selected accessions would provide an indication of the characteristics of a certain landrace group. If necessary, this could be completed by a more detailed evaluation of promising material.

Subsequently, two selection methods can be formulated, dependent upon the significance of the relationship between the observed plant character and environmental characteristics of the collection site. If such relationships are significant and causal, then preliminary selection of germplasm can be based upon collection site characteristics. An example is tolerance to late season frosts, and to a lesser extent some fungal disease resistance. If relevant relationships are difficult to establish, as for instance yield, then application of a crop growth simulation model appears a suitable technique in analysis of evaluation results of extensive germplasm collections, and for exploring growth and development under various environmental conditions. Whereas only a limited part of a large germplasm collection is evaluated multilocationally and multiseasonally, crop growth analysis can be applied to an entire collection. This would alleviate quantitative and qualitative limitations to evaluation programmes.

As mentioned in Chapter 6, for application of such models, data on plant characters for which model performance is sensitive are required. Partly, these can easily be recorded in customary routine evaluations, such as date of anthesis and the related temperature sum. Additionaly, basic information on for instance physiological characters is required. These may be determined experimentally on a limited number of selected genotypes, and then be applied more broady. Environmental input may be long-term wheather characteristics and preferably specific soil characteristics, if necessary completed by specific weather or soil data representing more favourable or adverse growing conditions.

It is difficult to derive detailed plant characteristics from information on the environmental characteristics of the collection region, for the purpose of model input. Firstly, the origin of the germplasm is not always known. Secondly, detailed knowledge on relations between environmental and plant characteristics would be required, which would be difficult to obtain. Thirdly, although regions can be classified on the basis of relatively uniform environmental conditions, their plant genotypes may be variable, which causes genotype x environment interaction and different phenotypes in other environments. As this would reduce the accuracy of simulation, experimentally obtained plant characteristics are preferred model input.

The heterogeneity of landrace populations complicates evaluation. Crop growth simulation models at the population level do not explain the consequences of heterogeneity in different environments. However, simulation at the population level (Chapter 6) was sufficiently accurate to justify application in interpretation of preliminary germplasm evaluation. In subsequent evaluation and selection, it may be necessary to quantify intrapopulation variation, to determine breeding potentials of best performing populations.

These observations and conclusions are valid for Syrian landraces of durum wheat, which is a self-pollinating field crop. Applicability to other crops and countries will vary, depending on conditions such as evolutionary history, geographical distribution of morphological groups, reproduction, cultivation, utilization, and seed exchange.

9.3 Landrace groups in germplasm evaluation

Durum wheat in Syria forms a continuum of morpho-types, which farmers classify in different landrace groups, each with distinct characteristics. Each landrace group is morphologically variable, which causes some overlap by their extremes. The classification in landrace groups is compatible with both farmer's perceptives and taxonomic rules, which is important as it provided a base for data structuring.

Within landrace groups, three patterns of geographical distribution can be distinguished (Chapter 3). Some are widely distributed over most of the country, whereas most others are regionally concentrated, either in a limited region or in a few villages. Distribution maps of all encountered landrace groups are given in Appendix I, and their herbarium specimen are preserved at the Herbarium of ICARDA and at the Herbarium Vadense of the Department of Plant Taxonomy, Wageningen Agricultural University.

If relations between plant characteristics and regions of origin could be established, the former could be derived from analysis of the region of origin. However, in this study, morphological characteristics were more related to landrace groups than to regions of origin (Chapter 4), and efforts to establish relations between agronomic characteristics and regions of origin have been moderately succesful (Chapter 5).

Morphological characterization is important in distinguishing groups (here, landrace groups) that are relatively homogeneous with respect to agronomic characteristics (Chapter 5). The latter are normally more important, but more difficult to assess. Morphological characterization can be used to stratify large germplasm collections, and increase the efficiency of agronomic evaluation.

9.4 Variation

Genetic diversity was observed at four levels: within field populations, among populations at farm or village level, and belong to the same or different landrace groups, among regions, and as species mixtures in mountainous areas.

Variation in morphological plant characteristics is considerably larger for the entire collection than for a single population (Chapter 3). When populations are combined into groups, then within-variation is widened. Variation is slightly lower within landrace groups than within regions of origin, similarly for fungal disease resistances. Landrace groups thus are slightly more homogeneous. However, as differences in degree of variation are small, it may be concluded that variation among landrace groups and among regions explain about similar fractions of the total variation.

Agronomists are primarily interested in variation in agronomic characteristics such as yield. However, as in preliminary evaluations it is easier to determine morphological characteristics, variation in these may be assessed. It is then difficult to estimate agronomic variation on the basis of morphological variation, due to the limited causal relation between the two. For example, although plant heigth and stature, leaf and spike characteristics and tiller production have an effect on dry matter production and distribution, these characteristics do not consequently show similar variation. For the same reason, it is equally difficult to estimate agronomic variation from variation in glutenin characteristics, which is often favoured as it is not affected by environmental conditions (Brown & Weir, 1983; Gepts, 1989), and may be positively related to morphological variation (van Hintum & Elings, 1991).

9.5 Domestication

Morphological discrimination was possible between many landrace groups, but difficult between populations from regions of origin; landrace groups were slightly more homogeneous for morphological characteristics and disease resistances than regions of origin; and it was easier to relate grain yield to landrace groups than to regions of origin. This relative uniformity of landrace groups seems contradictory to their geographic distribution, as that implies variation in environmental characteristics, which, in turn, would cause genetic variation.

It is argued in Chapter 5 that landrace groups have been domesticated or cultivated for a long period, within relatively small areas with specific climatic conditions, followed by dispersion of some groups without losing characteristics. This probably has occured only recently, as otherwise dispersed landrace groups would have been less uniform in agronomic characteristics due to environmental pressure.

These regions of domestication and routes along which germplasm has spread are not known. Electrophoretic analysis of glutenin composition may help to analyse this. Glutenin diversity studies (van Hintum & Elings, 1991) indicated that all glutenin alleles common in many landrace groups and are geographically widely distributed, were found in populations from the western parts of Syria. This indicates that genetic material has been introduced from other parts of the Mediterranean basin and possibly other regions into western Syria, from where alleles have been disseminated further.

9.6 Collection strategy

Three reasons justify representative sampling of both regions and landrace groups:
- differences in plant characteristics among both regions and landrace groups are large;
- the geographic distribution of landrace groups is heterogeneous;
- both, regions of origin and landrace groups contribute about equally to variation.

Hence, per agro-ecological region all landrace groups should be collected. Extension officers, village heads and farmers may provide information on presence of landrace groups. However, this approach does not guarantee acquisition of all landrace groups, as some may not be cultivated in a particular year, or due to time limits only few villages can be visited. Consequently, it is difficult to indicate what share of the total genetic variation is collected.

Moreover, from each population a sufficient number of genotypes should be obtained (Marshall & Brown, 1975). Although intrapopulation variation may be relatively low, it can be high in absolute terms, as in germplasm from mountainous areas (Chapter 4).

Agro-ecological zoning for Syria can be based upon rainfall patterns, as moisture availability is a dominant factor in dry matter production in arid regions. Taking into account other factors, such as other environmental characteristics, population density, government policies, etcetera, leads to a classification that better discriminates among various cropping systems. For Syria, this approach has resulted in 5 zones (ICARDA, 1989). However, in such large zones, environmental conditions may be still too heterogeneous to determine relations between environmental and plant characteristics. As large zones are therefore not helpful in elucidating distribution and variation patterns, and setting priorities, planning of collection missions requires therefore a more stratified regional classification. On the other hand, classification in many small regions neither provides much clarification, as neighbouring regions are then likely to be similar, which limits the possibilities for discrimination, except for small areas with specific characteristics that may provide rare genetic material.

The agro-ecological classification presented in Chapter 3 yielded 14 regions, which appeared to meet the above mentioned criteria. Variation within regions of origin and within landrace groups were about equal. If the latter is taken as a reference, it follows that the regions were small enough to show limited variation. Admittedly, however, the agro-ecological classification was only moderately successful in elucidating agronomic performance patterns. It is doubtful whether a more detailed classification would mprove that, as the moderate success is most likely associated with the supposed historic spread of landrace groups.

9.7 Implications for genebank management

When a simulation model for crop growth and development is to be used in analysis of evaluation results, the evaluations themselves should meet some specific demands. For instance, data on plant characteristics for which model performance is sensitive must be obtained. Some of these, such as date of anthesis and the related temperature sum can easily be recorded in routine preliminary evaluations, if necessary for all accessions. On the other hand, determination of basic information on for instance physiological and morphological characteristics requires careful experimentation, including growth analysis. As this is not feasible for all accessions, such characteristics can be determined for a limited number of selected genotypes. Subsequently, the information obtained for part of the germplasm has to be analyzed such that it represents the entire collection. The concept of classification into landrace groups may be applied in this research phase.

This implies that preliminary characterization, which could be combined with first seed increase, has to preceed preliminary evaluation, as its results may be needed to organize the evaluation. If the former is the only occasion that all germplasm is sown, characteristics that can easily be recorded (e.g. date of anthesis) should be observed then. Periodical harvesting requires relatively large evaluation fields, in a sufficient number of replicates, and determination of plant physiological characteristics requires specific equipment. Experiments under controlled conditions in a phytotron, which in most cases will not be available, should be avoided.

Crop growth simulation models may be used to explore crop behaviour under different environmental conditions. Firstly, this requires appropriate computer hard and software, which are widely available currently. Secondly, simulation models need to be available. For many crops, these have been developed for various levels of production. Although in this study a fairly complex model has been used, it may be more appropriate to apply summary models, such as SUCROS87 (Spitters et al., 1989). These are small, comprehensible, and easy to parameterize for other plant characteristics or for other crops. It may also appear necessary to improve existing models by fundamental research and developing specific subroutines. This, however, is done most efficiently by experts.

Crop growth simulation is an interdisciplinary activity, that makes knowledge available in comprehensive form to non-specialists. Nevertheless, training in crop growth modelling and simulation will be necessary for curators that are not familiar with this discipline. The required minimum level of skill would be the ability to understand and apply summary models. Curators of larger genebanks, who serve a wide range of environments and who are consequently faced with more diversity in growth-limiting factors, would benefit from a more thorough quantitative understanding of plant growth processes.

Extensive data sets containing long-term weather data and detailed soil characterization of locations in various agro-ecological regions have to be available at the genebank. Simulation results based on these environmental inputs provide a preliminary overview of an accession's potentials. As subsequently more information will be required on growth under particular environmental conditions, additional data sets comprising specific weather or soil data representing more favourable or adverse growing conditions are needed.

Germplasm documentation has to be reorganized, as more complete, and thus more complex, information on plant characteristics has to be processed and presented. Preliminary evaluation results, for instance, could be distributed in printed form or through computer networks. Germplasm for specific conditions could then be selected in interaction with the interisted agronomists, utilizing local environmental input.

Simulation results need to be confirmed by field evaluation of a representative selection of the collection. Therefore, a genebank needs access to evaluation sites characterized by distinct environmental conditions (see 9.2.4). Simulation of crop growth and development, however, can be sufficiently accurate to limit the number of evaluations that actually have to be carried out.

