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The effects of *Hordeum spontaneum* C. Koch. germplasm on barley production

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The effects of <u>Hordeum</u> <u>spontaneum</u> C. Koch. germplasm

on barley production

by

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INTRODUCTION

Much research has been focused on cytoplasmic inheritance in higher
plants since the discovery of DNA within cytoplasmic organelles (Gillham,
1978). It has been established that the cytoplasmic genome affects both
qualitative and quantitative traits in many crop species (Crane and
Nyquist, 1967; Nagaich et al., 1968; Tsuchiya, 1980). However, it is
doubtful that the cytoplasm affects traits solely. Rather, the cytoplasm
usually interacts with the nuclear genome.

Direction and magnitude of cytoplasmic effects vary with each nuclear-
cytoplasmic combination. Washington and Maan (1974) developed alloplasmic
lines of Triticum aestivum L. em. Thell., and found that cytoplasms af-
fected the reactions of 'Chris', 'Selkirk', and T. durum Sel. 56-1 nuclei
to three races of wheat leaf rust, Puccinia recondita Rob. ex. Desm. f. sp.
tritici. Selkirk was not susceptible to rust irrespective of cytoplasm
source, whereas Chris was resistant in the presence of T. aestivum cyto-
plasm and susceptible in the donor cytoplasm. Robertson (1980) found
that segregates from A. sterilis L. x A. sativa crosses that had A.
sterilis cytoplasm gave 16% higher grain yield than corresponding segre-
gates with A. sativa cytoplasm when CI9170 was the A. sativa parent, but
the grain yield advantage for derivatives with A. sterilis cytoplasm was
only 4% when 'Otee' was the cultivated oat parent (Robertson and Frey,
1984). Evidence from this study indicates that the cytoplasmic genome
generally interacts with the nuclear genome.

Hordeum spontaneum, C. Koch., the progenitor of cultivated barley, has
existed for more than 5,000 years in Israel (Harlan, 1979). H. spontaneum,

which grows in lush stands in Israel, has enormous variability for both molecular and phenotypic traits within and among populations (Nevo et al., 1984, 1979; Moseman et al., 1983). Hybrids between H. spontaneum and H. vulgare L. are easily attained and completely fertile (Nevo et al., 1984). Because of the immense reservoir of genetic variability H. spontaneum contains and the ease of gene flow in interspecific Hordeum crosses, H. spontaneum has been used extensively for both academic investigations and applied breeding programs.

The general objective of this study was to ascertain the value of H. spontaneum as a gene donor from both cytoplasmic and nuclear genomes for grain yield, straw yield, harvest index, plant height, unit straw weight, heading date, and vegetative growth index. Specifically, the objectives were to:

1. Determine whether cytoplasms from H. vulgare and H. spontaneum caused differential effects;

2. Discuss whether specific nuclear cytoplasmic genomic interactions occurred;

3. Ascertain the nature of nuclear-cytoplasmic interactions;

4. Compare segregates from northern, southern, central, and coastal H. spontaneum ecotypes from Israel combined with two barley cultivars, 'Bowers' and 'Robust'.

LITERATURE REVIEW

Extranuclear Effects

The earliest reports on extranuclear inheritance in plants came from studies of foliar variegation in the four-o'clock plant, Mirabilis jalapa (Bauer, 1909; Correns, 1909, in Kirk and Tilney-Bassett, 1967). Later, non-Mendelian inheritance was classified into the categories maternal inheritance, dauermodification, and cytoplasmic inheritance (Caspari, 1948). Maternal inheritance occurs when the female genotype has a transitory effect on a trait(s) of the offspring. Maternal effects are common for the offspring of animals, but among plants, they are less frequent. An example would be poor seed and seedling vigor due to inferior seed-producing ability of the mother plant. Dauermodifications are environmentally induced effects transmitted through the maternal parent for one or more generations. An example is the morphological abnormality caused on bean (Phaseolus vulgaris (L.)) leaves by chloral hydrate treatment (Strickberger, 1985). Cytoplasmic inheritance occurs when genes in the cytoplasm determine traits in the offspring (Beal and Knowles, 1978; Gillham, 1978). Therefore, cytoplasmic effects are heritable whereas maternal effects and dauermodifications are transitory.

Usually, studies of maternal effects in plants make use of reciprocal mating designs (Ellsworth and Peloquin, 1972; Miksch, 1980). However, the detection of true cytoplasmic inheritance requires backcrossing to both parents for several generations (Caspari, 1948; Bahn, 1964). Substitution lines of wheat (Kihara, 1951) and isopopulations

(Day et al., 1955; Burton, 1966) of oats (Avena sativa (L.) Koch) have been used to study cytoplasmic inheritance (Robertson and Frey, 1984).

The Cytoplasmic Genome

The discovery of DNA in cytoplasmic organelles (Gillham, 1978) and new knowledge about molecular biology have given an understanding of the structure and function of the cytoplasmic genome. Chloroplast DNA exists in a circular double helix with many copies per plastid (Gillham, 1978; Murphy and Thompson, 1988). It contains 135 - 160 kb in most angiosperms and it is highly conserved (Murphy and Thompson, 1988). If 1000 kb code for one protein, the entire chloroplast genome would encode for about 150 proteins.

The chloroplast genome tends to have a large single-copy region and two inverted repeats (ca. 10 - 30 kb) separated by another small single-copy region (ca. 12 - 28 kb) (Murphy and Thompson, 1988). Genes of the chloroplast are arranged in clusters and encode rRNA, tRNA, and proteins. Protein coding genes involved in light harvesting are psbA from photosystem II which contains 7 genes, psa from photosystem I which contains 2 genes, pet from the b_g and b_f which contains 3 genes, and catp which contains 6 genes. The most well-known gene in the chloroplast genome codes for the large subunit of rubisco-1,5-bisphosphate carboxylase (Murphy and Thompson, 1988).

The mitochondrial genome is larger and more variable in size than the chloroplast genome, ranging from 200 kb in Oenothera to 1600 kb in muskmelon (Cucumis melo). The DNA has many single copy sequences, but

some multiple-copy sequences occur either directly or as inverted repeats. There are approximately 20 genes in the mitochondrial genome (Murphy and Thompson, 1988). Genes in the mitochondrial genome code for rRNA, several ribosomal proteins, and components of the mitochondrial inner membrane and respiration apparatus (Murphy and Thompson, 1988). The gene that causes male sterility in plants is in the mitochondrial genome.

Nuclear-Cytoplasmic Male Sterility

The most economically important cytoplasmic trait in plants is cytoplasmic male sterility (cms). Actually, cms results from nuclear-cytoplasmic interaction. It was first discovered in maize, Zea mays (L.) (Rhoades, 1931), and has been utilized for hybrid seed production in several crops. The system was used extensively to produce hybrid seed in maize until the southern corn leaf blight, Bipolaris (Helminthosporium) maydis Nisikado and Miyari, race T, epidemic occurred in 1970 (Tatum, 1971). Nuclear-cytoplasmic (NC) male sterility makes it possible to produce hybrid seed of crops such as sorghum (Sorghum bicolor (L.) Moench) (Stephens and Holland, 1954) which have perfect flowers.

NC-male sterility has been induced in some crops by placing the nuclear genome into alien cytoplasms. Crops in which cms has been induced are wheat, Triticum spp, Aegilops spp (Kihara, 1951); barley, Hordeum spp (Foster and Schooler, 1971); tobacco, Nicotiana spp (Clayton, 1950); cotton, Gossypium spp (Meyer and Meyer, 1961; Richmond and Kohel, 1961); Brassica spp (Pearson, 1972); and tomato, Lycopersicon spp (Anderson, 1963, 1964).

Male sterile cytoplasms for maize are classified as types T, S, and C (Beckett, 1971). A study that compared T and S sterile with normal cytoplasm without restorer alleles indicated that T-cytoplasm altered grain yield, barrenness, tillering, and root lodging, whereas the S-cytoplasm affected only grain yield and barrenness (Duvick, 1958). Hybrids with normal cytoplasm and restorer alleles had a yield advantage over fertile plants with recessive restorer alleles. Stringfield (1958) concluded that hybrids with T-cytoplasm and restorer alleles gave greater grain yield than those with normal cytoplasm. Contradictory results were reported by Noble and Russell (1963) who found yields for hybrids with T-cytoplasm and restorer alleles were less than their counterparts with normal cytoplasm. T-cytoplasm and restorer alleles also may affect grain moisture and days to pollen shed (Russell and Marquez-Sanchez, 1966).

The 'milo' source of cytoplasmic male sterility is used to produce 97% of the hybrid seed of sorghum (Harvey, 1977). Six 'KS' sterility inducing cytoplasms were compared with milo cytoplasm, and hybrids with KS and milo cytoplasms gave identical performances for grain yield, days to flowering, and plant height (Ross and Kofoid, 1979; Lenz and Atkins, 1981).

Agronomic Traits

Numerous studies about reciprocal effects on agronomic characters have been conducted with maize, soybean (Glycine max (L.) Merrill), cowpea (Vigna sinesis (L.) Walp.) and other species. Flint and dent maize cytoplasms showed no reciprocal effects for grain yield (Dimmock and

Donovan, 1956). However, a study with diverse alloplasmic maize lines with the WF9 nucleus showed that certain exotic cytoplasms were superior to the normal counterpart for grain yield, percent moisture, and lodging (Crane and Nyquist, 1967). No reciprocal effect has been shown for any agronomic traits of soybean (Wilcox and Simpson, 1977) or cowpea (Kheradnam et al., 1975). Reciprocal effects were found in several Gossypium spp for plant height, yield, and boll size (Meyer, 1973). Reciprocal effects were found in alfalfa (Medicago sativa (L.)) for seedling height and forage yield (Carnahan, 1963), and in barley (H. vulgare (L.)) for grain yield, yield components, and plant height (Riggs and Hayter, 1973; Fejer and Fedak, 1976; Kaz'min et al., 1980).

