Netherlands Journal of Agricultural Science 49 (2001) 95-112

Competition and niche differentiation in barley *(Hordeum vulgare)* and wheat *(Triticum aestivum)* mixtures under rainfed conditions in the Central Highlands of Eritrea

A. WOLDEAMLAK[1,2], L. BASTIAANS[2] AND P.C. STRUIK[2] *

[1] University of Asmara, College of Agriculture and Aquatic Sciences, Department of Plant Science, P. O. Box 1220, Asmara, Eritrea
[2] Wageningen University, Department of Plant Sciences, Crop and Weed Ecology Group, Haarweg 333, NL-6709 RZ Wageningen, The Netherlands
* Corresponding author (fax: +31-317-485572; e-mail: paul.struik@cwe.dpw.wau.nl)

Received 23 February 2001; accepted 30 June 2001

Abstract

Barley and wheat mixtures were grown in the field using additive and replacement ratios at two locations (Halhale and Mendefera) in Eritrea during the 1997 and 1998 seasons. The aim was to assess yield advantage and to analyse competition and niche differentiation using a hyperbolic regression model. It proved advantageous to grow barley and wheat in mixtures because more land area was required to obtain the same yield in sole crops. The hyperbolic regression approach confirmed that barley and wheat grown in mixtures resulted in yield advantages as a result of complementary use of resources. Barley showed greater competitive ability than wheat; for wheat, interspecific competition was larger than the intraspecific competition while for barley the intraspecific competition was greater than the interspecific competition. Niche differentiation indices were always above 1.0 indicating that the component crops did not inhibit each other from sharing resources in a complementary way.

Key words: Competition, niche differentiation, yield advantage, mixed cropping, barley, wheat

Introduction

The cropping system *hanfetz* is practised in the highlands of Eritrea. *Hanfetz* is the Tigrigna word for mixed cropping of barley and wheat. The mixtures are sown under rainfed conditions from the end of June until the first week of July. Farmers traditionally broadcast the mixtures in a ratio of 67% barley and 33% wheat. Additionally, 50% barley and 50% wheat is sometimes used (Woldeamlak & Struik, 2000).

Total plant density is important in sole cropping but especially in mixed cropping. Excessively dense plant stands can result in misuse of limiting resources and may lead to weaker plants and lower productivity (Martin & Snaydon, 1982). Sowing density below the optimum leads to inefficient utilization of soil resources by the plants resulting in inadequate yield. Optimum plant density and proportion in mixed cropping may generally help to facilitate and ensure penetration of more solar radiation towards the undergrowing component crop of the system (Singh & Chauhan, 1991).

Competition occurs when the use of some resources by one species or an individual plant is at the expense of the use of the same resources by another. The competition between plants of the same species is called intraspecific competition; interspecific competition is the competition of plants of different species. These competitive forces determine the response of individual plant biomass to plant density, but also have consequences for crop yield. When crop species show a yield advantage in mixed cropping it may imply that they are complementary; intraspecific competition usually exceeds interspecific competition.

Most of the earlier studies done in intercropping are either replacement series or additive series focused on determination of yield advantage and productivity of mixtures. In additive series, the total population density in mixtures (and thus the population pressure) exceeds that of the sole crops. The total proportion is greater than 100%. When the crop ratio of component crops increases the total density also increases (Willey & Osiru, 1972). The disadvantage of this approach is that it is difficult to identify whether yield advantage results from growing two crops in mixtures or from an increased total plant density, as both these factors are confounded. In replacement series, the mixing ratio varies but the total density remains constant. The total proportion adds up to 100%. Spitters (1983) proposed a hyperbolic regression approach in which the crop yield-plant density relation is used to determine the competitive relation between component crops and niche differentiation. This analysis requires crops to be grown in a range of densities either in an additive or a replacement design.

Up to now there are no concrete, science-based studies done on the competition and niche differentiation of barley and wheat mixtures either using replacement or additive series. The objective of this study was to assess yield advantage of mixed cropping of barley and wheat and additionally to analyse competition and niche differentiation between these crops, using the Spitters regression model.

Materials and Methods

Location

Four field experiments were conducted at two research sites in the highlands of Eritrea (Halhale Research Station and Mendefera) during the rainy periods of 1997 and 1998. The amount of rainfall at Halhale was 580 mm in 1997 and 656 mm in 1998, and that at Mendefera was 710 mm in 1997 and 784 mm in 1998.