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Abstract

Abstract

The need for an efficient evaluation method

Evaluation results have often limited applicability, due to the considerable genotype x environment interaction. Extensive multilocational or multiseasonal evaluation would be needed to assess plant characteristics, but this expensive procedure can often not be applied to large germplasm collections. Moreover, extensive evaluations may still not lead to unequivocal results. Therefore, an efficient method is developed that allows the assessment of plant characteristics of large numbers of accessions under various environmental conditions, utilizing a limited amount of evaluation results.

Collection of durum wheat landraces

A total of 185 landrace populations of durum wheat [Triticum turgidum L. var. durum (Desf.) MK] was collected in the Syrian Arab Republic in 1987 and 1988. During the collection missions, attention was paid to recording passport and collection information, and providing an agro-ecological description of each site. Farmers were asked for information on the landraces and their farm management practices.

Grouping of the 166 collection sites, based on four climatological variables, resulted in 14 relatively homogeneous regions of origin with respect to agro-ecological characteristics. Fifty-nine populations had their putative origin at or in the vicinity of their collection sites, and were considered representative for the respective environments.

A brief morphological description was given of the landrace groups as distinguished by farmers. Each group has distinct morphological characteristics, and is referred to by a local name that is often derived from a striking character or supposed origin. Some landrace groups are widely distributed over most of the country, whereas most others are regionally concentrated, either in a limited region or a few villages.

Agronomic evaluation

Thirty-eight populations were evaluated for agronomic performance at four locations, characterized by different long-term rainfall averages, over two seasons, and at two levels of nutrient availability. Actual seasonal rainfall was below average (viz. below 300 mm), although at the location with highest average yield, residual moisture had to be assumed.

Considerable differences in average yield were observed among experiments. Performance per population varied highly among locations, and populations showing superior performance under all conditions could not be identified. Modern varieties (incorporated in the experiments as check varieties) showed superior performance under best growing conditions, and landraces appeared competitive under more marginal conditions. Both modern varieties and landraces were not able to maintain yield levels under adverse growing conditions. Fertilizer application resulted in many cases in decreased kernel density, and delay of anthesis by one day, which could be an indirect effect of nitrogen shortage through increased canopy temperature.

Analysis of variance

Analysis of variance showed that most year, location, population and fertilizer effects were significant, as were interactions between year and location. Yield stability, which is an important characteristic of landraces, was indicated by the absence of significant effects for grain yield between years, within sites, and by the absence of a population effect for total dry matter production.

Through ANOVA, sources of variation are identified. This technique is therefore useful in preliminary, qualitative analysis of evaluation trials. However, it does not contribute to an understanding of processes underlying variation, and has therefore little capabilities in exploring plant behaviour under other environmental conditions.

Simulation of growth and development

Analysis of growth and development with a simulation model showed that total dry matter production was higher at higher total, and higher spring rainfall, and that at higher levels of moisture availability, more aboveground dry matter was produced per unit rainfall. Moisture and nitrogen availability interacted: at very low levels of moisture availability, this was the dominant growth limiting factor, whereas at higher levels, nitrogen recovery increased, and nitrogen availability became an additional growth limiting factor.

Under favourable environmental conditions, differences in weather conditions are reflected in the source size, i.e. the residual reserve carbohydrates at the end of grain fill. Genotypical differences in the balance between maintenance requirements and assimilation after anthesis determine to what extent the reserves are distributed to the sink. Under adverse growing conditions, severe drought stress after anthesis results in rapid senescence and cessation of grain fill, so that the reserve pool is not depleted. Under these conditions, higher grain yields are the result of increased remobilization of reserve carbohydrates, mainly due to higher kernel density.

The crop growth simulation model presented a comprehensive tool to increase insight in plant growth processes. Despite some shortcomings, the model simulated a recognizable durum wheat crop and reproduced in a consistent way genotype x environment interactions and their effects on yields. The model could be used in exploring crop behaviour under different environmental conditions, and replace extensive multilocational and multiseasonal evaluations.

Environmental characterization

It appeared possible to relate some collection site and plant characteristics at evaluation, which could be used to select germplasm on the basis of knowledge on the environment in the region of provenance. As this approach provides only general understanding, it is useful in preliminary evaluations that are aimed to identify groups of accessions in which further selections best can be made.

The germplasm was additionally evaluated for early and late season frost tolerance. All populations were well adapted to moderate early season frosts, which is characteristic for the Syrian climate. However, tolerance to late season frosts, which is uncharacteristic, was highest in populations from the inland, where minimum winter temperatures are lowest. Application of this relation is straightforward: in search for late season frost tolerance, breeding material can best be selected from inland populations, where chances of success are highest.

For fungal disease resistances, however, relations were not always cases clear. Only in the case of two of the three evaluated diseases, host resistance was highest in germplasm originating from regions with environmental characteristics favourable for development and incidence of the concerned disease. An efficient evaluation method is therefore difficult to formulate. Moreover, as the frequency of plants with specific vertical resistance can be very low, it may remain necessary to evaluate an entire collection.

Evaluation methods

It is useful to evaluate at least part of a germplasm collection at several locations over a number of seasons. This will provide data to analyze the variation patterns with ANOVA, validate a crop growth model, and determine possible relations between plant and collection site characteristics.

Subsequently, two evaluation methods can be followed, dependent upon the significance of the relationship between the observed plant character and environmental characteristic of the collection site. If such relationships are significant and causal, then preliminary selection of germplasm can be based upon collection site characteristics. Example are tolerance to late season frosts, and to a lesser extent some fungal disease resistance. If such relationships are difficult to establish, as for instance yield, then application of a crop growth simulation model appears a suitable technique in analysis of evaluation results of extensive germplasm collections, and for exploring growth and development under various environmental conditions. Whereas only a limited part of a large germplasm collection is evaluated multilocationally and multiseasonally, crop growth analysis can be applied to an entire collection. This would alleviate quantitative and qualitative limitations to evaluation programmes.

Landrace groups were generally more homogeneous for plant characteristics than regions of origin. Therefore, a pre-selection of germplasm could be made on the basis of landrace groups to restrict the number of accessions to evaluate. Of each group a small number of populations could be chosen, randomly or on the basis of origin, and evaluated, which would provide an indication of the characteristics of certain landrace groups. If necessary, this could be completed by a more detailed evaluation of promising material.

Variation

Genetic diversity was observed at four levels: within field populations, among populations at farm or village level, and belong to the same or different landrace groups, among regions, and as species mixtures in mountainous areas.

The heterogeneity of landrace populations complicates evaluation. Crop growth simulation models at the population level do not explain the consequences of heterogeneity in different environments. However, simulation at the population level was sufficiently accurate to justify application in interpretation of preliminary evaluation. In subsequent evaluation and selection, it may be necessary to quantify intrapopulation variation, to determine breeding potentials of best performing populations.

Domestication

It is argued that landrace groups have been domesticated or cultivated for a long period, within relatively small areas with specific climatic conditions, followed by dispersion of some groups without losing characteristics. This probably has occurred only recently, as otherwise dispersed landrace groups would have been less uniform in agronomic characteristics due to environmental pressure.

Collection methods

Both regions and landrace groups must be sampled representatively. Hence, per agro-ecological region all landrace groups should be collected. Moreover, from each population a sufficient number of genotypes must be obtained. Although intrapopulation variation may be relatively low, it can be high in absolute terms, as in germplasm from mountainous areas.

Collection missions require a regional classification, such that the regions are relatively homogeneous with respect to environmental characteristics. In large zones, environmental conditions may be too heterogeneous to determine relations between environmental and plant characteristics. Therefore, large zones are not helpful in elucidating distribution and variation patterns, and setting priorities, whereas classification in many small regions neither provides much clarification, as neighbouring regions are then likely to be similar, which limits the possibilities for discrimination.

Implications for genebank management

If a crop growth model is to be used in analysis of evaluation results, the evaluations themselves should meet some specific demands. Data on plant characteristics for which model performance is sensitive must be obtained. Some can easily be recorded in routine preliminary evaluations, if necessary for all accessions. Characteristics that require much effort to record, can be determined on few selected genotypes, and subsequently interpreted such that they are representative for the entire collection.

Appropriate computer hard- and software is required, and simulation models need to be available. Although for this study a fairly complex model was used, it may be more appropriate to apply summary models. These are small, comprehensive, and easy to parameterize for other plant characteristics or other crops. Training in modelling and simulation will be necessary for curators who are unacquainted with this.

Extensive data sets containing weather data and detailed soil characterization of locations in various agro-ecological regions have to be available at the genebank. Germplasm documentation has to be reorganized, as the more complex information on plant characteristics has to be processed and presented.

Simulation results need to be confirmed by field evaluation of a part of the collection. Therefore, a genebank will need access to evaluation sites characterized by distinct environmental conditions.

Samenvatting (in Dutch)

De behoefte aan een efficiënte evaluatiemethode

Als gevolg van aanzienlijke genotype x omgevingsinteractie hebben evaluatieresultaten hebben vaak een beperkte geldigheid. Een uitgebreide evaluatie gedurende meerdere seizoenen op meerdere locaties zou nodig zijn om planteigenschappen te bepalen, maar deze kostbare methode kan vaak niet worden worden toegepast in het geval van grote genenbankverzamelingen. Bovendien zou een uitgebreide evaluatie nog steeds geen eenduidige resultaten kunnen opleveren. Daarom is er een efficiënte evaluatiemethode ontwikkeld, die het mogelijk maakt planteigenschappen van grote aantallen nummers in verschillende milieus te bepalen, daarbij gebruik makend van een beperkte hoeveelheid evaluatieresultaten.

De verzameling van durum tarwe landrassen

In 1987 en 1988 werden 185 landraspopulaties van durum tarwe [Triticum turgidum L. var. durum (Desf.) MK] verzameld in de Syrisch Arabische Republiek. Tijdens de verzamelreizen werd aandacht besteed aan het vastleggen van de paspoort- en collectiegegevens, en aan het geven van een agro-ecologische beschrijving van ieder verzamelpunt. Bij boeren werd informatie ingewonnen omtrent de landrassen en de bedrijfsvoering.

Groepering van de 166 verzamelpunten op basis van vier klimatologische variabelen resulteerde in 14 oorsprongsgebieden die relatief homogeen waren met betrekking tot agro-ecologische karakteristieken. De veronderstelde oorsprong van 59 populaties lag op of in de nabijheid van het verzamelpunt, en deze populaties werden representatief geacht voor hun respectievelijke milieus.

Van iedere landrasgroep, zoals boeren deze onderscheiden, is een beknopte morfologische beschrijving gegeven. Iedere groep heeft bepaalde morfologische kenmerken, en draagt een locale naam die vaak afgeleid is van een opvallend kenmerk of van de veronderstelde oorsprong. Sommige landrasgroepen zijn wijd verspreid over het grootste deel van het land, terwijl andere plaatselijk geconcentreerd zijn in een beperkt gebied of in een aantal dorpen.

Landbouwkundige evaluatie

Gedurende twee seizoenen werden 38 populaties op vier locaties en op twee niveaus van nutriëntenbeschikbaarheid geëvalueerd met betrekking tot hun landbouwkundige prestaties. De locaties werden gekenmerkt door verschillende lange-termijn regenvalgemiddelden. De gemeten seizoensregenval lag onder het gemiddelde (namelijk onder 300 mm), alhoewel op de locatie met de hoogste gemiddelde opbrengst de aanwezigheid van overgebleven vocht moest worden aangenomen.