Reciprocal effects can be partitioned into cytoplasmic and maternal effects if progenies from reciprocal matings are backcrossed several times to the parents. Alloplasmic wheat lines with Aegilops ovata (L.) cytoplasm were later, taller, and had increased numbers of tillers and spikelets per spike than their normal cytoplasm counterparts (Tahir, 1971), whereas those with T. timopheevi Zhuk. cytoplasm showed no differences in performance. Reciprocal effects were found for days to heading and tiller number of spring and winter oats (A. sativa). These differences were due to maternal influences (Muehlbauer et al., 1971). Consistent superior performance due to A. sterilis cytoplasm had been found after three backcrosses indicating cytoplasmic inheritance for grain yield and heading date (Robertson and Frey, 1984).

Physiological Traits

Reciprocal effects have been noted for chilling injury in maize
(Cal and Obendorf, 1972; Pinnell, 1949) and cotton (Christiansen and
Lewis, 1973; Maroni and Dag, 1962). Mitochondria from cold tolerant maize
are more flexible under chilling stress than are the susceptible types
(Lyons et al., 1964). Reciprocal differences among populations of oats
for freezing resistance and winterhardiness were significant but they
were inconsistent over testing sites (Muehlbauer et al., 1970). Seed
viability in maize is influenced by cytoplasmic effects (Rao and Fleming,
1978) and chlorophyll mutations in barley may be maternally inherited
(Tsuchiya, 1980).

In peanuts (Arachis hypogea (L.)), the V4 cytoplasm produces runner
or bush growth habit depending upon a specific allele in the nuclear
genome (Ashri, 1964). With all other cytoplasms, the growth habit is
runner if at least three dominant alleles are present in the nuclear
genome. With two or less, the growth habit is bush. Respiratory and
photosynthetic rates in alloplasmic lines of Aegilops spp and Triticum
spp have been assigned to cytoplasmic-nuclear interactions (Iwanaga
et al., 1978).

Quality Traits

Reciprocal differences for oil content were found in maize matings
(Jellum, 1966), and these were due to both maternal and cytoplasmic
effects (Garwood et al., 1970; Ruskova, 1975). Reciprocal effects caused

differences in soybean oil quantity and fatty acid content (Brim et al., 1968), but the differences were due to maternal effects (Singh and Hadley, 1968). Reciprocal effects have caused differences in oil content of sunflower (Helianthus annuus (L.)) (Thompson et al., 1979) and safflower (Carthamus tintorius (L.)). Maternal and reciprocal effects influence oil percentage of oats (Brown and Aryeetey, 1973; Elliot, 1975).

Reciprocal differences have been noted for protein (Garwood and Lambert, 1967) and amylose (Loesch and Zuber, 1964) content of maize, but dent x flint crosses did not show reciprocal effects for protein content (Pollmer et al., 1979). Protein percentage of spring wheat was increased by several Aegilops cytoplasms (Sasaki et al., 1978), but it was due to yield component compensation (i.e., a smaller protein available sink). T. timopheevi cytoplasm did not affect grain protein percentage in wheat (Rooney et al., 1969) and no maternal effects were found for groat protein content of oats (Ohm and Patterson, 1973).

Reciprocal differences for sugar content in soybean F1s were due to maternal effects (Openshaw and Hadley, 1978).

Bread-making traits of two hard red spring wheat varieties were unchanged when their nuclei were substituted into several Aegilops spp cytoplasms (Busch and Maan, 1978; Rooney et al., 1969), and diverse barley cytoplasms had no significant effect on malting quality traits (Lee et al., 1987).

Disease Resistance

Susceptibility of T-cytoplasmic male sterile lines of maize to B. maydis, race T, was reported nearly 30 years ago by Mercado and Lantican (1961), and 30 sources of cytoplasmic male sterility that condition susceptibility to this pathogen were identified (Smith et al., 1971).

G. harknessi Brandagee cytoplasm enhanced resistance to bacterial blight Xanthomonax malvacearum E. F. Sm. Dowson, for both resistant and susceptible lines of G. hirsutum (L.). This cytoplasmic effect was stable over several environments and it accounted for 12% greater resistance (Mahill and Davis, 1978).

Cytoplasms from several wheat species (i.e., T. araraticum Jakubz, T. timopheevi Zhuk., T. macha De. and Men., T. boeoticum Boiss., Ae. ovata (L.), and Ae. speltoides Tausch) influenced the reaction of T. aestivum to rust (i.e., Puccinia recondita Rob. ex. Desm. f. sp tritici). Selkirk cultivar was resistant to rust under all circumstances and Chris changed from resistant to susceptible with the donor cytoplasm. Alloplasmic lines of T. durum had slower rates of uredial development than did the control (Washington and Maan, 1974).

The cytoplasms of Capsicum pendulum Willd. and C. annuum (L.) resulted in resistance and susceptibility, respectively, to potato virus X (Nagaich et al., 1968).

Recent Advances

A more detailed knowledge of the cytoplasmic genome is being dis-
covered with the use of molecular biology techniques. Restriction frag-
ment length polymorphisms (RFLPs) are being utilized to confirm cyto-
plasmic genomic diversity in wheat (Vedel and Quetier, 1978), soybean
(Shoemaker et al., 1986), and barley (Holwerda et al., 1986). The de-
velopment of linear models that incorporate frequency of restriction
sites have been proposed for characterizing cytoplasmic diversity (Nei
and Li, 1979).

Soybean lines that possessed four different chloroplast genomes
(based on RFLP analysis) were crossed reciprocally to a common high
photosynthetic parent to study the effect of diverse chloroplast
genomes on traits related to photosynthesis. CO_2 exchange, photosynthetic
electron transport, rubisco activity, and soluble protein content were
not influenced differentially by cytoplasms (Diethelm et al., 1989).

Digests of chloroplast and mitochondria DNA from H. vulgare and
H. spontaneum lines made with 17 and 16 hexanucleotide restriction enzymes,
respectively, were evaluated to assess variability and evolutionary di-
vergence between the two species. Chloroplast genomes evolved at a slower
rate than mitochondrial genomes. Variability for chloroplast DNA was
nearly equal for the two species, but H. vulgare was more variable than H.
spontaneum for the mitochondrial genome (Holwerda et al., 1986).

Variability of H. spontaneum Within Israel

In Israel, H. spontaneum occupies a wide range of habitats from mesic
Mediterranean to xeric desert conditions (Nevo et al., 1979). Harlan
and Zohary (1966) classified H. spontaneum accessions into races or eco-
types which differed both in ecology and morphology. Two extreme races
are found in Israel. The xeric ecotype, which grows in the desert and
steppic habitats, has long, slender, grassy-like leaves, whereas the
"Jordan Rift Valley" race, a mesic ecotype that grows in lush rainy habi-
tats, has large seeds and long awns.

Nevo et al. (1979) investigated genetic variability for allozyme
alleles among and within 28 H. spontaneum populations within Israel.
Allelic variation at the allozyme loci was significantly correlated with
climatic and soil characteristics at the sites of origin. Most of the
allozyme variability was expressed within populations and the allozyme
alleles were carried primarily as homozygotes within the populations.
Brown et al. (1978) subdivided the allozyme variability and showed that
17% of the variation occurred among regions, 32% occurred among popula-
tions within regions, and 51% occurred within populations.

H. spontaneum has been found to carry genes that condition resis-
tance to powdery mildew, Erysiphe graminis DC Ex. Merat. f. sp hordei
(Em. Marchal) (Baenziger et al., 1981, Fischbeck et al., 1976).
Moseman et al. (1983) found that, of 235 H. spontaneum accessions from
Israel, 35% were resistant and 71% moderately resistant to three powdery
mildew cultures that possessed virulence genes corresponding to most
known resistance genes in cultivated barley. Resistance to leaf rust

(Puccinia hordei Otth.) (Manisterski et al., 1986), scald (Rhynchosporium secalis Oud.), and net blotch (Pyrenophora teres Dreschs.) (Baenziger et al., 1981) also have been found in H. spontaneum.

Nevo et al. (1984) investigated the phenotypic variability of agronomic traits among H. spontaneum accessions from a wide range of habitats in Israel. Genetic variation was found among and within populations at each sampling site for earliness, grain yield, and biomass.

Explanation of Dissertation Format

This dissertation contains two sections. Section I investigates the differential effects of H. spontaneum and H. vulgare cytoplasms on agronomic traits of barley. Section II describes mean performance of segregates from crosses of H. spontaneum ecotypes in combination with two barley cultivars. Each section is in the form of a complete manuscript that will be submitted for publication with little or no modification. References are cited in Additional References Cited following the general conclusions.

SECTION I. CYTOPLASMIC EFFECTS ON AGRONOMIC TRAITS IN
INTERSPECIFIC MATINGS OF <u>HORDEUM</u> SPP

ABSTRACT

The cytoplasmic genome affects both physiological and agronomic

traits in many crop species. It can affect a trait directly or by in-

teracting with the nuclear genome. The objectives of this study were to

(1) determine whether Hordeum vulgare L. and H. spontaneum C. Koch. cyto-

plasmic genomes differentially affect grain yield, straw yield, harvest

index, plant height, unit straw weight, heading date, and vegetative

growth index, (2) determine whether nuclear-cytoplasmic genomic inter-

actions occur, and (3) ascertain the nature of nuclear cytoplasmic inter-

actions. Eighty-four populations of 14 lines each, representing recipro-

cal crosses of the BC0, BC1, and BC2 generations from all possible matings

among seven H. spontaneum and two H. vulgare cultivars were evaluated in

the field in two years. Cytoplasmic effects were significant for grain

yield, straw yield, harvest index, unit straw weight, and vegetative

growth index. Lines with H. spontaneum cytoplasm had greater means for

straw yield, unit straw weight, and vegetative growth index than did

lines with H. vulgare cytoplasm. Conversely, lines with H. vulgare

cytoplasm showed a greater mean grain yield and harvest index. Cyto-

plasmic effects were consistent through backcross generations for straw

yield, unit straw weight, and vegetative growth index; however, cyto-

plasmic effects did interact with generations for grain yield and har-

vest index. Cytoplasm x mating interaction was significant in all gen-

erations for straw yield but only in the BC2 for unit straw weight and

vegetative growth index, indicating specific nuclear-cytoplasmic genomic

interactions. Cytoplasm x mating interactions for straw yield re-
sulted from H. spontaneum cytoplasm by H. vulgare nuclear genome inter-
actions. Cytoplasm x generation interactions for grain yield and harvest
index resulted from differential responses of H. spontaneum and H. vulgare
nuclear genomes or combinations of both, within their respective cyto-
plasms.