Treatments and design

Genotypes Yeha (barley) and Mana (wheat), the most popular combination in *hanfetz,* were grown at three basic sowing densities (100% =100, 200 or 300 plants m^{-2})

in crop ratios with additive and replacement series. In the additive design, the barley (B) / wheat (W) crop ratios in % included were 25/100, 50/100, 75/100, 100/25, 100/50, 100/75. In the replacement series, the barley and wheat crop ratios evaluated were in %, 0/100 (wheat sole crop) 33/67, 50/50, 67/33 and 100/0 (barley sole crop). The amounts of seed needed to obtain these ratios were assessed based on the thousand-grain weight of both crops. The amount of seed planted was assumed to have 100% germination based on a germination test conducted before planting.

The treatments were arranged in two-factor factorial experiments in a Randomized Complete Block Design in 4 replications and an individual plot size of 3.75 m^2. The sowing densities and crop ratios were factorially combined to give 27 mixed cropping treatments and 6 sole crops.

Agronomic practices

Seed was broadcasted during the end of June at both locations and both years. A basal dressing of fertilizer was applied to all plots during planting at a rate of 100 kg ha^{-1} Di-Ammonium Phosphate (DAP, 18% N and 46% $P_2 0_5$) and 50 kg ha^{-1} Urea (46% N). These amounts guaranteed no limitation of nitrogen in the soil as evidenced by the grain yield per kg of N. No irrigation or pest control was carried out. Weeds were removed manually twice at 30 and 45 days after sowing the crop. Crops of the two seasons and two years were harvested at 88 to 90 days after sowing (DAS) for barley and 100 to 103 DAS for wheat.

Data collected

The plants of the component crops in the mixture were harvested at physiological maturity and weighed separately. Data on grain yield were based on 12.5% moisture content reflecting practical conditions. The biomasses and grain yield of the two component crops were added to get the total above ground biomass or grain yield of each mixture and this sum was converted into kg ha^{-1}.

Yield advantage analysis

Land Equivalent Ratio (LER)
The yield advantage in the additive series was calculated using the land equivalent ratio.

$$LER = L_1 + L_2 = (Y_{12} / Y_{11}) + (Y_{21} / Y_{22}) \quad (1)$$

where L_1 and L_2 are the land equivalent ratios of barley and wheat, respectively; Y_{11} and Y_{22} are the yields of the sole crops of barley and wheat at the relevant plant density in the sole crop, respectively; Y_{12} and Y_{21} are the yields in mixtures of barley and wheat, respectively. The LER expresses the relative land area under sole cropping that is required to give the same yield of each species in mixtures. Hyperbolic regression analysis (Equation 3) of sole crop yields against plant density was used to estimate the reference yields for some densities of the sole crops used in the additive design. If LER > 1, a larger land area is required to produce the same yield of the mixtures in sole cropping which means that there is a yield advantage. If LER = 1, it does not make any difference to grow either a mixture or the sole crop, because the yield obtained in mixed cropping can be obtained by growing the same area of land in sole cropping. In very rare cases LER can be lower than 1; in those cases the yields obtained in mixtures are lower than those in sole cropping. It implies that a larger area under mixed cropping gives the same yield as a smaller land area planted with sole crops.

Relative Yield Total

The yield advantage in the replacement series was estimated using the relative yield total (RYT):

$$RYT = RY_1 + RY_2 = (Y_{12} / Y_{11}) + (Y_{21} / Y_{22}) \qquad (2)$$

where RY_1 and RY_2 are the relative yields of barley and wheat, respectively; Y_{12} and Y_{21} are the yields of barley and wheat in the mixtures, respectively; Y_{11} and Y_{22} are the yields of the sole crops of barley and wheat, respectively. RYT values greater than 1 indicate that there is at least to some extent complementarity in resource use. RYT values less or equal to 1 indicate that the species fully share the common limiting resources, i.e. they compete fully and show no resource complementarity.

Hyperbolic regression model

Crop biomass yield is related to plant density according to (Spitters, 1983):

$$Y_1 = N_1 / (b_{10} + b_{11} N_1) \qquad (3)$$

in which Y_1 is the yield (g m^{-2}) of the crop in monoculture; N_1 is the plant density of the crop (plants m^{-2}); b_{10} and b_{11} are constants. From Equation 3 the average weight per plant (W_1; g $plant^{-1}$) can be derived as:

$$W_1 = Y_1/N_1 = 1/(b_{10} + b_{11}N_1) \qquad (4)$$

To estimate b_{10} and b_{11} this expression can be rewritten in a linear regression form as:

$$1/W_1 = b_{10} + b_{11}N_1 \qquad (5)$$

where b_{10} is the intercept and b_{11} is the slope of the linear relationship between $1/W_1$ and N_1.