Tussen experimenten werden aanzienlijke verschillen in opbrengst waargenomen. Het gedrag per populatie wisselde sterk per locatie, en populaties met een onder alle omstandigheden superieur gedrag werden niet geïdentificeerd. Moderne variëteiten, die als controles in de experimenten waren opgenomen, vertoonden een superieur gedrag onder de beste groeiomstandigheden, en landrassen bleken concurrerend onder meer marginale omstandigheden. Zowel moderne variëteiten als landrassen waren niet in staat om hun opbrengstniveaus onder slechte groeiomstandigheden te handhaven. Kunstmestgift resulteerde in veel gevallen in een verminderde korreldichtheid, en een uitstel van de bloeidatum met een dag, wat een indirect gevolg zou kunnen zijn van stikstoftekort via verhoogde bladtemperatuur.

Variantieanalyse

Variantieanalyse (ANOVA) toonde aan dat de meeste jaar-, locatie-, populatie-, en kunstmesteffecten significant waren, net als de interacties tussen jaar en locatie. De afwezigheid van significante effecten voor korrelopbrengst tussen jaren, binnen locaties, en de afwezigheid van een populatie-effect voor totale drogestofproduktie, duidden op opbrengststabiliteit, dat een belangrijk kenmerk is van landrassen.

Door middel van ANOVA worden variatiebronnen geïdentificeerd. Deze techniek is daarom zinvol in een voorlopige, kwalitatieve analyse van evaluaties. Het draagt echter niet bij aan een begrip van de onderliggende processen die de variatie veroorzaken, en het biedt dus weinig mogelijkheden ten aanzien van het onderzoeken van plantgedrag onder andere milieuomstandigheden.

Simulatie van groei en ontwikkeling

Analyse van groei en ontwikkeling met een simulatiemodel toonde een hogere totale drogestofproduktie bij een hogere totale regenval, en bij een hogere voorjaarsregenval, en een hogere bovengrondse drogestofproduktie per eenheid regenval bij hogere niveaus van vochtbeschikbaarheid. Vocht- en stikstofbeschikbaarheid vertoonden interactie: bij lage niveaus van vochtbeschikbaarheid was dit de dominante groeibeperkende factor, terwijl bij hoger niveaus de stikstofbenutting toenam en stikstofbeschikbaarheid een additioniële groeibeperkende factor vormde.

Bij gunstige milieuomstandigheden reflecteren verschillen in weersomstandigheden in de omvang van de 'source', in de vorm van overgebleven reservekoolhydraten aan het einde van de korrelvulling. Genotypische verschillen in de balans na de bloei tussen onderhoudsbehoeften en assimilatie bepalen in welke mate de reserves worden geredistribueerd naar de 'sink'. Onder slechte groeiomstandigheden resulteert een sterk watertekort na de bloei in een snelle afsterving en een beëindiging van de korrelvulling, waardoor de reserves niet uitgeput raken. Onder deze omstandigheden zijn hogere korrelopbrengsten het resultaat van een toegenomen remobilisatie van reservekoolhydraten, voornamelijk als gevolg van een grotere korreldichtheid.

Milieukarakteristieken

Het bleek mogelijk enkele milieukarakteristieken van de verzamelpunten en planteigenschappen bij evaluatie aan elkaar te relateren. Dit zou kunnen worden gebruikt in de selectie van genetisch materiaal op basis van kennis omtrent het milieu in het oorsprongsgebied. Aangezien deze benadering slechts een algemeen begrip verschaft, is het van nut in voorlopige evaluaties die tot doel hebben groepen nummers te identificeren waarin het best verder geselecteerd kan worden.

Het materiaal werd eveneens geëvalueerd met betrekking tot vroege en late vorsttolerantie. Alle populaties waren goed aangepast aan matige vroege vorst, welke karakteristiek is voor het Syrische klimaat. Daarentegen was late vorsttolerantie, welke niet karakteristiek is, het grootst in populaties afkomstig uit het binnenland, waar de minimim wintertemperaturen het laagst zijn. De toepassing van dit verband is duidelijk: bij het zoeken naar late vorsttolerantie kan veredelingsmateriaal het beste worden geselecteerd uit populaties afkomstig van het binnenland, waarin de kansen op succes het grootste zijn.

In het geval van resistentie tegen schimmelziekten daarentegen, waren de verbanden niet steeds duidelijk. Slechts in het geval van twee van de drie geëvalueerde ziekten was de waardplantresistentie het grootst in materiaal afkomstig uit gebieden met gunstige milieukarakteristieken voor de ontwik-keling en het voorkomen van de desbetreffende ziekte. Het is daarom moeilijk een efficiënte evaluatiemethode te formuleren. Bovendien, omdat de frequentie van planten met specifieke verticale resistenties erg laag kan zijn, kan het noodzakelijk blijven om een volledige collectie te evalueren.

Evaluatiemethoden

Het is zinvol om tenminste een deel van de collectie gedurende een aantal seizoenen op meerdere locaties te evalueren. Dit zal de gegevens verschaffen om variatiepatronen met behulp van ANOVA te analyseren, een gewasgroeimodel te valideren, en mogelijke relaties tussen plant en locatiekarakteristieken te bepalen.

Vervolgens kunnen er twee evaluatiemethoden worden gevolgd, afhankelijk van de significantie van relaties tussen waargenomen planteigenschappen en milieukarakteristieken van het verzamelpunt. Als zulke relaties significant en oorzakelijk zijn, dan kan de voorlopige evaluatie gebaseerd worden op karakteristieken van het verzamelpunt. Voorbeelden hiervan zijn late vorsttolerantie, en in mindere mate een aantal resistenties tegen schimmelziekten. Als zulke relaties moeilijk te bepalen zijn, zoals in het geval van opbrengst, dan blijkt de toepassing van een simulatiemodel voor gewasgroei een geschikte techniek om evaluatieresultaten van uitgebreide collecties te analyseren, en om de groei en ontwikkeling onder andere milieuomstandigheden te onderzoeken. Terwijl slechts een beperkt deel van een grote collectie op meerdere locaties gedurende meerdere seizoenen wordt geëvalueerd, kan gewasgroeianalyse op een volledige collectie worden toegepast. Dit vermindert de kwantitatieve en kwalitatieve beperkingen van evaluatieprogramma's.

Landrasgroepen waren in het algemeen homogener ten aanzien van planteigenschappen dan oorsprongsgebieden. Daarom zou een voorselectie van genetisch materiaal kunnen worden gebaseerd op landrasgroepen, teneinde het aantal te evalueren nummers te beperken. Van iedere groep zou een klein aantal populaties kunnen worden gekozen, willekeurig of op basis van hun oorsprong, en worden geëvalueerd, wat een indicatie van de karakteristieken van bepaalde landrasgroepen zou opleveren. Indien noodzakelijk, zou dit kunnen worden gecompleteerd met een meer gedetailleerde evaluatie van het veelbelovende materiaal.

Variatie

Genetische diversiteit werd waargenomen op vier niveau's: binnen veldpopulaties, tussen populaties op een boerderij of in een dorp, en die tot dezelfde of verschillende landrasgroepen behoren, tussen regio's, en in de vorm van soortenmengsels in bergachtige gebieden.

De heterogeniteit van landraspopulaties compliceert de evaluatie. Simulatiemodellen voor gewasgroei op populatieniveau verklaren niet de gevolgen van heterogeniteit in andere milieu's. De simulatie op populatieniveau was echter nauwkeurig genoeg om de toepassing ervan in de interpretatie van voorlopige evaluaties te verantwoorden. In hierop volgende evaluatie en selectie zou het nodig kunnen zijn om de intrapopulatievariatie te kwantificeren, teneinde de veredelingspotentiëlen van de best presterende populaties te bepalen.

Domesticatie

Het wordt beargumenteerd dat landrasgroepen in relatief kleine gebieden met specifieke klimaatomstandigheden werden gedomesticeerd of gedurende een lange periode werden gecultiveerd, gevolgd door een verspreiding van enige groepen zonder dat daarbij hun karakteristieken verloren gingen. Dit heeft waarschijnlijk onlangs plaatsgevonden, aangezien anders de verspreide landrasgroepen minder uniform zouden zijn geweest als gevolg van milieudruk.

Verzamelmethoden

Zowel regio's als landrasgroepen moeten representatief worden bemonsterd, dus dienen per agro-ecologische regio alle landrasgroepen te worden verzameld. Bovendien moet er van iedere populatie een voldoende aantal genotypen worden verkregen. Hoewel de intropopulatie variatie relatief klein kan zijn, kan dit in absolute termen groot zijn, zoals in materiaal uit bergachtige gebieden.

Verzamelreizen vereisen een dusdanige regionale klassificatie dat de regio's relatief homogeen zijn ten aanzien van milieuomstandigheden. In grote regio's kunnen de milieuomstandigheden te heterogeen zijn om relaties tussen milieu- en plantkarakteristieken te bepalen. Daarom zijn grote gebieden niet behulpzaam in het verhelderen van distributie- en variatiepatronen en in het bepalen van prioriteiten, terwijl een klassificatie in vele kleine regio's eveneens weinig helderheid verschaft, aangezien naburige regio's dan waarschijnlijk soortgelijk zijn, wat de onderscheidingsmogelijkheden beperkt.

Gevolgen voor genenbankbeheer

Als een gewasgroeimodel gebruikt gaat worden in de analyse van evaluatieresultaten, dan dienen de evaluaties zelf aan enige specifieke eisen te voldoen. Gegevens omtrent planteigenschappen waarvoor de modelwerking gevoelig is moeten worden verkregen. Sommige kunnen eenvoudig worden vastgelegd in de standaard uitgevoerde voorlopige evaluaties, indien noodzakelijk voor alle nummers. Eigenschappen die slechts met veel moeite kunnen worden verkregen, kunnen worden bepaald aan enkele geselecteerde genotypen, om daarna zodanig geïnterpreteerd te worden dat ze representatief zijn voor de volledige verzameling.

Geschikte apparatuur en programmatuur is vereist, en simulatiemodellen moeten beschikbaar zijn. Hoewel voor deze studie een redelijk complex model werd gebruikt, zou het beter zijn overzichtmodellen toe te passen. Deze zijn klein, begrijpelijk, en eenvoudig te parameteriseren voor ander planteigenschappen of andere gewassen. Onderwijs in modelleren en simuleren zal een noodzaak zijn voor curators die hiermee onbekend zijn.

Uitgebreide gegevensbestanden met weergegevens en gedetailleerde grondkarakterisaties van locaties in diverse agro-ecologische regio's moeten beschikbaar zijn op de genenbank. De genenbank-documentatie moet worden gereorganiseerd, aangezien de meer complexe informatie ten aanzien van planteigenschappen moet worden verwerkt en gepresenteerd.

Simulatieresultaten moeten worden bevestigd door evaluatie van een deel van de collectie in het veld. Daarom zal een genebank toegang moeten hebben tot evaluatieplaatsen die worden gekarakteriseerd door onderscheiden milieuomstandigheden.