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Additional index words: Hordeum spontaneum C. Koch., Hordeum
vulgare L., barley.

INTRODUCTION

Much effort has been focused on cytoplasmic inheritance in higher plants since the discovery of DNA within cytoplasmic organelles (Gillham, 1978). Cytoplasmic inheritance for grain yield (Crane and Nyquist, 1967; Rao and Fleming, 1978; Kofoid and Maan, 1982), heading date (Tahir, 1971; Robertson and Frey, 1984), seed quality (Jellum, 1966; Openshaw and Hadley, 1978), and physiological traits (Cal and Obendorf, 1972; Christiansen and Lewis, 1973; Ashri, 1964) have been well documented. However, aside from nuclear-cytoplasmic male sterility, the cytoplasmic genome has found limited usage in applied breeding programs.

Direction and magnitude of cytoplasmic effects on plant traits vary with each nuclear-cytoplasmic combination. Washington and Maan (1974) found that cytoplasms from several species related to wheat (Triticum araraticum Jakubz, T. timopheevi Zhuk., T. macha De. and Men., T. boetoticum Boiss., Aegilops ovata L., and Ae. speltoides Tausch) influenced the reaction of T. aestivum to leaf rust (Puccinia recondita Rob. ex. Desm. f. s tritici). The cultivar 'Selkirk' was not affected by rust, whereas 'Chris' was resistant in the presence of T. aestivum cytoplasm and susceptible in a donor cytoplasm. Segregates with Avena sterilis L. cytoplasm showed a 16% higher grain yield than corresponding segregates with A. sativa cytoplasm when CI9170 was used as a parent, but there was only a 4% grain yield advantage for A. sterilis cytoplasm from matings involving 'Otee' (Robertson and Frey, 1984). Evidence from these studies indicates that the cytoplasmic genome frequently interacts with the nuclear

genome over a range of traits and crop species.

Hordeum spontaneum, the progenitor of cultivated barley, has been used in barley breeding programs. Resistance to powdery mildew Erysiphe graminis DC, Ex Merat. F. sp hordei (em. Marchal) (Moseman and Craddock, 1976), the complete fertility of its crosses with H. vulgare and the immense reservoir of variability for other characteristics that this species encompasses (Nevo et al., 1984) have been reasons for H. spontaneum being a good species for introgression studies.

Objectives of this study were to (1) determine whether cytoplasms from H. vulgare and H. spontaneum caused differential effects on grain yield, straw yield, harvest index, plant height, unit straw weight, heading date, and vegetative growth index; (2) determine whether specific nuclear-cytoplasmic genomic interactions occur; and (3) ascertain the nature of nuclear cytoplasmic interactions.

MATERIALS AND METHODS

Seven accessions of H. spontaneum (PI 466302, PI 466363, PI 466394, PI 466410, PI 466434, PI 466514, and PI 466561), collected in Israel, were mated reciprocally with two cultivated varieties of H. vulgare ('Bowers' and 'Robust') in a Design II mating system (Comstock and Robinson, 1952) to give 28 BC0s. The 28 BC0s were backcrossed to their respective H. vulgare parent twice to give BC1s and BC2s. (BC0, BC1, and BC2 refer to single cross, backcross one, and backcross two, respectively.) Thus, 84 populations were developed consisting of two cytoplasms within each of 14 matings in the BC0, BC1, and BC2 generations. The BC0 crosses were made in the field and the BC1 and BC2 were made in the greenhouse, with H. vulgare being used as the male for the backcrosses. All generations of all matings were advanced to the F_3 in the greenhouse. To provide an experimental format for contrasting the effects of spontaneum and vulgare cytoplasms, the "isopopulation method" (Day et al., 1955; Burton, 1966) was used. This method makes the assumption that, on average, the nuclear genetic composition of the sets of lines in the reciprocal populations of a mating in the same backcross generation will be identical, and thus, a significant difference between the reciprocals for any trait is due to the effects of the spontaneum and vulgare cytoplasms, or to cytoplasmic-nuclear interaction.

F_3 seeds from the BC0, BC1, and BC2 generations of the matings were space planted in the field, and 14 nonshattering plants were chosen from each of the BC0, BC1, and BC2 of each reciprocal cross from each mating.

The seeds from an F_3 plant were used to establish an F_3-derived line which was evaluated in field trials. The lines were $F_{3:4}$ and $F_{3:5}$ when evaluated in 1987 and 1988.

There were 84 barley populations each with 14 F_3-derived lines for a total of 1176 entries. In 1987 and 1988, the F_3-derived lines along with parental entries, which consisted of 14 entries of each H. vulgare parent and two entries of each H. spontaneum parent, were evaluated in field experiments utilizing a randomized complete-block design with two replications each at Ames, Kanawha, and Nashua, Iowa. A plot was a hill sown with 30 seeds, and hills were spaced 30.5 cm apart in perpendicular directions. Two rows of border hills were sown around each replication to provide competition for peripheral hills. In 1987, the plots were sown on 12 March, 7 and 8 April at Ames, Kanawha, and Nashua, respectively, and in 1988, they were sown on 23 March, 1 and 7 April at Ames, Kanawha, and Nashua, respectively. Soil types in Ames, Kanawha, and Nashua are Nicollet silty loam (fine-loamy, mixed, mesic Aquic Hapludoll), Webster silty clay (fine-loamy, mixed, mesic Typic Hapluquoll), and Kenyon loam (fine-loamy, mixed, mesic Typic Hapludoll), respectively. The previous crop was always soybean (Glycine max L.). Nitrogen, P_2O_5, and K_2O were applied broadcast before sowing at rates of 34-52-52 kg ha^{-1} in both years at Ames, 50-50-101 kg ha^{-1} in 1987 and 50-0-67 kg ha^{-1} in 1988 at Kanawha, and 50-98-99 kg ha^{-1} in both years at Nashua.

The experiments in both years were hand-weeded and Bayleton (1-(4-chlorophenoxyl)-3,3-dimethyl 1-1-(1-H-1, 2 4-triazol-1-yl)-

2-butone), a systemic fungicide, was sprayed onto the barley plants at anthesis for control of fungal foliar diseases. The spikes of the H. spontaneum entries were bagged two weeks after anthesis with delnet PG218 nonwoven mesh bags (hi-density polyethylene, manufactured by Hercules Inc., Wilmington, DE 19899) to catch shattered seed.

Heading date was recorded in a plot as the number of days from planting to when 50% of the spikes were fully emerged. Plant height was the distance from ground level to the average of the tips of the spikes in the plot two weeks after anthesis. When mature, a plot was cut at ground level, dried, and weighed for biomass (Mg ha^{-1}). Next, the bundle of culms was threshed and grain was weighed to give grain yield (Mg ha^{-1}). Straw yield (Mg ha^{-1}) was obtained by subtracting grain yield from biomass; harvest index was calculated as (grain yield)(100)/(straw yield); unit straw weight (grams cm^{-1}) was computed as (straw yield)/(plant height); and vegetative growth index (Mg ha^{-1} da^{-1}) was calculated as (straw yield)/(heading date). Heading date, plant height, unit straw weight, and vegetative growth index were measured or computed only for the replications grown at Ames. Grain yield, straw yield, and harvest index were measured for all three locations in both years.

Combined analyses of variance over years, locations (each year location combination is equivalent to an environment), generations, and matings were conducted for grain yield, straw yield, and harvest index. Combined analyses of variance over years were calculated for the traits measured only at Ames. Parents, populations, generations, cytoplasms,

and matings were considered as fixed variables, whereas years, locations,

and lines within populations were considered random variables.

RESULTS

When averaged over backcross generations and matings, there were significant cytoplasmic effects for grain yield, straw yield, harvest index, unit straw weight, and vegetative growth index (Table 1). These results could have been due to superior effect of either cytoplasm, the interaction of the nuclear genomes with cytoplasmic genomes, or both. On average, H. spontaneum cytoplasm gave significantly superior performance over H. vulgare cytoplasm for straw yield, unit straw weight, and vegetative growth index, whereas H. vulgare cytoplasm gave significantly greater grain yield and harvest index (Table 2). Cytoplasm had no differential effects on plant height or heading date.

Generation means were significantly different for all traits except vegetative growth index when averaged over cytoplasms and matings (Table 1). Means for grain yield and harvest index increased significantly from both BC0 to BC1 and from BC1 to BC2, whereas for straw yield, unit straw weight, and days to heading, the means increased significantly only between BC0 and BC1. Plant height did not change significantly over generations (Table 3).