The intercept b_{10} (plant g^{-1}) is the reciprocal of the biomass or yield of an isolated plant ($W_1 = 1/b_{10}$). The slope (b_{11}, m^2 g^{-1}) measures how $1/W_1$ increases, and hence how the per plant weight (W_1) decreases with any plant added to the population. The coefficient b_{11} is the reciprocal of the maximum yield per unit area achieved at infinite density. The ratio b_{11}/b_{10} is a measure of intraspecific competition.

If adding plants of one species affects 1/W additively, then it seems reasonable to assume that adding plants of another species also linearly affects $1/W_1$. Based on this assumption the reciprocal of the per plant weight of Species 1 in a mixture with Species 2 can be calculated as:

$$1/W_1 = b_{10} + b_{11}N_1 + b_{12}N_2 \qquad (6)$$

The coefficient b_{11} measures the effect of intraspecific competition whereas b_{12} measures the effect of interspecific competition. The ratio b_{11}/b_{12} measures the relative competitive ability (Spitters *et al.*, 1989).

By deriving this ratio for the two component crop species of a mixture the niche differentiation index (NDI) can be estimated:

$$NDI = (b_{11} / b_{12}) \times (b_{22} / b_{21}) \qquad (7)$$

This index represents the ratio between intraspecific (b_{11} and b_{22}) and interspecific (b_{12} and b_{21}) competition. If NDI > 1, there is niche differentiation indicating that the intraspecific competition exceeds interspecific competition. Plants in the mixtures are sharing resources better than plants of a sole crop, which means that competition for the same resources is less. If NDI= 1, the two species are competing equally for the same resources, whereas a NDI < 1 suggests that the species are hampering one another (Spitters *et al.*, 1989).

Analysis of the model

From Equation 6 the model can be written as

$$Y_{12} = N_1 / (b_{10} + b_{11} N_1 + b_{12} N_2) \qquad (8a)$$

Final biomass and grain yield data were analysed using a slightly re-written version of Equation 8a:

$$\begin{aligned} Y_{12} &= N_1 \times (1 / b_{10}) / (1 + b_{11} / b_{10}(N_1 + (b_{12} / b_{11} N_2))) \\ &= N_1 \times W_{10} / (1 + a_{12} (N_1 + (1/c_{12}) \times N_2)) \qquad (8b) \end{aligned}$$

where N_1 is the plant density of the component crop (plants m^{-2}); W_{10} is the apparent weight of an isolated plant ($1/b_{10}$) in g $plant^{-1}$; a_1 is a parameter characterizing intraspecific competition (b_{11}/b_{10}) and c_{12} is the relative competitive ability (b_{11}/b_{12}) describing how many individuals of Species 2 are equivalent to each individual of Species 1. The maximum attainable yield can be estimated as the reciprocal of b_{11} (i.e. $1/b_{11}$) (Watkinson, 1981).

Alike for Species 2:

$$Y_2 = N_2 \times W_{20} (1+a_{21} (N_2+(1/c_{21}) \times N_1)) \qquad (8c)$$

The nonlinear regression procedure of SPSS was used to fit the different versions of the model (Equations 8a, 8b and 8c) in order to determine the parameter values b_0, b_1, b_2, W, c and a for both species.

Results

Biomass yield in additive series

There was a significant density effect in Halhale 1997, and averaged over the two years for both locations, with S_3 giving the highest biomass yield. There was no significant effect of additive series on total biomass yield of the mixtures in both locations and years (Table 1). The mean biomass yield was higher in the additive crop ratios as compared with that in the replacement series (Tables 1 and 3).

Table 1. Biomass yields (kg ha^{-1}) in additive crop ratios at three sowing densities (S_1–100; S_2–200 and S_3–300 plants m^{-2}) of barley (B) and wheat (W) in mixed cropping at Halhale and Mendefera, Eritrea 1997–1998. The results are averages over the crop ratios or densities.

Density / Crop ratio	Halhale			Mendefera		
	1997	1998	Mean	1997	1998	Mean
Density						
S_1–100	6194 b[1]	8875	7535	5665	9147	7406 b
S_2–200	6667 b	8521	7594	6290	9239	7765 ab
S_3–300	8340 a	8846	8593	6437	9475	7956 a
Mean	7067	8747	7907	6131	9287	7709
Crop ratio B/W						
25/100	7046	8826	7936	5911	9973	7942
50/100	7833	8972	8403	6177	9533	7855
75/100	7322	8851	8087	5974	9356	7665
100/25	6953	8469	7711	5848	8935	7392
100/50	6400	8421	7411	6301	9622	7962
100/75	6827	9023	7925	6355	8989	7672
Mean	7067	8747	7907	6131	9287	7709
LSD 5%[2]						
Density	869	NS[3]	NS[4]	NS	NS	477
Crop ratio	NS	NS	NS	NS	NS	NS
Density × crop ratio	NS	NS	NS	NS	NS	NS
CV%[5]	21.4	15.6	14.9	22.6	9.6	10.6

[1] Means within a column followed by the same letter are not significantly different at $P \leq 0.05$. [2] Least significant difference at $P = 0.05$. [3] NS=not significant at $P \leq 0.05$.
[4] significant at $0.05 < P \leq 0.10$. [5] CV%= coefficient of variation (%).