Tables and figures

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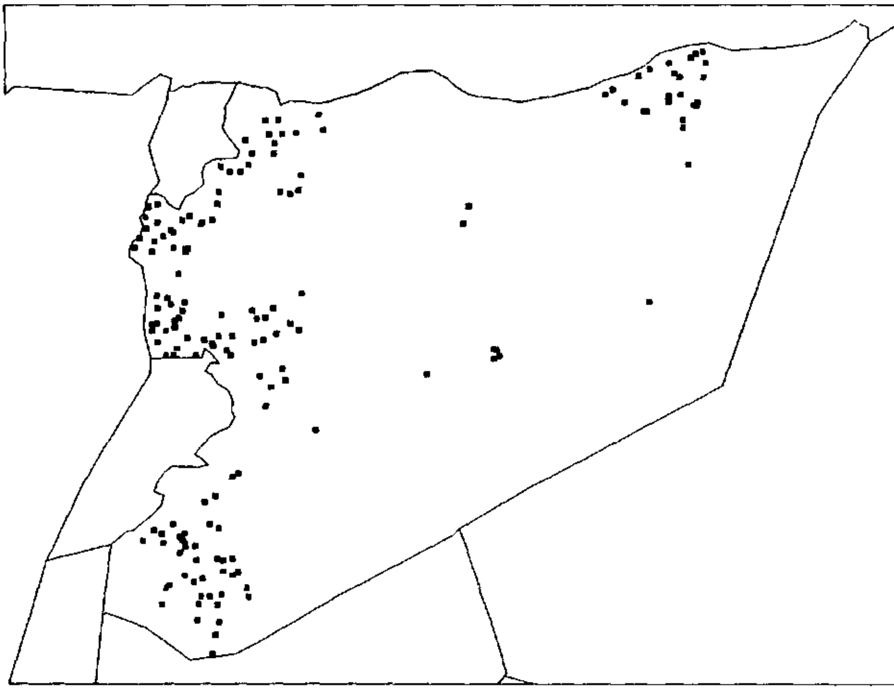
Abbreviations

ANCOVA	Analysis of Covariance
ANOVA	Analysis of Variance
B.C.	Before Christ
CABO	Centre for Agrobiological Research, Wageningen, The Netherlands
CGN	Centre for Genetic Resources The Netherlands, Wageningen, The Netherlands
CPRO	Centre for Plant Breeding and Reproduction Research, Wageningen, The Netherlands
cv	coefficient of variation
DGIS	Directorate General International Cooperation, Ministry of Foreign Affairs, The Hague, The Netherlands
DLO	Directorate Agricultural Research
E	East
FDR	Relative Frost Damage Rate
GRU	Genetic Resources Unit
ICARDA	International Center for Agricultural Research in the Dry Areas, Aleppo, Syria
ITC	International Institute for Aerospace Survey and Earth Sciences, Enschede, The Netherlands
IvP	Department of Plant Breeding, Wageningen Agricultural Univeristy, Wageningen, The Netherlands
N	Nitrogen, North
P	Phosphorus
PCA	Principal Component Analysis
RCB	Randomized Complete Block (design)
SDA	Stepwise Discriminant Analysis
TPE	Department of Theoretical Production Ecology, Wageningen Agricultural University, Wageningen, The Netherlands
WAU	Wageningen Agricultural University, Wageningen, The Netherlands

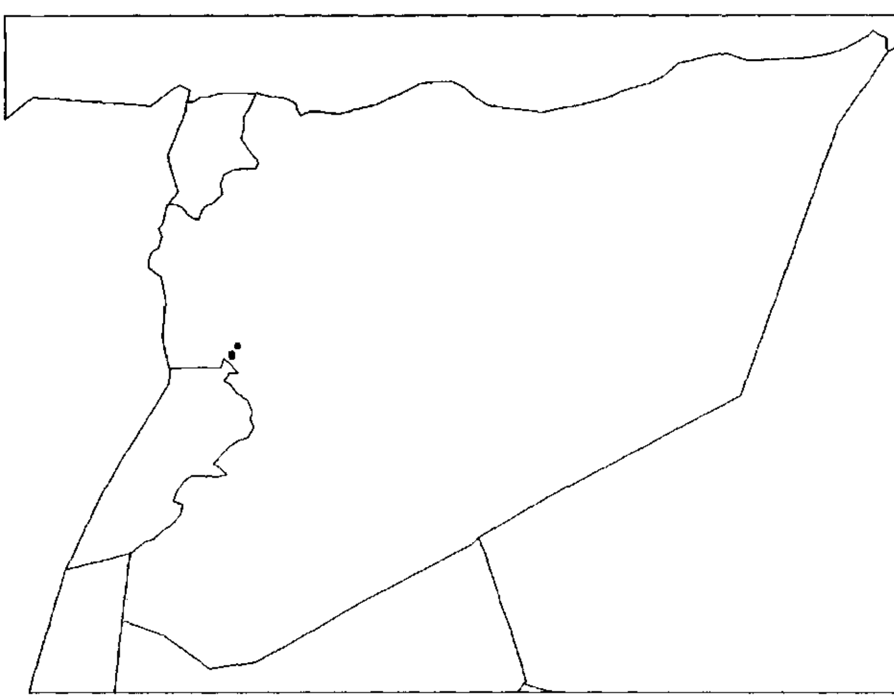
Curriculum vitae

Anne Elings was born at August 9th 1960, as the second of five children of Rint Elings and Tini Kuipers in Sint Annaparochie, where he went to kinder garten and primary school. In 1978, he completed the Atheneum β secondary education at the 'Rijksscholengemeenschap' in Leeuwarden, and started in Wageningen his study Plant Breeding at the Agricultural University. He spent a 7-months practical training period at the All-India Coordinated Rice Improvement Project (AICRIP) in Hyderabad, India, and graduated in April 1986, after passing MSc exams in plant breeding, theoretical production ecology, phytopathology, the plant production of crops, and agricultural economics and policy. In 1987, he was contracted by DGIS and stationed at the International Center for Agricultural Research in the Dry Areas (ICARDA) in Aleppo, Syria, to research evaluation methods of large germplasm collections of durum wheat landraces, which has resulted in this dissertation. From January to April 1992, he spent a short sabbatical at the Malang Research Institute for Food Crops (MARIF), in Malang, Indonesia, to evaluate its soybean germplasm collection for resistance against bean fly. Presently, he is Coordinator Crop Protection for the Simulation and Systems Analysis for Rice Production (SARP) project, and based at the DLO-Centre for Agrobiological Research (DLO-CABO), Wageningen.

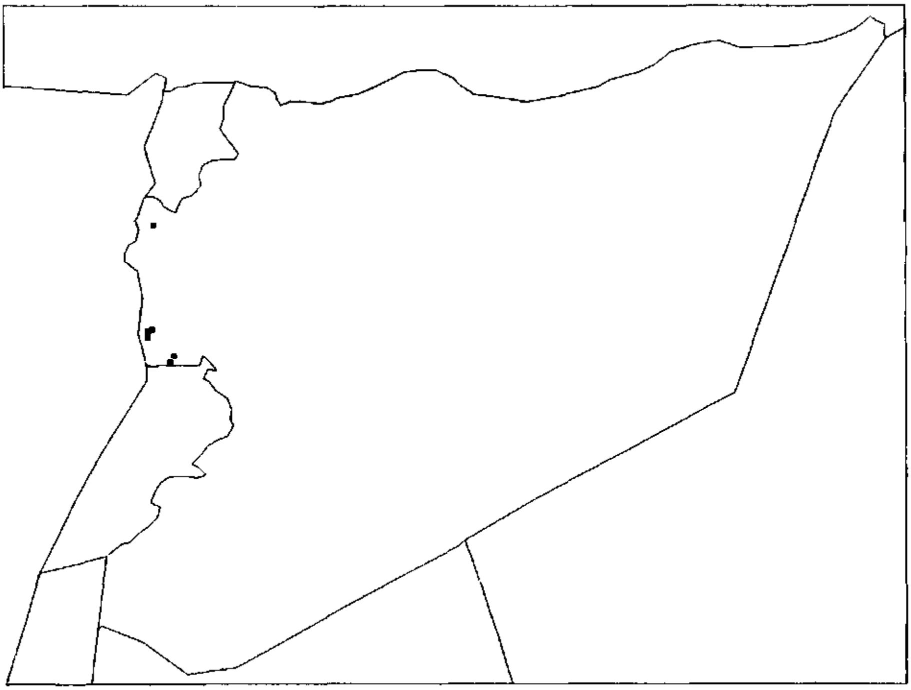
Distribution maps



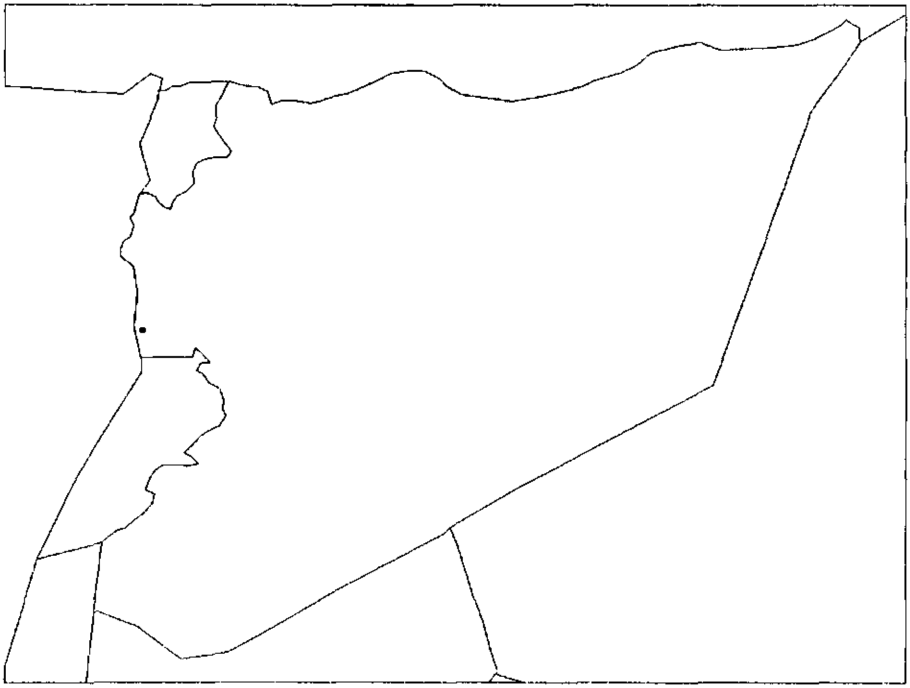
Map 1. Distribution of collection sites of all durum wheat landrace populations.