The interaction of cytoplasms and generations was significant for grain yield, harvest index, and plant height (Table 1). H. vulgare cytoplasm gave a larger mean than did the H. spontaneum cytoplasm in each backcross generation for both grain yield and harvest index, so the cytoplasm-generation interaction for these traits was due only to magnitude of difference across generations (Table 4). For grain yield, the

Table 1. Mean squares of cytoplasm, generation, mating, and all possible interaction effects for grain yield, straw yield, harvest index, plant height, unit straw weight, heading date, and vegetative growth index of segregates from matings of Hordeum vulgare and H. spontaneum

	Trait						
Source of variation	Grain yield ------(Mg ha^{-1})------	Straw yield	Harvest index (%)	Plant height (cm)	Unit straw weight (g cm^{-1})	Heading date (da)	Vegetative growth index (Mg ha^{-1} da^{-1})
Cytoplasm (C)	94.0**	92.8**	2.07**	33.5	0.73**	0.001	0.69**
Generation (G)	1601.5**	123.6**	8.28**	1247.0**	0.69**	3473.4**	0.18
Mating (M)	38.0**	47.1**	0.32**	2594.3**	0.75	493.9**	0.20**
C x G	37.5**	1.6	0.21**	207.3**	0.08	17.2	0.03
C x M	14.1**	8.1**	0.14**	328.3**	0.09	128.5**	0.09
G x M	36.3**	12.9**	0.39**	585.1**	0.06	188.6**	0.08
C x G x M	12.9**	7.6**	0.12**	539.9**	0.06	59.1	0.07

**Significantly different at the 0.01 probability level.

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Table 2. Means for grain yield, straw yield, harvest index, plant
height, unit straw weight, heading date, and vegetative growth
index for F_3-derived lines with H. vulgare or H. spontaneum
cytoplasm averaged over matings and backcross generations

| Trait | No. of replicates | Cytoplasm | |
		H. spontaneum	H. vulgare
Grain yield (Mg ha^{-1})	12	2.83	2.99**
Straw yield (Mg ha^{-1})	12	3.75**	3.58
Harvest index (%)	12	42.9	45.3**
Plant height (cm)	4	69.9	69.9
Unit straw weight (g cm^{-1})	4	0.559**	0.535
Heading date (da)	4	69.5	69.6
Vegetative growth index (Mg ha^{-1} da^{-1})	4	0.0601**	0.0575

**Significantly different at the 0.01 probability level.

Table 3. Means[a] of the BC0, BC1, and BC2 F_3-derived lines of barley
for grain yield, straw yield, harvest index, plant height,
unit straw weight, heading date, vegetative growth index
when averaged over matings and cytoplasms

Trait	Backcross generation		
	BC0	BC1	BC2
Grain yield ($Mg\ ha^{-1}$)	2.27a	3.04b	3.42c
Straw yield ($Mg\ ha^{-1}$)	3.48a	3.79b	3.72b
Harvest index (%)	39.7a	44.5b	48.0c
Plant height (cm)	70.9a	70.0ab	69.1b
Unit straw weight ($g\ cm^{-1}$)	0.524a	0.565b	0.552b
Heading date (da)	67.9a	70.1b	70.7b
Vegetative growth index ($Mg\ ha^{-1}\ da^{-1}$)	0.0585	0.0601	0.0578

[a]Means not followed by the same letter are significantly different
at the 0.01 probability level.

Table 4. Means of the BC0, BC1, and BC2 F_3-derived lines of barley with H. vulgare or H. spontaneum cytoplasm for grain yield, straw yield, harvest index, plant height, unit straw weight, heading date, and vegetative growth index averaged over matings

| Trait | Cytoplasm | Backcross generations | | |
		BC0	BC1	BC2
Grain yield	H. spontaneum	2.27	2.98	3.24
(Mg ha^{-1})	H. vulgare	2.72**	3.10**	3.59**
Straw yield	H. spontaneum	3.55**	3.89**	3.80**
(Mg ha^{-1})	H. vulgare	3.42	3.70	3.64
Harvest index	H. spontaneum	39.2	43.3	46.2
(%)	H. vulgare	40.2	45.8**	49.8**
Plant height	H. spontaneum	71.2	69.7*	68.8**
(cm)	H. vulgare	70.5	70.3	69.4
Unit straw weight	H. spontaneum	0.529	0.579*	0.571**
(g cm^{-1})	H. vulgare	0.519	0.551	0.533
Heading date	H. spontaneum	67.9	70.0	70.7
(da)	H. vulgare	67.8	70.3	70.6
Vegetative growth index	H. spontaneum	0.0593	0.0615	0.0595
(Mg ha^{-1} da^{-1})	H. vulgare	0.0578	0.0587	0.0561

*,**Significantly different at the 0.05 and 0.01 probability levels, respectively.

means were greater in the BC0 and BC2 than in the BC1, but for harvest index, the difference between the cytoplasmic means became greater over generations (Table 4), with the _vulgare_ mean being 3.6% greater in the BC2. _H. spontaneum_ cytoplasm gave a greater mean plant height in BC0 than did _H. vulgare_, while the reverse was true in the BC1 and BC2.

Mating effects were significant for all traits except unit straw weight (Table 1). For all traits except unit straw weight and vegetative growth index, matings tended to interact significantly with cytoplasms and backcross generations. Of course, different genetic situations exist among backcross generations because the BC0, BC1, and BC2 are expected to have 50%, 75%, and 87.5% of the _H. vulgare_ nuclear genome, respectively. This situation could enhance or decrease the opportunity for interaction of cytoplasmic and nuclear genomes. To obtain a better understanding of the differential effects of cytoplasms among generations, a separate analysis of variance was computed for each backcross generation, and matings mean square was partitioned into _vulgare_, _spontaneum_, and _vulgare-spontaneum_ effects within each generation (Tables 5, 6, and 7). In the BC0, _H. vulgare_ and _H. spontaneum_ parents gave significant variation for straw yield, harvest index, plant height, and heading date, whereas only _H. spontaneum_ gave significant variation for grain yield. There was significant _H. vulgare_ x _H. spontaneum_ interaction for all traits except vegetative growth index. In the BC1, both _H. vulgare_ and _H. spontaneum_ gave significant variation for harvest index, plant height, and heading date. Only _H. spontaneum_ gave significant variation for straw yield and vegetative growth index, and only _H. vulgare_ gave significant

Table 5. Mean squares from partitioning of BCO mating effects and the interactions of cytoplasm x mating for grain yield, straw yield, harvest index, plant height, unit straw weight, heading date, and vegetative growth index

Source of variation	Trait						
	Grain yield (Mg ha^{-1})	Straw yield (Mg ha^{-1})	Harvest index (%)	Plant height (cm)	Unit straw weight (g cm^{-1})	Heading date (da)	Vegetative growth index (Mg ha^{-1} da^{-1})
Mating	10.497**	15.289**	0.834**	1796.022**	0.03215	402.890**	0.07248
H. vulgare	1.396	39.36**	0.1613*	1117.9**	0.00139	966.4**	0.00053
H. spontaneum	12.867**	19.167**	0.07057*	2794.5**	0.03278	495.4**	0.12008
H. vulgare x H. spontaneum	9.6441**	7.3979*	0.08322*	910.44**	0.03665	216.45**	0.03688
Cytoplasm x mating	5.455**	9.493*	0.081**	739.44**	0.03276	108.819	0.04720
Cytoplasm x H. vulgare	0.234	6.964	0.0142	33.74	0.04101	162.6	0.13495
Cytoplasm x H. spontaneum	5.405	6.234	0.0796*	909.26**	0.02854	96.03	0.032017
Cytoplasm x H. vulgare x H. spontaneum	6.376*	13.17**	0.0936**	687.23**	0.03562	112.64	0.04777

*,**Significantly different at the 0.05 and 0.01 levels of probability, respectively.

Table 6. Mean squares from partitioning of BC1 mating effects and the interaction with cytoplasm x matings for grain yield, straw yield, harvest index, plant height, unit straw weight, heading date, and vegetative growth index

Source of variation	Trait						
	Grain yield (Mg ha^{-1})	Straw yield (Mg ha^{-1})	Harvest index (%)	Plant height (cm)	Unit straw weight (g cm^{-1})	Heading date (da)	Vegetative growth index (Mg ha^{-1} da^{-1})
Mating	18.949**	23.329**	0.1910**	1464.072**	0.03772	216.648**	0.1163**
H. vulgare	62.45**	3.030	0.309**	1696.531**	0.00849	101.53**	0.104
H. spontaneum	2.61	43.679**	0.334*	2532.788**	0.03722	282.47**	0.212**
H. vulgare x H. spontaneum	4.54	6.362*	0.029*	356.6131**	0.04309	170.00**	0.0228
Cytoplasm x mating	31.629**	7.5154**	0.2611**	446.818**	0.05477	85.3223	0.04663
Cytoplasm x H. vulgare	0.886	4.157	0.0797	2.3731	0.02144	15.322	0.02713
Cytoplasm x H. spontaneum	35.395**	8.939**	0.3038**	418.904*	0.04519	74.334	0.04194
Cytoplasm x H. vulgare x H. spontaneum	32.99**	6.6519*	0.2486**	548.806**	0.06991	107.977	0.05541

*,**Significantly different at the 0.05 and 0.01 probability levels, respectively.

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Table 7. Mean squares from partitioning of BC2 mating effects and the interaction of cytoplasm x matings for grain yield, straw yield, harvest index, plant height, unit straw weight, heading date, and vegetative growth index

Source of variation	Trait						
	Grain yield ($Mg\ ha^{-1}$)	Straw yield ($Mg\ ha^{-1}$)	Harvest index (%)	Plant height (cm)	Unit straw weight ($g\ cm^{-1}$)	Heading date (da)	Vegetable growth index ($Mg\ ha^{-1}\ da^{-1}$)
Mating	36.794**	24.629**	0.3206**	504.305**	0.13091**	251.545**	0.16465**
H. vulgare	213.77**	76.85**	0.2518**	797.15**	0.2441**	1164.03**	0.00119
H. spontaneum	32.108**	37.94**	0.5769**	733.43**	0.2267**	241.64**	0.3353**
H. vulgare x H. spontaneum	11.982**	2.618	0.0757*	226.37	0.01624	109.36**	0.02127
Cytoplasm x mating	25.0191**	10.0695**	0.2946**	221.852	0.12512**	52.5352	0.13857**
Cytoplasm x H. vulgare	0.0013	1.5778	0.01533	516.58	0.02833	0.0057	0.004075
Cytoplasm x H. spontaneum	52.129**	19.547**	0.6059*	193.12	0.24076**	63.477	0.2576**
Cytoplasm x H. vulgare x H. spontaneum	2.0787	3.9577	0.2981	201.5	0.02561	50.348	0.04204

*,**Significantly different at the 0.05 and 0.01 probability levels, respectively.