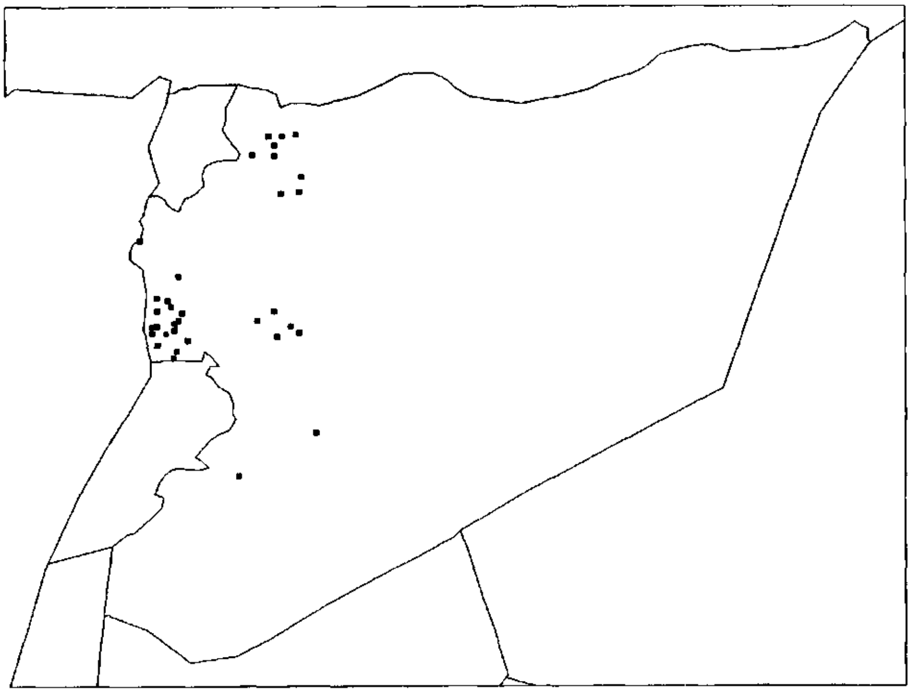
Map 2. Distribution of collection sites of *Abssieh* durum wheat landrace populations.



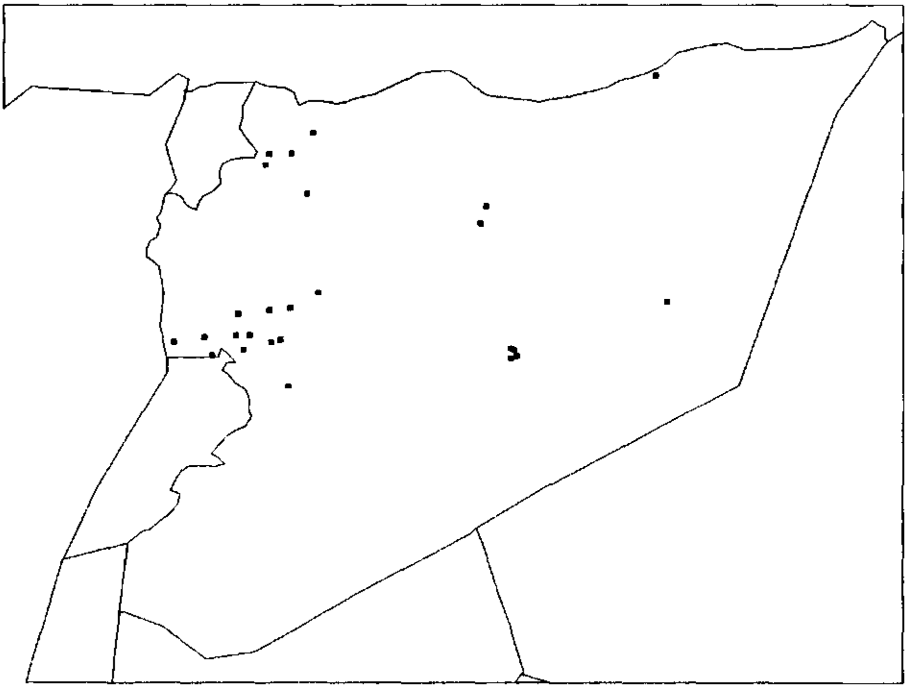
Map 3. Distribution of collection sites of *Ahmar* durum wheat landrace populations.



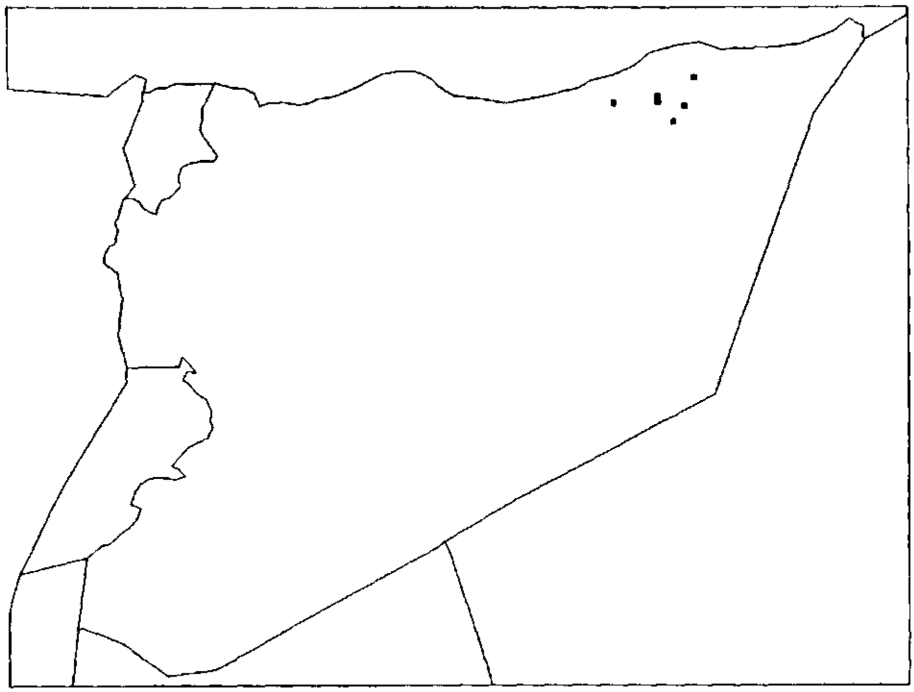
Map 4. Distribution of collection sites of *Akraa* durum wheat landrace populations.



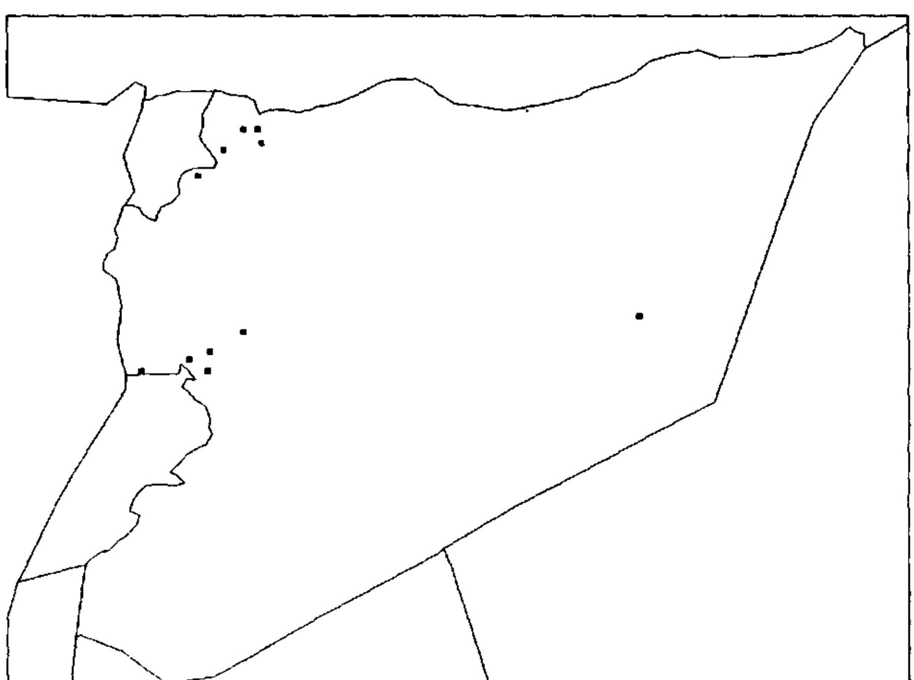
Map 5. Distribution of collection sites of *Baladi* durum wheat landrace populations.



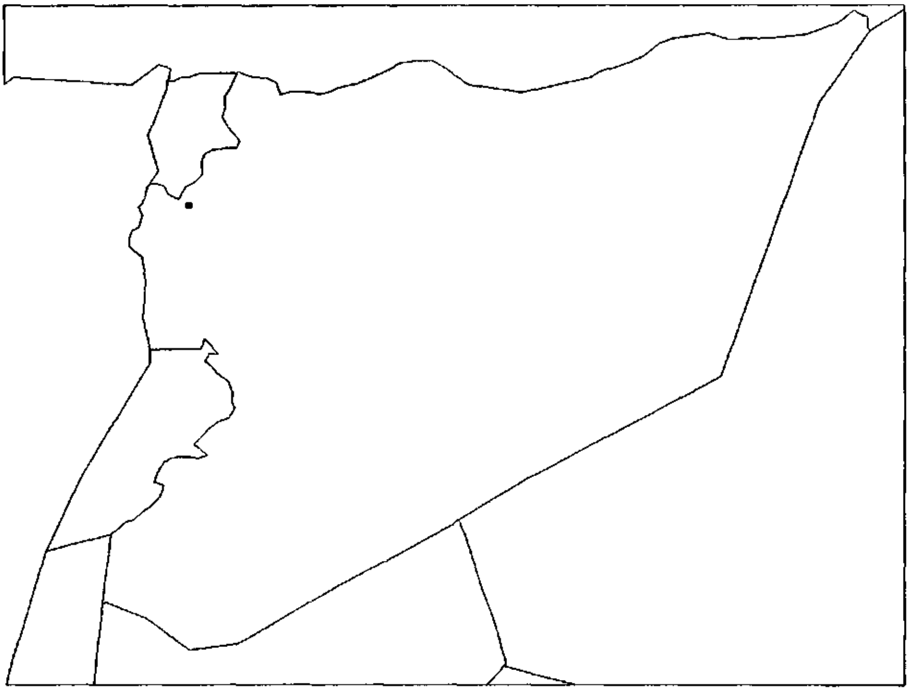
Map 6. Distribution of collection sites of *Bayadi* durum wheat landrace populations.



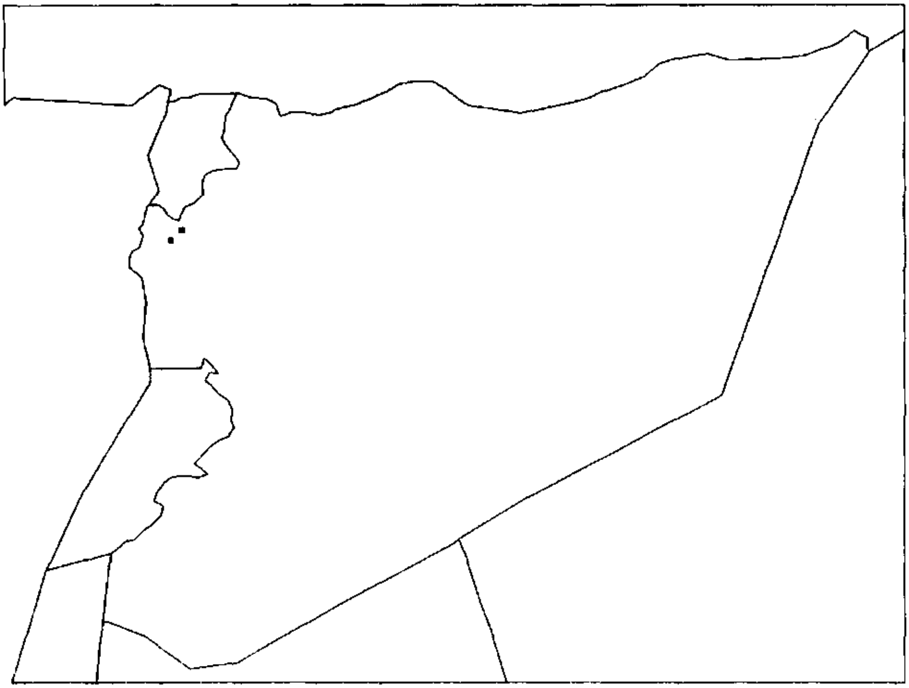
Map 7. Distribution of collection sites of *Halabi* durum wheat landrace populations.



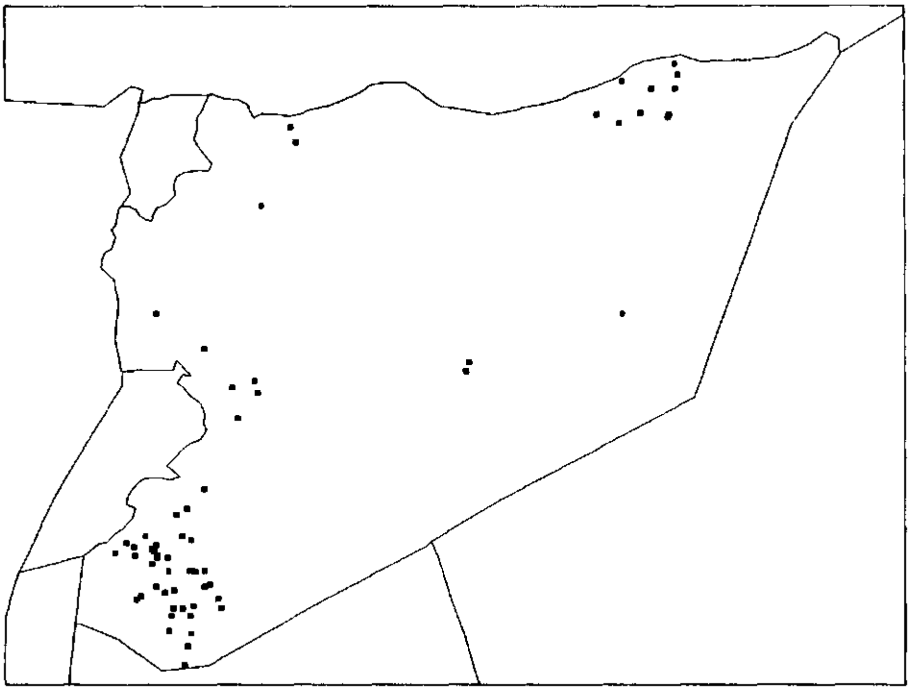
Map 8. Distribution of collection sites of *Hamari* durum wheat landrace populations.



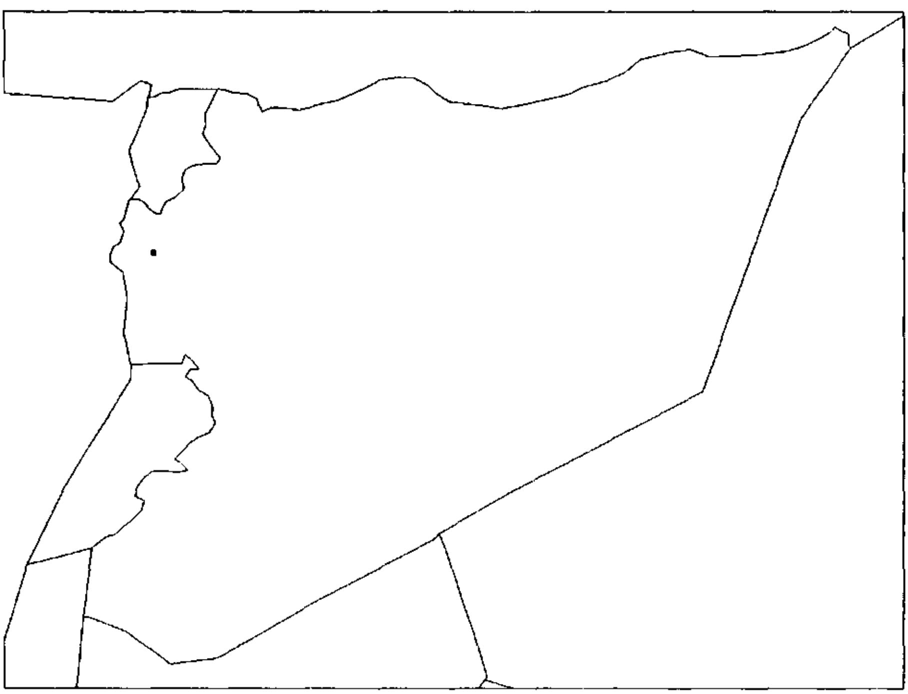
Map 9. Distribution of collection sites of *Harami* durum wheat landrace populations.



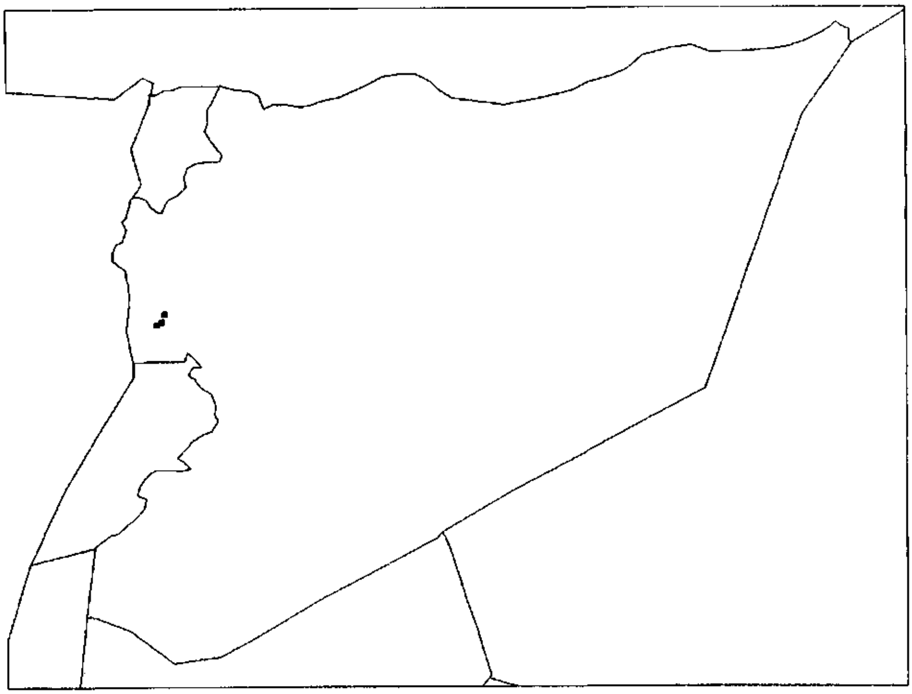
Map 10. Distribution of collection sites of *Haririeh* durum wheat landrace populations.



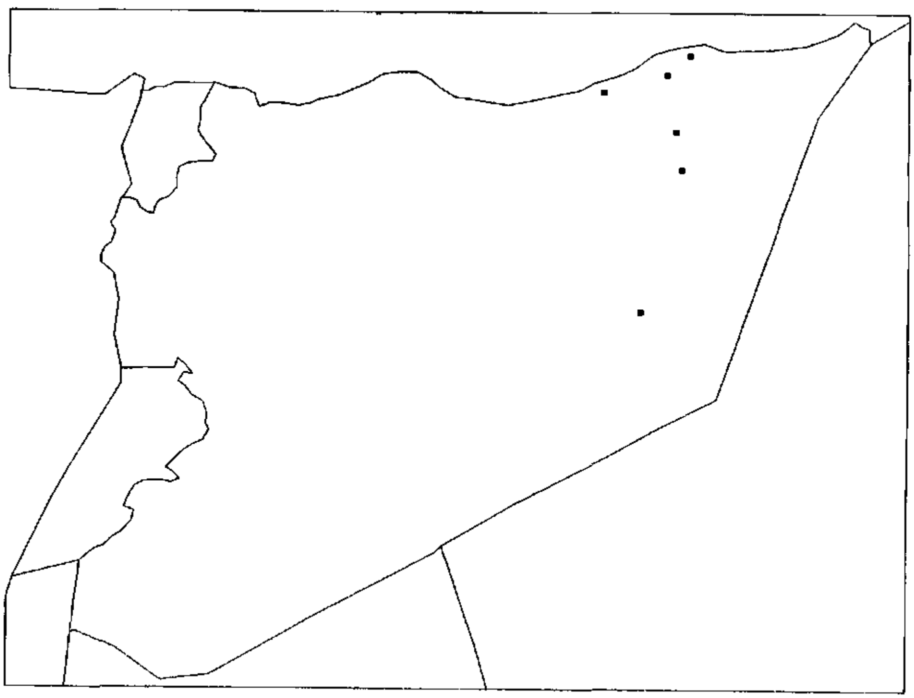
Map 11. Distribution of collection sites of *Haurani* durum wheat landrace populations.



Map 12. Distribution of collection sites of *Hredieh* durum wheat landrace populations.



Map 13. Distribution of collection sites of *Hridini* durum wheat landrace populations.



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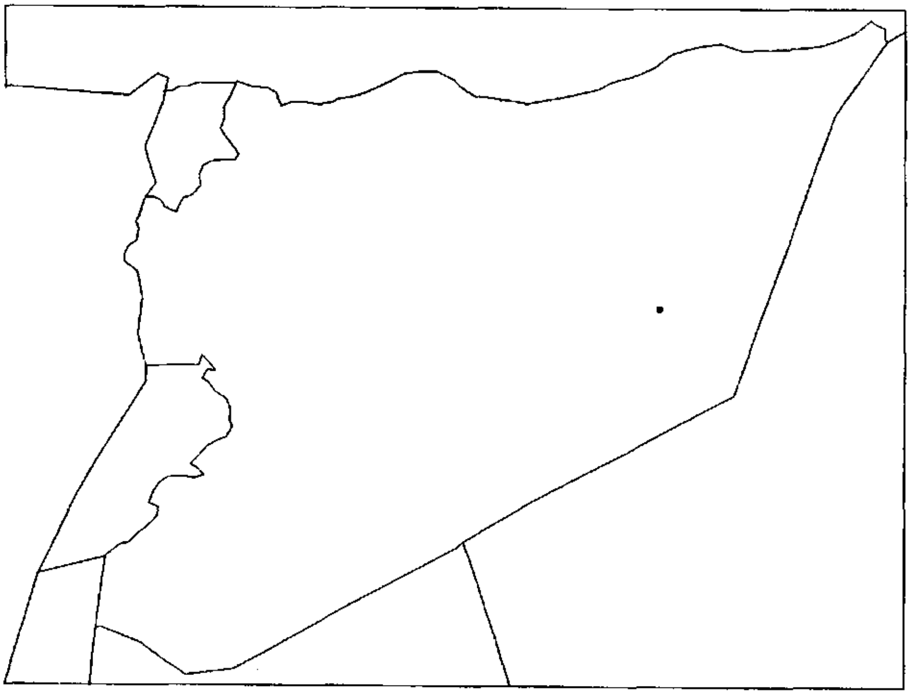