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variation for grain yield. There was significant H. vulgare x H. spontaneum interaction for straw yield, harvest index, plant height, and heading date. In the BC2, H. vulgare and H. spontaneum gave significant variation for all traits except vegetative growth index, which was significant only for H. spontaneum. There was significant H. vulgare x H. spontaneum variation for grain yield, harvest index, and heading date. There were significant cytoplasm-vulgare-spontaneum interactions for grain yield, straw yield, harvest index, and plant height in the BC0 and BC1, but this interaction was not significant for any trait in the BC2. Harvest index had a significant cytoplasm-spontaneum mean square for all three generations, whereas this interaction for plant height was significant only in the BC0 and BC1. Grain yield and straw yield had significant cytoplasm-spontaneum mean squares in both the BC1 and BC2 but not in the BC0. The only significant interaction for unit straw weight and vegetative growth index was cytoplasm-spontaneum in the BC2. No significant cytoplasm vulgare interaction was found for any trait in any generation.

These interactions show that genes from H. spontaneum parents did interact with cytoplasms and with H. vulgare nuclear genes to affect certain traits. It is noteworthy that the H. spontaneum x cytoplasm interaction persisted throughout all backcrosses, whereas the cytoplasm x H. vulgare x H. spontaneum interaction dissipated by BC2. This means that for grain and straw yields, specific nicking ability of vulgare-spontaneum nuclear genomes seems to have been diluted by continued

backcrossing. However, significant cytoplasm-<u>spontaneum</u> and cytoplasm-<u>vulgare</u>-<u>spontaneum</u> interactions for these traits indicate that neither specific cytoplasms nor nuclear genotypes have complete control over them.

DISCUSSION

The cytoplasm of a cell consists of subcellular organelles, some of which contain DNA. Many quantitative traits are end products of metabolic processes that occur within the cytoplasm, e.g., vegetative biomass, which is the end product of photosynthesis and respiration. In this study, cytoplasmic effects of particular interest were those where a H. spontaneum cytoplasm causes a trait mean to be greater than the mean with a H. vulgare cytoplasm. This occurred for straw yield, unit straw weight, and vegetative growth index. The effect, however, could have been due to either the cytoplasmic genome or to its interaction with nuclear genomes.

The cytoplasmic genomes from diverse barley species (H. agriocrithon, H. spontaneum var. lagunculiforme) did not affect various agronomic (plant height, lodging, grain yield) and malting quality (malt extract, diastatic power, kernel protein) traits according to Lee et al. (1987). These researchers probably were testing only the direct effects of cytoplasms because they used lines that had been backcrossed to the recurrent parent seven times.

With the "isopopulation method", there is a confounding effect of cytoplasm and nuclear genome interaction because even in the BC2, 12.5% of H. spontaneum nuclear genes are expected to remain. Thus, the H. vulgare or H. spontaneum cytoplasm has a sizable portion of its own nuclear genome with which to interact, and assignment of effects on plant traits directly to H. spontaneum and H. vulgare cytoplasms

usually is not possible. However, assuming that cytoplasms among
parents within H. spontaneum and with H. vulgare are homogenous, analyses
within backcross generations would indicate whether direct cytoplasmic
effects and/or cytoplasmic-nuclear interactions are of greatest importance.

As an example, H. spontaneum cytoplasm gave superior performance for
straw yield, unit straw weight, and vegetative growth index, but none of
these traits showed a cytoplasmic generation interaction. This result
provides evidence that the cytoplasmic genome probably contributed
directly to the performance of those traits. It indicates that there
probably are genes present in H. spontaneum cytoplasm that enhance these
traits in cultivated barley. However, cytoplasms did interact with
matings for straw yield in each generation, and for unit straw weight
and vegetative growth index in the BC2. So obviously, interactions of
cytoplasmic and nuclear genomes did occur. These findings are in accord
with studies that have shown that many cytoplasmic functions depend upon
enzymes encoded by both the nuclear and cytoplasmic genes (cytoplasmic-
nuclear interaction). Examples are the light harvesting complex of
chloroplast (Dunsmuir et al., 1983), the ATP synthetase complex
(Huttly and Gray, 1984), and the Rubisco enzyme (Highfield and Ellis,
1978).

A lack of significant cytoplasm x generation interactions for straw
yield, unit straw weight, and vegetative growth index implies that the
H. spontaneum and H. vulgare cytoplasms reacted similarly to differing
proportions of the H. spontaneum nuclear genome when averaged across
all matings. However, the significant cytoplasm x mating interaction for

straw yield indicates that the two cytoplasms do not react similarly
to all parental nuclear genomes; therefore, the H. spontaneum cytoplasmic
genome must have interacted with the H. vulgare nuclear genome.

The presence of a significant cytoplasm x mating interaction for
grain yield and harvest index in each backcross generation provides
further evidence of specific nuclear x cytoplasmic genome interactions
for these traits. Because the theoretical percentage of the H. spontaneum
nuclear genome decreased from 50% to 25% to 12.5% as backcrossing pro-
ceeded, the interactions between the cytoplasms and the H. spontaneum
nuclear genome should have decreased over generations. The significant
cytoplasm x generation interactions for grain yield and harvest index
indicate that the expected reductions in interactions between the propor-
tion of H. spontaneum nuclear genome present and cytoplasm was not the
same for both cytoplasms. This suggests that interactions occurred be-
tween (a) cytoplasms and H. spontaneum nuclear genes or (b) cytoplasms
and various combinations of both H. spontaneum and H. vulgare nuclear
genomes. Of course, other possibilities are that the actual percentages
of the H. spontaneum nuclear genome present in the different cytoplasms
and generations did not fit the theoretical expected percentages or
major H. spontaneum nuclear genes may have persisted through sampling.

In this study, both H. spontaneum cytoplasmic effects and intro-
gressed nuclear germplasm from H. spontaneum may have contributed to
superior performance for straw yield, unit straw weight, and vegetative
growth index. Complex interactions between Hordeum spp cytoplasms and

nuclear genomes probably were the primary causes of the superior per-

formance. These results suggest that plant breeders may be able to

improve barley by utilizing cytoplasms and perhaps nuclear genes from

H. spontaneum.

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SECTION II. AGRONOMIC PERFORMANCE OF SEGREGATES FROM
INTERSPECIFIC MATINGS OF <u>HORDEUM</u> SPP

ABSTRACT

Immense variability exists among and within populations of Hordeum

spontaneum C. Koch. in Israel. Gene transfer from H. spontaneum to cul-

tivated barley, H. vulgare L., can be accomplished easily, thereby making

H. spontaneum a valuable species for introgression studies in barley. In

this study, comparisons were made among H. spontaneum ecotypes from

northern, central, southern, and coastal Israel as sources of genes for

improving barley. Seven H. spontaneum accessions were crossed and back-

crossed twice with 'Bowers' and 'Robust' cultivars to give 84 populations

each with 14 F_3-derived lines. The 84 populations, which consisted of

the BC0, BC1, and BC2 generations of all possible matings among the

seven H. spontaneum and two H. vulgare cultivars with reciprocals, were

evaluated in the field for two years.

Segregates from matings with the coastal ecotype, on average, had

higher straw yield, plant height, and vegetative growth index, but lower

harvest index than segregates from matings involving northern, central,

or southern H. spontaneum ecotypes. Segregates from matings involving

northern and southern ecotypes had the highest harvest index.

Additional index words: Hordeum spontaneum C. Koch., Hordeum

vulgare L., barley, germplasm.

INTRODUCTION

Hordeum spontaneum, the progenitor of cultivated barley, has existed for more than 5,000 years in Israel (Harlan, 1979), and presently, grows in wild stands throughout the country. Studies of H. spontaneum show that it has immense diversity for allozymes, agronomic traits, and disease resistance within and among populations in Israel (Nevo et al., 1986, 1984, 1979; Moseman et al., 1983).

H. spontaneum is a self-pollinating diploid (2n = 14) that crosses with H. vulgare naturally to give fertile hybrids (Nevo et al., 1984). Gene flow between the two species occurs easily, thereby making H. spontaneum a species of choice for introgression research.

The objective of this study was to compare the value of H. spontaneum ecotypes from northern, southern, central, and coastal Israel as donors of genes for agronomic traits in crosses with two H. vulgare cultivars, 'Bowers' and 'Robust'. The ecotype effects were judged by evaluating segregates from backcross generations for grain yield, straw yield, harvest index, plant height, unit straw weight, heading date, and vegetative growth index.

MATERIALS AND METHODS

Seven accessions of H. spontaneum (PI 466302, PI 466363, PI 466394, PI 466410, PI 466434, PI 466514, and PI 466561), collected in Israel, were mated reciprocally with two cultivated varieties of H. vulgare ('Bowers' and 'Robust') in a Design II mating scheme (Comstock and Robinson, 1952) to give 28 BC0s. The H. spontaneum accessions were two each from Southern, Northern, and Central Israel and one from the Coastal zone of Israel (Table 1). The 28 BC0s were backcrossed to their respective H. vulgare parents twice to give BC1s and BC2s (BC0, BC1, and BC2 refer to single cross, backcross one, and backcross two, respectively). The BC0 crosses were made in the field and the BC1 and BC2 crosses were made in the greenhouse with H. vulgare being used as the male parent. All matings were advanced to the F_3 in the greenhouse.