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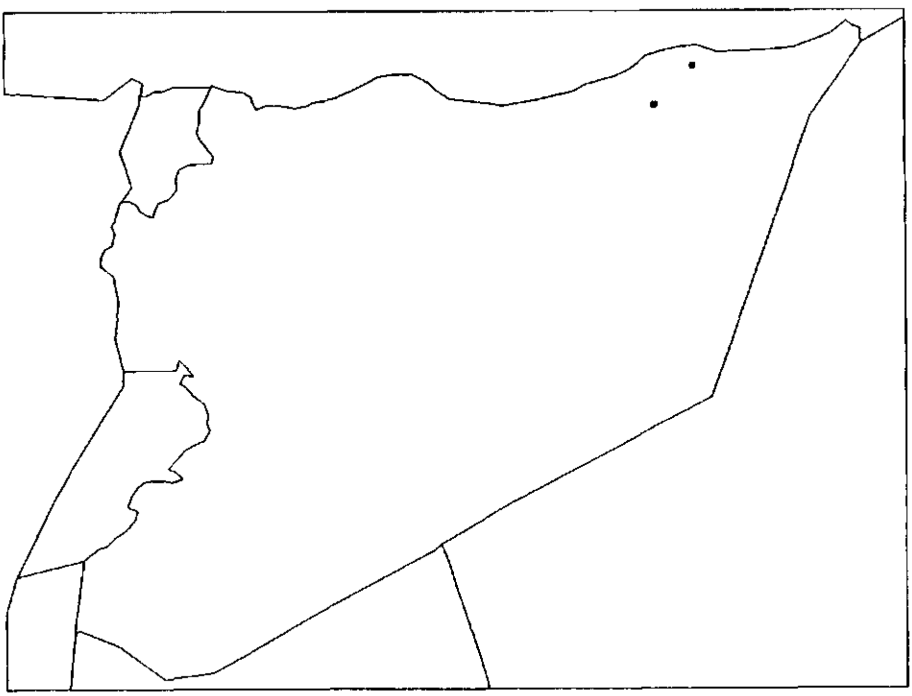

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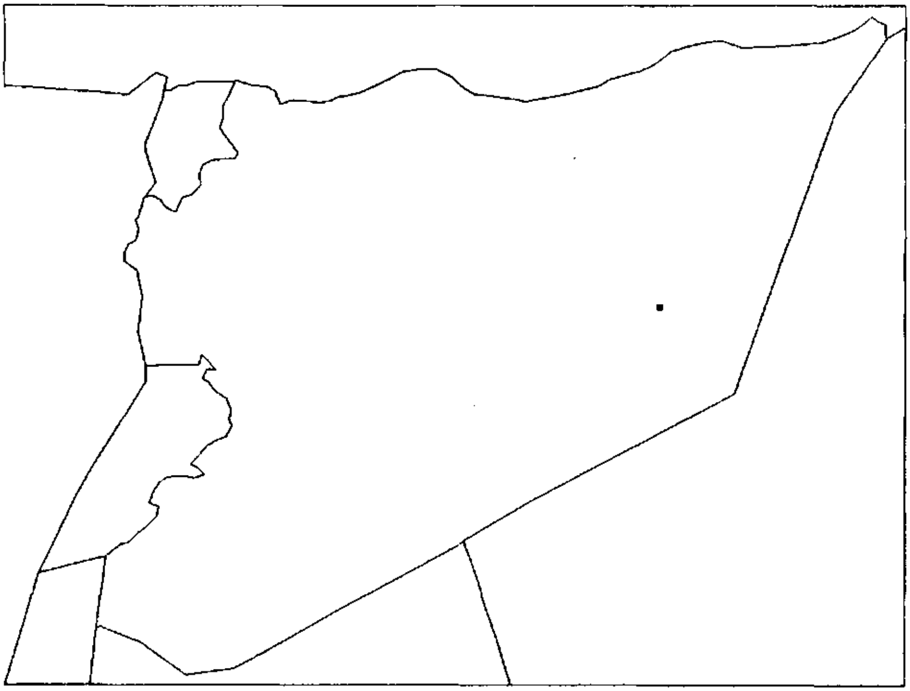
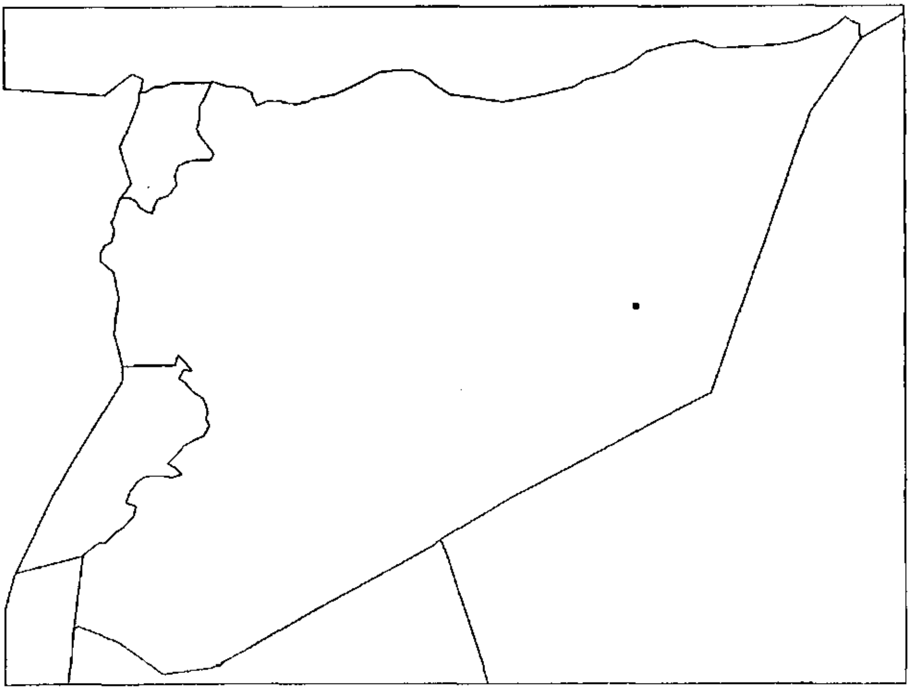


Map 17. Distribution of collection sites of *Mousseirieh* durum wheat landrace populations.



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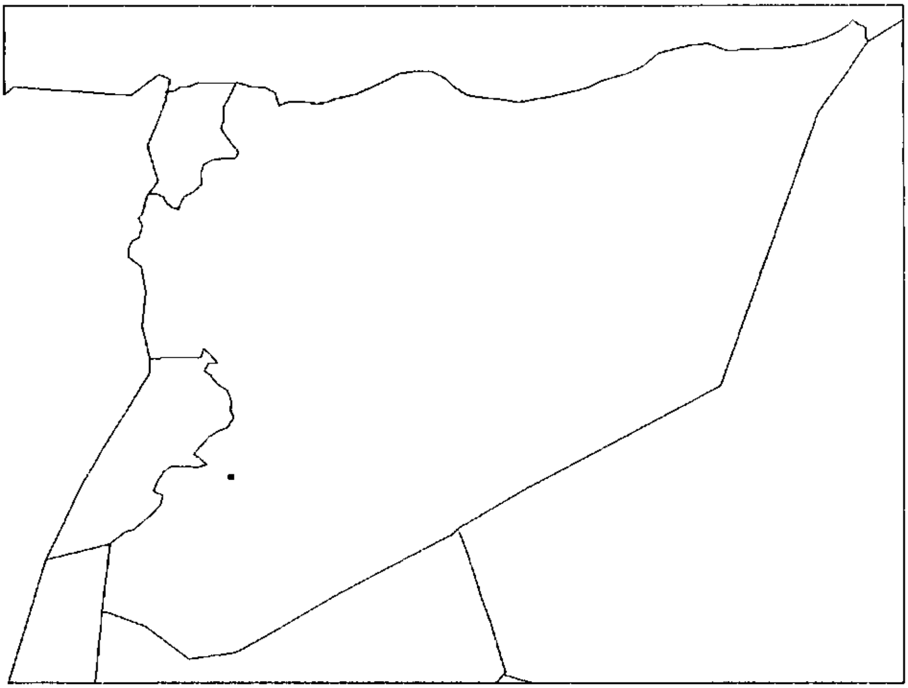
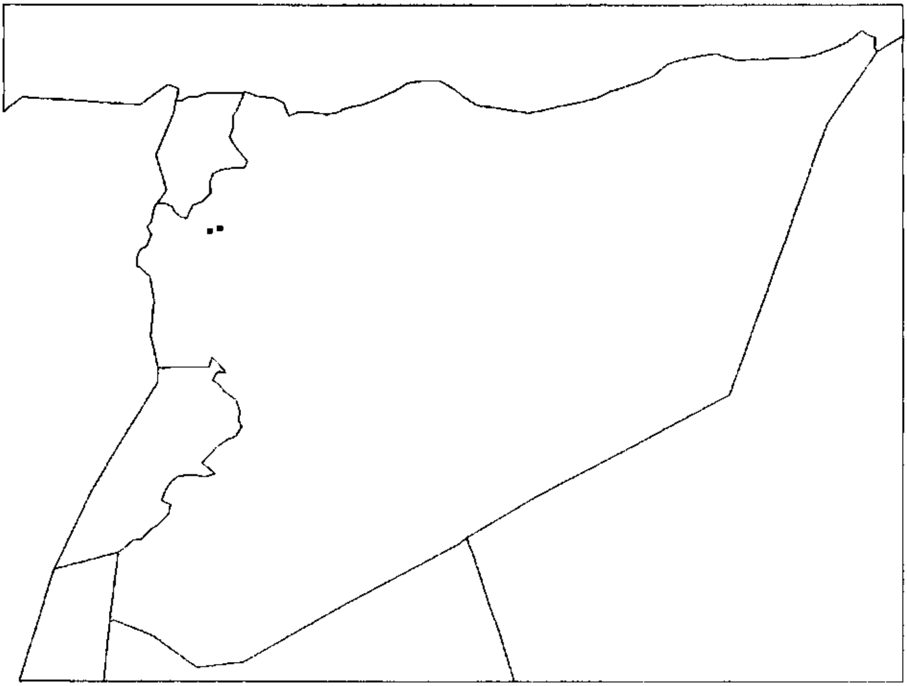
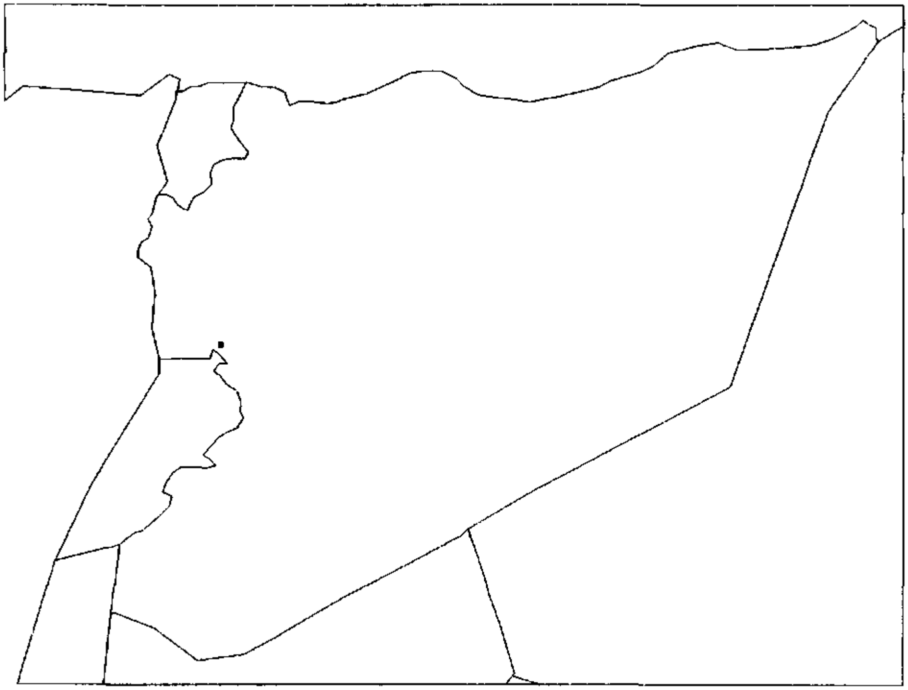