F_3 seed from the BC0s, BC1s, and BC2s were space-planted in the field, and 14 random nonshattering plants were chosen from the BC0, BC1, and BC2 of each reciprocal cross of each mating. The bulked seed from a plant was used to establish an F_3-derived line. These lines as $F_{3:4}$ and $F_{3:5}$ were evaluated in field trials in 1987 and 1988, respectively.

A total of 84 barley populations existed (i.e., the BC0, BC1, and BC2 of the reciprocals of 14 matings), each with 14 F_3-derived lines for a total of 1176 entries. In 1987 and 1988, the F_3-derived lines, the H. vulgare parents each entered 14 times, and the H. spontaneum parents each entered twice were evaluated in field experiments utilizing a randomized complete-block design with two replications at each of the sites: Ames, Kanawha, and Nashua, Iowa. A plot was a hill sown with

Table 1. PI number or name and site of collections for 7 H. spontaneum accessions and 2 H. vulgare cultivars used as parents in a Design II mating plan

Parental line	Origin
	H. spontaneum
PI 466394	Tabigha (Northern Israel)
PI 466410	Tabigha (Northern Israel)
PI 466434	Mehola (Central Israel)
PI 466514	Beit Shean (Central Israel)
PI 466302	Eyzariya (Southern Israel)
PI 466451	Wadi Quilt (Southern Israel)
PI 466363	Ashqelon (Coastal Israel)
	H. vulgare
Bowers	Michigan
Robust	Minnesota

30 seeds, and hills were spaced 30.5 cm apart in perpendicular directions. Two rows of hills were sown around each replication to provide competition for peripheral plots. Sowing dates in 1987 were 12 March, 7 and 8 April in Ames, Kanawha, and Nashua, respectively. Plots in 1988 were sown on 23 March, 1 and 7 April in Ames, Kanawha, and Nashua, respectively. Soil types at Ames, Kanawha, and Nashua are Nicollet silty loam (fine-loamy, mixed, mesic Aquic Hapludoll), Webster silty clay (fine-loamy, mixed, mesic Typic Hapluquoll), and Kenyon loam (fine-loamy, mixed, mesic Typic Hapludoll), respectively. The previous crop at all sites in both years was soybeans (<u>Glycine</u> <u>max</u> L.). Nitrogen, P_2O_5, and K_2O were applied at rates of 34-52-52 kg ha^{-1} in both years at Ames, 50-50-101 kg ha^{-1} in 1987 and 50-0-67 kg ha^{-1} in 1988 at Kanawha, and 50-98-99 kg ha^{-1} in both years at Nashua.

In both years, the experiments were hand weeded and Bayleton (1-(4-chlorophenoxy)-3.3-dimethyl 1-1-(1-H-1, 2 4-triazol-1-yl)-2 butone), a systemic fungicide, was sprayed onto the barley plants at anthesis to prevent fungal foliar diseases. The spikes of the <u>H</u>. <u>spontaneum</u> entries were bagged two weeks after anthesis with delnet PG218 nonwoven mesh bags (hi-density polyethylene, manufactured by Hercules Inc., Wilmington, DE 19899) to catch shattered seed.

Heading date was recorded for a plot as the number of days from planting to when 50% of the spikes were fully emerged. Plant height was the distance from ground level to the average top of the spikes measured two weeks after anthesis. When mature, the plants in a plot were cut at ground level, dried, and weighed to obtain biomass (Mg ha^{-1}). Next,

the bundle of culms was threshed and the grain was weighed (Mg ha^{-1})
to give grain yield. Straw yield (Mg ha^{-1}) was obtained by subtracting
grain yield from total biomass; harvest index (in percent) was computed
as (grain yield)/(biomass); unit straw weight (g cm^{-1}) was obtained as
(straw yield)/(plant height); and vegetative growth index (Mg ha^{-1} da^{-1})
was calculated as (straw yield)/(heading date). Heading date, plant
height, unit straw weight, and vegetative growth index were measured or
computed only on the Ames replications, whereas grain yield, straw
yield, and harvest index were measured at all three locations in both
years.

Combined analyses of variance over years, locations (each year-
location combination is equivalent to an environment), generations, and
matings were conducted for grain yield, straw yield, and harvest index,
whereas combined analyses for heading date, plant height, unit straw
weight, and vegetative growth index were computed only over years, gen-
erations, and matings. Parents, generations, and matings were considered
as fixed variables, whereas years, locations, and lines within matings
were considered as random variables.

Appropriate error mean squares were used to test significance of
all sources of variation except (among H. spontaneum accessions) and (H.
vulgare x among H. spontaneum ecotypes), which were tested with their
respective pooled (within H. spontaneum) sources of variation.

A least significant difference (LSD) among ecotypes, between acces-
sions within ecotypes, and between accessions within ecotype-H. vulgare
parental combinations was:

$$LSD = t_{0.01} \left[(1/rb - 1/rc)MS_E \right]^{\frac{1}{2}}$$

where $t_{0.01}$ is the tabular value of t at the 0.01 level of significance; r is equal to the number of replications; b and c are equal to the number of entries in either each ecotype accession or accession-H. vulgare parental combination; and MS_E is the appropriate error mean square (Steel and Torrie, 1980). For the purposes of this study, a transgressive segregate was defined as a line whose mean was greater than the recurrent parent mean. Percentages of F_3-derived lines that were transgressive for a trait were computed for each H. spontaneum ecotype in combination with Bowers and with Robust. Transgressive segregates were greater than the recurrent parent mean for grain yield, straw yield, harvest index, unit straw weight, and vegetative growth index, and less than the recurrent parent mean for heading date and plant height.

RESULTS

Mean squares for between H. vulgare varieties were significant for grain and straw yields, harvest index, and heading date, whereas the mean squares among H. spontaneum accessions were significant for all traits except unit straw weight (Table 2). When the H. spontaneum accessions were grouped into northern, central, southern, and coastal ecotypes, differences among ecotypes were significant for straw yield, harvest index, plant height, and vegetative growth index. Differences among ecotypes were not significant for grain yield and unit straw weight. Further, variability within ecotypes was significant for all traits except unit straw weight and vegetative growth index. H. vulgare varieties interacted with H. spontaneum accessions for grain yield, straw yield, plant height, and heading date. When these interactions were partitioned into (H. vulgare varieties) x (among H. spontaneum ecotypes) and (H. vulgare varieties) x (within H. spontaneum ecotypes), the mean squares for (varieties) x (within ecotypes) were significant for grain yield, straw yield, plant height, and heading date.

Grain Yield

The means for grain yield of segregates from the matings of H. spontaneum with H. vulgare ranged from 3.01 Mg ha^{-1} for the northern ecotypes to 2.77 Mg ha^{-1} for the coastal ecotype, but the extreme values were not significantly different (Table 3). However, the means among H. spontaneum between accessions within ecotypes were significantly different within the northern, central, and southern ecotypes (Table 4).

Table 2. Pertinent mean squares from partitioning the sums of squares for among matings of Hordeum spontaneum with H. vulgare for grain yield, straw yield, harvest index, plant height, unit straw weight, heading date, and vegetative growth index

		Trait						
Source of variation	df	Grain yield ---(Mg ha⁻¹----	Straw yield	Harvest index (%)	Plant height (cm)	Unit straw weight (g cm⁻¹)	Heading date (da)	Vegetative growth index (Mg ha⁻¹ da⁻¹)
Among H. vulgare varieties	1	187.0**	93.8**	0.14**	431.7	0.10	1889.1**	0.032
Among H. spontaneum accessions	6	41.7**	78.0**	0.62**	1836.9**	0.10	602.8**	0.411**
Among H. spontaneum ecotypes	3	19.6	134.4**	1.09**	8361.1**	0.15	303.7	0.739**
Within H. spontaneum ecotypes	3	63.8**	21.5**	0.16**	1311.4**	0.06	401.9**	0.081
H. vulgare varieties x H. spontaneum accessions	6	9.4*	8.4**	0.04	712.1**	0.04	152.4**	0.020
H. vulgare varieties x among H. spontaneum ecotypes	3	7.9	5.2	0.06	391.1	0.02	148.2	0.005
H. vulgare varieties x within H. spontaneum ecotypes	3	10.9**	11.6**	0.016	823.2*	0.08	156.6*	0.002

*,**Denotes the mean squares are significantly different at the 0.05 and 0.01 probability levels, respectively.

Table 3. Means[a] of segregates from matings of Hordeum spontaneum with H. vulgare averaged according to ecotype of the H. spontaneum parents for grain yield, straw yield, harvest index, plant height, unit straw weight, heading date, and vegetative growth index

	Trait						
Ecotype	Grain yield -----(Mg ha^{-1})----	Straw yield	Harvest index (%)	Plant height (cm)	Unit straw weight (g cm^{-1})	Heading date (da)	Vegetative growth index (Mg ha^{-1} da^{-1})
Northern	3.01	3.67b	44.9a	70.3b	0.5447	70.0	0.0585bc
Central	2.87	3.63b	44.0b	70.3b	0.5385	69.8	0.0589b
Southern	2.94	3.52b	45.2a	67.2c	0.5457	69.2	0.0565c
Coastal	2.77	4.06a	40.5c	74.6a	0.5696	70.9	0.0640a

[a]Means followed by the same letter are not significantly different at the 0.01 probability levels.