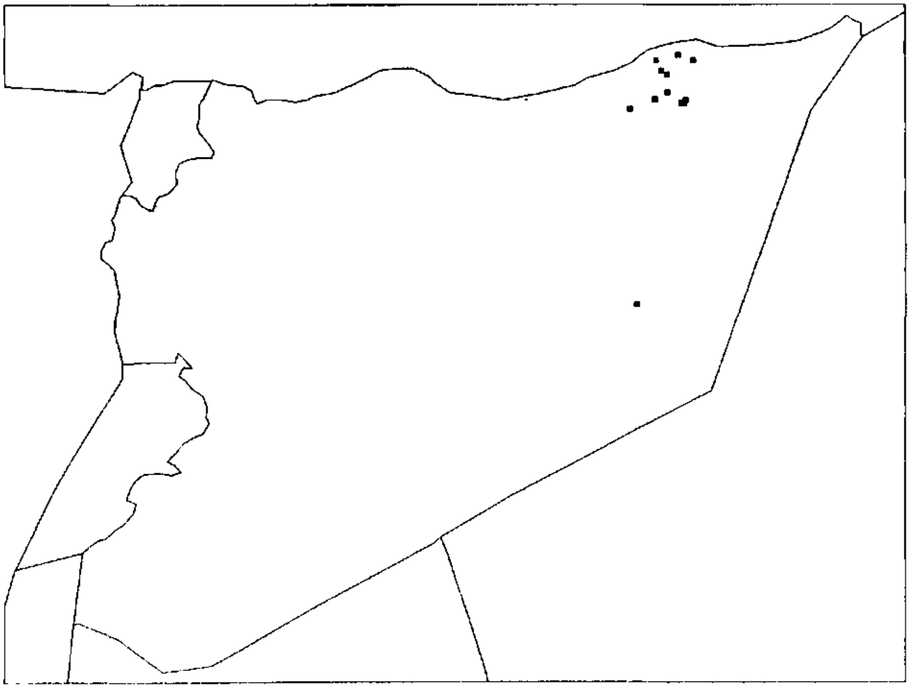
Map 19. Distribution of collection sites of *Salamieh* durum wheat landrace populations.



Map 20. Distribution of collection sites of *Shamieh* durum wheat landrace populations.



Map 21. Distribution of collection sites of *Sheirieh* durum wheat landrace populations.



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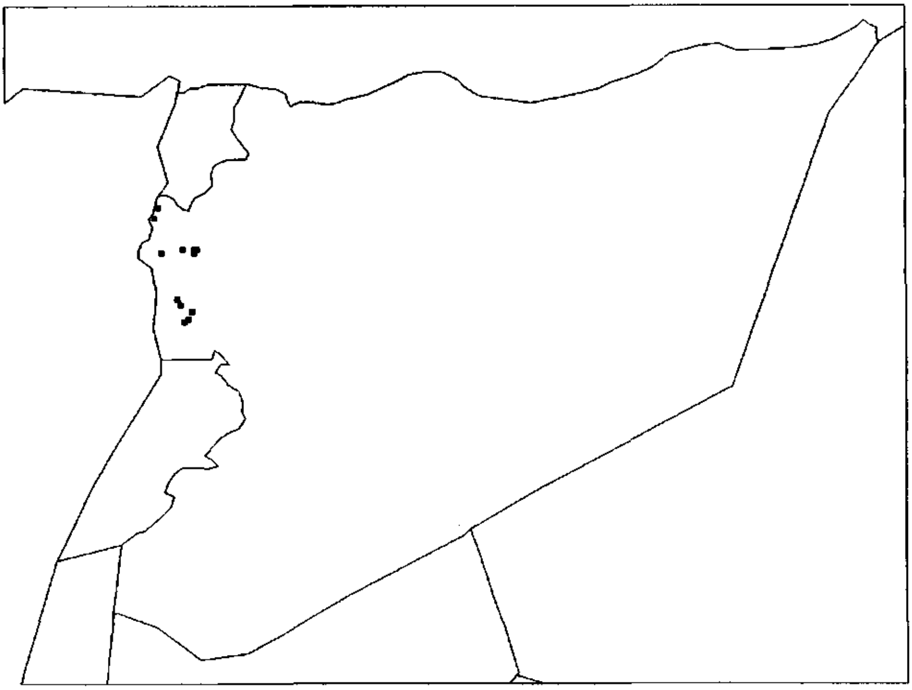

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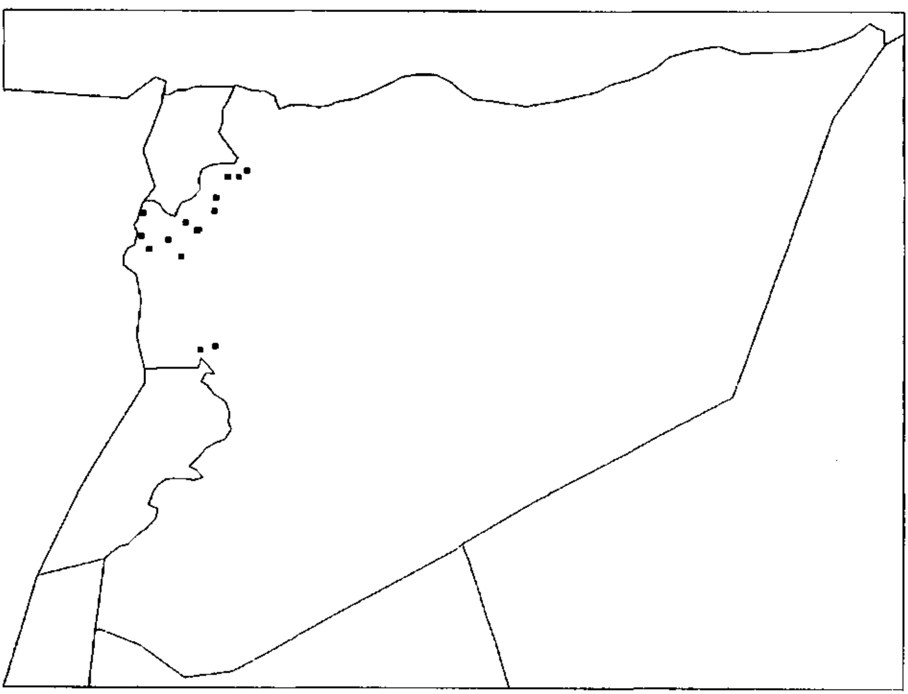

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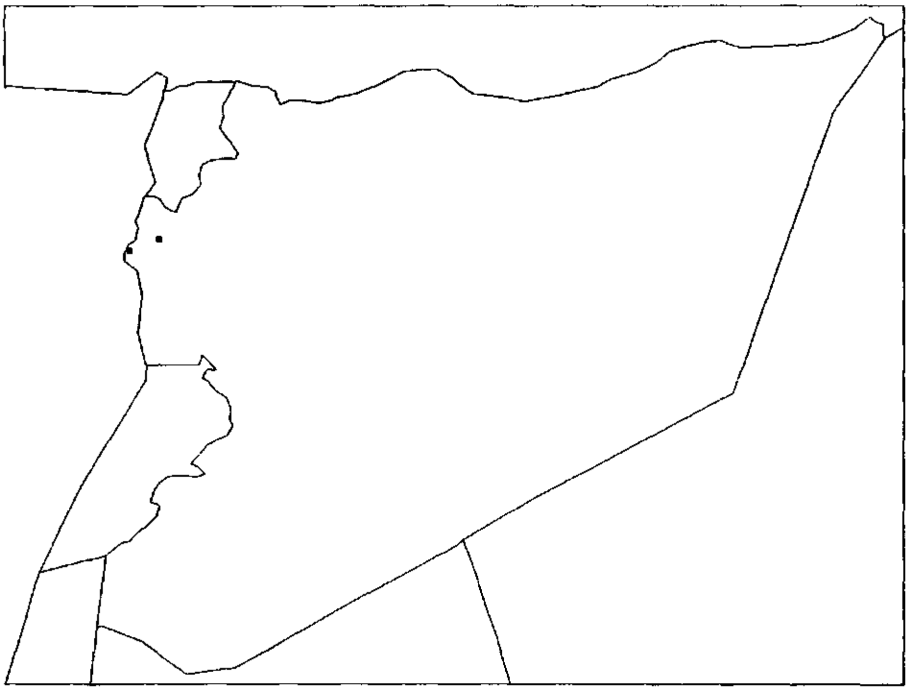

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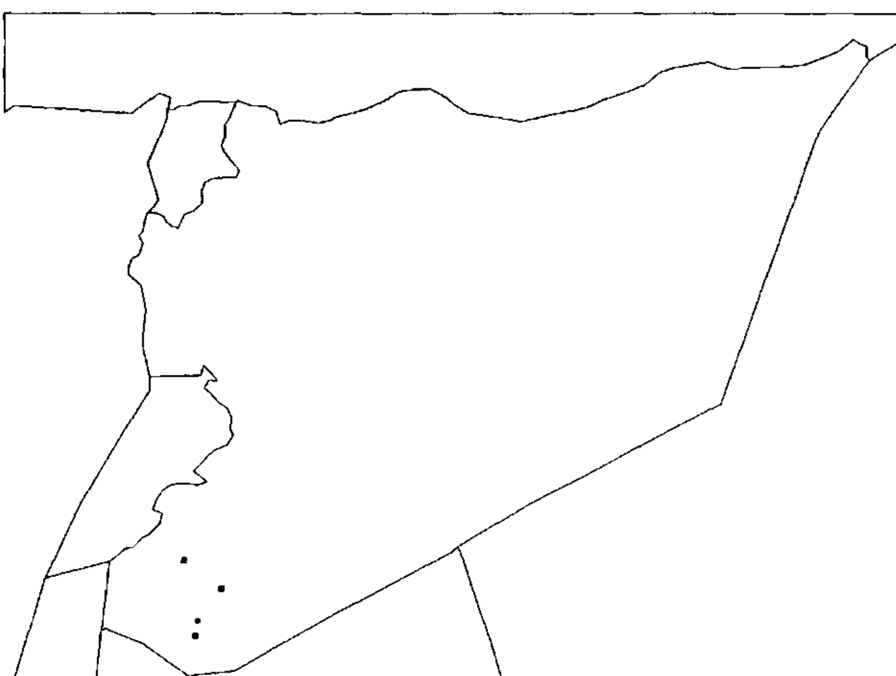

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