Table 4. Means of segregates from matings of <u>Hordeum</u> <u>spontaneum</u> with <u>H</u>. <u>vulgare</u> averaged according to <u>H</u>. <u>spontaneum</u> accession for grain yield, straw yield, harvest index, plant height, unit straw weight, heading date, and vegetative growth index

Ecotype and accession	Grain yield ----(Mg ha^{-1})----	Straw yield	Harvest index (%)	Plant height (cm)	Unit straw weight (g cm^{-1})	Heading date (da)	Vegetative growth index (Mg ha^{-1} da^{-1})
Northern							
PI 466394	2.85	3.67	44.3	70.0	0.5380	70.2	0.0572
PI 466410	3.16**	3.77**	45.5	70.6	0.5513	69.8	0.0599
Central							
PI 466434	2.96**	3.61	44.9**	71.2**	0.5296	69.2	0.0585
PI 466514	2.78	3.65	43.0	69.4	0.5473	68.3	0.0595
Southern							
PI 466302	3.03**	3.59**	45.3	68.6**	0.5499	70.0**	0.0568
PI 466561	2.84	3.44	45.0	65.8	0.5464	68.4	0.0562

**Denotes that PI accession means within an ecotype are significantly different at the 0.01 probability level.

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PI 466410, PI 466434, and PI 466302 gave segregates with significantly greater grain yield than their counterparts within the northern, central, and southern ecotypes, respectively. Within the northern ecotype, PI 466410 was superior to PI 466394 when crossed to either Bowers or Robust, but within the central and southern ecotypes, H. spontaneum accessions did not show consistent reactions when mated with the two H. vulgare varieties (Table 5). PI 466434 was superior to PI 466514 within the central ecotype when mated to Bowers, but not when mated to Robust. Also, within the southern ecotype, PI 466302 was superior to PI 466561, when mated to Robust, but not when mated to Bowers. The differential reactions of PI accessions within ecotypes when crossed to Robust and Bowers is responsible for the significant interaction of H. vulgare varieties x within H. spontaneum ecotypes. The percentages of segregate means that exceeded their respective recurrent parents increased over backcross generations for both H. vulgare varieties and for all H. spontaneum ecotypes (Tables 6 and 7). The northern and southern ecotypes gave the highest percentages of high transgressive segregates in the BC2 (Table 6).

Straw Yield

The mean straw yield for segregates from matings involving the coastal ecotype of H. spontaneum was significantly greater than the means from matings involving the other ecotypes. The straw yield mean for segregates from the northern, central, and southern H. spontaneum ecotypes did not differ significantly (Table 3). Within the northern and

Table 5. Means of segregates from matings of _Hordeum spontaneum_ with _H. vulgare_ for grain yield, straw yield, harvest index, plant height, unit straw weight, heading date, and vegetative growth index

Mating combination[a]	Grain yield ----(Mg ha^{-1})----	Straw yield	Harvest index (%)	Plant height (cm)	Unit straw weight (g cm^{-1})	Heading date (da)	Vegetative growth index (Mg ha^{-1} da^{-1})
				Trait			
Bowers x N PI 466394	2.89	3.62	44.3	69.0	0.5488	71.3**	0.0566
Bowers x N PI 466410	3.22**	3.80**	45.5	71.0**	0.5409	70.2	0.0586
Bowers x C PI 466434	3.11**	3.77	45.1	71.1**	05390	70.3**	0.0585
Bowers x C PI 466514	2.89	3.67	43.5	69.1	0.5473	68.7	0.0588
Bowers x S PI 466302	3.08	3.65	45.2	67.7	0.5543	70.2	0.0569
Bowers x S PI 466561	3.06	3.62	45.5	67.2	0.5482	69.5	0.0567
Robust x N PI 466394	2.81	3.51	44.3	70.9	0.5271	69.1	0.0577
Robust x N PI 466410	3.09**	3.74**	45.4	70.1	0.5617	69.3	0.0611
Robust x C PI 466434	2.80	3.44	44.6	71.2**	0.5201	68.1**	0.0584
Robust x C PI 466514	2.61	3.63*	42.6	69.6	0.5472	67.1	0.0601

Robust x S						
PI 466302	2.97**	3.52**	45.5	69.5**	0.5355	69.7**	0.0566
Robust x S						
PI 466561	2.81	3.26	44.5	64.3	0.5445	67.2	0.0557

[a]N = northern, C = central, S = southern ecotypes.

**Denotes that PI accession means combined with H. vulgare varieties within an ecotype are significantly different at the 0.01 probability level.

Table 6. Percentages of F_3-derived lines from matings of Bowers with <u>H. spontaneum</u> accessions that exceeded the mean of Bowers for grain yield, straw yield, harvest index, unit straw weight, vegetative growth index, and were less than the mean of Bowers for plant height or heading date within BC0, BC1, and BC2

Ecotype	Grain yield ----(Mg ha^{-1})----	Straw yield	Harvest index (%)	Plant height (cm)	Unit straw weight (g cm^{-1})	Heading date (da)	Vegetative growth index (Mg ha^{-1} da^{-1})
BC0							
Northern	0.0	1.8	3.6	9.8	1.8	36.7	7.1
Central	0.0	2.7	6.3	1.3	0.0	48.0	2.7
Southern	0.0	4.5	2.7	24.1	0.9	35.7	5.4
Coastal	0.0	5.4	1.8	10.7	1.8	41.1	7.1
BC1							
Northern	7.1	5.4	22.3	17.0	2.7	26.8	8.0
Central	4.5	7.1	17.0	19.6	0.9	29.5	8.9
Southern	7.1	1.8	32.1	20.5	1.8	39.3	3.6
Coastal	5.3	14.3	14.3	2.7	7.1	23.2	16.1
BC2							
Northern	20.5	2.7	37.5	14.3	1.8	29.5	1.8
Central	16.1	1.8	35.7	17.0	0.9	27.7	5.4
Southern	24.1	0.9	42.9	20.5	1.8	26.8	0.9
Coastal	17.9	14.3	30.4	8.9	6.3	21.4	14.3

Table 7. Percentages of F_3-derived lines from matings of Robust with H. spontaneum accessions that exceeded the mean of Robust for grain yield, straw yield, harvest index, unit straw weight, vegetative growth index, and were less than the mean of Robust for plant height or heading date within BC0, BC1, and BC2

	Trait						
Ecotype	Grain yield ----(Mg ha^{-1})----	Straw yield	Harvest index (%)	Plant height (cm)	Unit straw weight (g cm^{-1})	Heading date (da)	Vegetative growth index (Mg ha^{-1} da^{-1})
BC0							
Northern	0.9	7.1	9.8	18.8	8.0	17.0	17.0
Central	0.0	1.8	5.4	18.8	2.7	15.2	14.3
Southern	0.0	0.9	5.4	30.4	7.1	17.0	1.8
Coastal	0.0	7.1	7.1	3.6	0.9	1.8	7.1
BC1							
Northern	8.9	10.7	20.5	8.9	10.7	3.6	10.7
Central	0.9	3.6	17.9	21.4	7.1	5.4	6.3
Southern	6.3	6.3	19.6	25.9	11.6	2.6	14.3
Coastal	5.4	28.6	12.5	3.6	7.1	0.0	19.6
BC2							
Northern	13.4	0.0	42.9	13.4	0.9	1.8	3.6
Central	15.2	5.4	33.0	16.1	7.1	2.7	8.9
Southern	12.5	0.0	35.7	25.9	2.7	7.1	5.4
Coastal	8.9	19.6	16.1	8.9	8.0	0.0	19.6

southern ecotypes of H. spontaneum segregates from matings involving

PI 466410 and PI 466302 gave significantly greater straw yields than

their respective counterparts (Table 4). The H. spontaneum accessions

within ecotypes were inconsistent in how they reacted in crosses with

Robust and Bowers for straw yield (Table 5). Within the northern ecotype,

segregates from matings involving PI 466410 had greater straw yield means

than those from matings involving PI 466394 when crossed to either Bowers

or Robust. In contrast, Bowers when mated with H. spontaneum accessions

within the central and southern ecotypes did not give differential straw

yields, whereas matings of Robust with PI 466514 in the central and

PI 466302 in the southern ecotypes were superior to matings of Robust

with their respective counterparts. On average, the percentages of F_3-

derived line transgressive segregates for straw yield were greatest in

the BC1 (Tables 6 and 7). The coastal ecotype consistently gave the

highest percentage of transgressive segregates. The highest percentage

was 28.6% from the BC1 of the coastal ecotype x Robust mating (Table 7).

Harvest Index

Harvest index means ranged from 45.2% for segregates from matings

involving southern H. spontaneum ecotypes to 40.5% for matings involving

the coastal ecotype. Means for segregates from northern and southern eco-

types were not significantly different, but the mean for segregates from

the coastal ecotype was significantly lower than the means for segregates

from all other ecotypes (Table 3). Only within the central ecotype did

the H. spontaneum accessions give significantly different harvest index

means. The percentages of transgressive segregates for harvest index
increased through the BC2 generation for each H. vulgare variety and for
all H. spontaneum ecotypes (Tables 6 and 7). The highest percentage of
high transgressive segregates came from the northern and southern eco-
types when mated with both Robust and Bowers, respectively (Tables 6
and 7).

Plant Height

Segregates from matings involving the coastal ecotype averaged 4-7
cm taller than those from matings involving all other ecotypes (Table 3).
Segregate means from matings involving northern and central ecotypes did
not differ but matings involving southern ecotypes gave the shortest
segregates. Within the central and southern ecotypes, segregates from
matings involving PI 466434 and PI 466302 had significantly greater plant
heights than their respective counterparts (Table 4). Within the central
ecotype, segregates from matings involving PI 466434 were taller than
segregates from matings involving PI 466514 when crossed to either Robust
or Bowers. However, H. spontaneum accessions within the southern and
central ecotypes combined differentially with Robust and Bowers for plant
height. The percentages of transgressive segregates for plant height were
inconsistent over backcross generations within each H. vulgare variety
(Tables 6 and 7). The southern ecotype gave the highest percentage of
short F_3-derived line means regardless of H. vulgare parent or backcross
generation, whereas the coastal ecotype gave the lowest percentage of
transgressive segregates. The highest percentage of transgressive

segregates was 30.4% from the BC0 of the southern ecotype x Robust mating (Table 7).

Unit Straw Weight

The percentages of transgressive segregates for unit straw weight were smaller in the Bowers matings than in the Robust matings. The highest percentage of Bowers transgressive segregates was 6.3% for the BC2 of the coastal ecotype x Bowers mating (Table 6). Generally, the Robust matings gave increases of percentages of transgressive segregates from BC0 to BC1 but reduced percentages from BC1 to BC2. The highest percentage of Robust transgressive segregates for this trait was 11.6% in the BC1 of southern ecotype x Robust mating (Table 7).

Heading Date

Means for heading dates of segregates did not differ significantly among ecotypes (Table 3); however, segregate means from crosses involving H. spontaneum accessions within the southern ecotype were significantly different (Table 4). Crosses involving PI 466302 averaged 1.6 days later than those involving PI 466561. PI 466438 gave later segregates than did PI 466514 when crossed to either Robust or Bowers (Table 5). Within the northern and southern ecotypes, the H. spontaneum accessions gave differential results when combined with Robust and Bowers. The percentage of transgressive segregates for heading date was much smaller for the Robust than for the Bowers matings in all backcross generations (Tables 6 and 7). The highest percentage of transgressive segregates for

this trait was 48.0% from the BC0 of the central ecotype x Bowers
mating (Table 6).

Vegetative Growth Index

Segregate means for vegetative growth index ranged from 0.064
Mg ha^{-1} for matings involving the coastal ecotype to 0.057 Mg ha^{-1} from
matings involving southern ecotypes (Table 3). The coastal ecotype was
significantly superior to all other ecotypes for vegetative growth index,
whereas the southern ecotype was significantly inferior to central and
coastal ecotypes. The percentage of transgressive segregates for vege-
tative growth rate increased from the BC0 to BC1 and then decreased in
the BC2 for Bowers matings (Table 6), whereas Robust matings were in-
consistent over backcrosses (Table 7). The coastal ecotype showed
the highest percentage of transgressive segregates in the BC1 and BC2
from both Robust and Bowers matings (Table 7). The highest percentage
of transgressive segregate means was 19.6% from the BC1 of the coastal
ecotype x Robust mating.

DISCUSSION

Genes from wild and weedy relatives of cereals have been used successfully for improving oats (Avena sativa (L.)), sorghum (Sorghum bicolor (L.) Moench), barley, and pearl millet (Pennisetum americanum (L.) Leeke). Among the traits improved are productivity, seed composition, and disease resistance (Frey et al., 1988; Cox et al., 1984; Vega and Frey, 1980; Rogers, 1982; Bramel-Cox et al., 1986).

Several studies have shown that H. spontaneum contains potentially useful genes for improving agronomic traits of cultivated barley (Rogers, 1982; Vega and Frey, 1981; Vega and Frey, 1980). These studies showed as many as 9.1% high transgressive segregates for grain yield from H. spontaneum and H. vulgare crosses (Rogers, 1982). Some segregates gave up to 167% heterosis for grain yield. In this study, accessions of H. spontaneum from Israel that were crossed with two H. vulgare varieties were classified into ecotypes from northern, central, southern, and coastal Israel. The accessions used originated two each from northern, central, and southern Israel and one from the coast. Even though the ecotypes are represented by few accessions, there is some evidence that ecotypes do differ as sources of genes for superior performance of agronomic traits. For example, the segregates derived from the coastal ecotype had means for straw yield, plant height, and vegetative growth index that were significantly greater than comparable means from any other ecotype. Further, the coastal ecotype produced higher percentages of transgressive segregates for straw yield and vegetative growth index than did any other ecotype. In general, the coastal ecotype gave

segregates with significantly inferior harvest index. The results suggest that the northern and southern ecotypes of H. spontaneum carry genes for efficient partitioning of biomass into grain. The coastal ecotype, even though its derivatives had superior straw yield, did not carry genes for superior biomass production.

Among the three H. spontaneum accessions used by Vega (1979), two of the accessions were collected from the southwest area of Iran approximately 200 kilometers north of the Persian Gulf (PI 227301 and PI 227019) and the third accession was from central Israel (PI 296870). The Iranian H. spontaneum accessions resulted in 134.4% and 167% heterosis for grain yield, whereas the accession from Israel resulted in only 15% heterosis. Also, one of the matings with an Iranian accession (PI 227301) resulted in a large percentage of transgressive segregates.

Seven H. spontaneum accessions used by Rogers (1982) were collected from different localities within Israel. These seven accessions can be categorized into four ecotypes: northern, central, southern, and coastal. The central ecotype gave segregates with the highest grain yields in his study. In our study, Bowers x PI 466434 resulted in the second highest grain yield of all matings.

Although not conclusive, these two studies do provide evidence of ecotype superiority as donors of genes for specific agronomic traits. Certainly, the evidence is sufficiently positive to encourage additional studies to better understand ecotypic variability of H. spontaneum and its relationship to sources of genes for agronomic traits.

Bailey (1977), on theoretical grounds, showed that the optimum

backcross generation for obtaining segregates that were superior to the recurrent parent for quantitatively inherited traits was between one and four. Rogers (1982), who studied segregates from BC0 - BC4 of H. spontaneum x H. vulgare crosses, found that the BC4 was the optimum generation for selecting superior progenies for grain yield. No particular backcross generation was associated with superior straw yield. In this study, percentages of line transgressive segregates tended to increase through the BC2 for grain yield. Whether this trend would have continued through the BC4 can only be speculative. Percentages of segregates that exceeded the recurrent parents for straw yield tended to be as high in the BC1 as in the BC2.

A practical implication from this study is that knowledge about the geographic origin of an accession of a wild species may be useful in predicting its value as a source of genes for improving a specific trait. For example, herein is suggested that H. spontaneum accessions from the coastal area near Ashqelon, Israel may carry genes for high straw yield, whereas those from the other regions of Israel carry genes for high harvest index. This information might be useful for a barley breeder who is developing barley varieties for pasture, a situation where high vegetative production would be desired. Of course, more accessions of H. spontaneum must be studied before one can conclude that associations exist whereby certain ecotypes represent good sources of genes for specific traits.

Choice of germplasm plays an important role in any breeding program, whether the objective is line development or germplasm enhancement

(Hallauer and Miranda, 1988). This study along with those of Rogers (1982) and Vega and Frey (1980) suggest that agronomic traits of culti- vated barley can be improved by introgression of genes from H. spontaneum for either long- or short-term breeding goals. Even though the coastal ecotype gave segregates with superior straw yield, biomass was not im- proved. A few segregates from crosses involving the coastal ecotype showed harvest index superior to the recurrent parent. So, if a large number of coastal ecotype accessions was used, some superior progenies might have both superior grain and straw yields. These data and those from Vega (1979) and Rogers (1982) show that H. spontaneum accessions from the Fertile Crescent may possess useful genes for agronomic traits when introgressed into the cultivated barley gene pool. Utilizing such germplasm in a population improvement program likely would produce gene pools with favorable genetic variability.

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GENERAL CONCLUSIONS

H. spontaneum, the progenitor of cultivated barley, possesses immense variability for allozymes, agronomic traits, and disease resistance (Nevo et al., 1984, 1979; Moseman et al., 1983). This study investigated (a) H. spontaneum accessions as donors of cytoplasmic and nuclear genes for agronomic traits and (b) whether a relationship existed between useful cytoplasmic and nuclear genes from H. spontaneum accessions and the sites from which the accessions originated.

In section I, the "isopopulation method" was used to determine whether H. spontaneum cytoplasm had direct effects upon barley traits. H. spontaneum cytoplasms gave greater means for straw yield, unit straw weight, and vegetative growth index than did H. vulgare cytoplasms. Conversely, H. vulgare cytoplasms gave greater means for grain yield and harvest index than did H. spontaneum cytoplasms. Probably, both H. spontaneum cytoplasms and nuclear genes contributed to superior straw yield, unit straw weight, and vegetative growth index. The effects of interaction between cytoplasmic and nuclear genomes in interspecific barley crosses on agronomic traits were clearly illustrated. To better utilize the genetic variability of interspecific crosses, care must be taken in selecting parents and which parent will be the female. Only when plant breeders understand the importance of specific nuclear-cytoplasmic combinations will they begin to fully utilize the genetic potential and variability of wild crop species. Based upon these data, improved barley variaties can result from the utilization of both cytoplasmic and nuclear genes from H. spontaneum.

In section II, seven H. spontaneum accessions were categorized as northern, southern, central, and coastal ecotypes. Then, segregates from interspecific matings in which these accessions were used as parents were evaluated on the basis of variation within and among ecotypes. The data suggest that superior performance of segregates for specific traits resulted, in part, due to genes from specific ecotypes. The most obvious effect was superior straw yield for segregates from matings in which the coastal ecotype was used as a parent. This could be an important discovery for a barley breeder who is developing barley varieties for use as pasture or forage. Extensive genetic variability found among and within ecotype matings for other traits suggests that improvement of all of them might be possible if large numbers of progenies per mating were evaluated.

That genetic traits may be associated with H. spontaneum ecotypes provides some interesting conclusions. Sampling a wild species to maximize the probability that the accessions of it will possess useful germplasm is an overwhelming task because one encounters almost endless variability. The ubiquity of H. spontaneum in the Fertile Crescent area of the Middle East is a case in point. If this vast area with natural stands of this species could be partitioned into ecosystems, efficiency of sampling and the probability of obtaining superior accessions for specific traits would be greatly enhanced. The results from this study, even though based upon our small number of H. spontaneum accessions from Israel, do suggest that ecotypes and specific traits were associated. It is essential to assess the value of an accession by evaluating its segregates. Only a few of the accessions possess genes that combine and function well in a

cultivated barley genetic background.

Both sections of this study provide evidence that H. spontaneum possess genes that give useful interactions in a H. vulgare genetic background for improving agronomic traits.

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