The mean biomass values for the different sowing density × crop ratio combinations are shown in Figure 1. The interactions between the two factors were not significant. At Halhale, when averaged over the two years, S_3 (300 plants m^{-2}) at 50/100 gave maximum biomass yield. At Mendefera, S_3 at 25/100 gave the maximum biomass yield.

Grain yield in additive series

There were no significant effects of sowing densities or crop ratios (nor significant interactions between these two factors) on grain yield at both locations. Grain yields were higher in 1998 than in 1997 (Table 2). In the barley additive series, yields were highest at 50/100 and in the wheat additive series at 100/50 when averaged over the

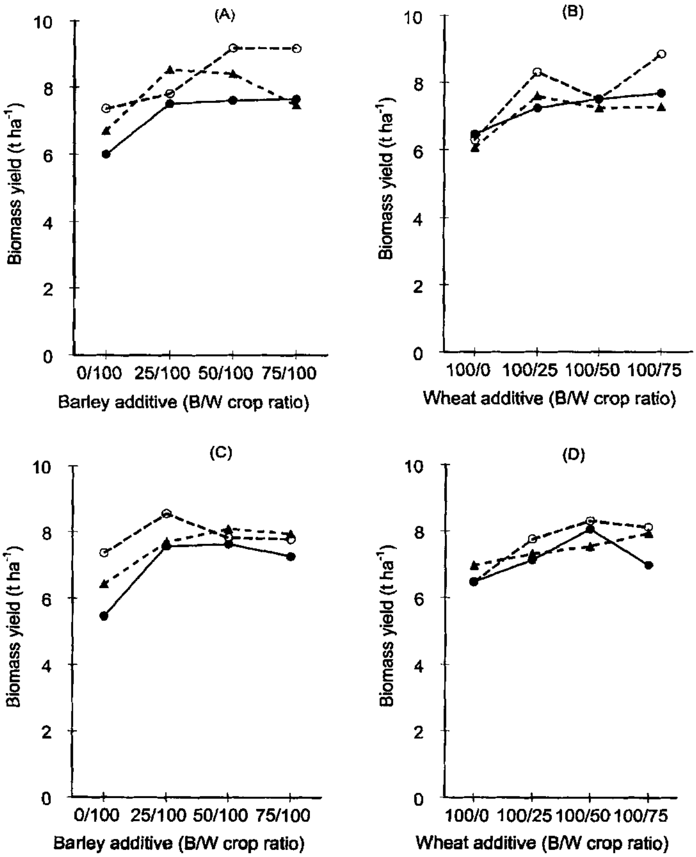

Figure 1. Effect of density and crop ratio (B/W) in the additive series on the mean biomass yield of mixed cropping of barley and wheat at two locations. (A) Barley additive, mean of 2 years at Halhale; (B) Wheat additive, mean of 2 years at Halhale; (C) Barley additive, mean of 2 years at Mendefera; (D) Wheat additive, mean of 2 years at Mendefera. ●–S_1 (100%=100 plants m^{-2}), ▲–S_2 (100%=200 plants m^{-2}) and O–S_3 (100%=300 plants m^{-2}).

Table 2. Grain yields (kg ha^{-1}) in additive crop ratios at three sowing densities (S_1–100; S_2–200 and S_3–300 plants m^{-2}) of barley (B) and wheat (W) in mixed cropping at Halhale and Mendefera, Eritrea 1997–1998. The results are averages over the crop ratios or densities.

Density / Crop ratio	Halhale			Mendefera		
	1997	1998	Mean	1997	1998	Mean
Density						
S_1–100	1874	2514	2194	1614	1968	1791
S_2–200	2119	2192	2156	1502	2196	1849
S_3–300	2086	2177	2132	1644	2030	1837
Mean	2026	2294	2161	1586	2065	1826
Crop ratio B/W						
25/100	1780	2445	2113	1736	2391	2064
50/100	1953	2343	2148	1470	2017	1744
75/100	1800	2106	1954	1718	1964	1841
100/25	2145	2336	2241	1655	2067	1861
100/50	2176	2372	2275	1541	2270	1906
100/75	2058	2314	2186	1548	2005	1777
Mean	2026	2294	2161	1586	2065	1826
LSD 5%[1]						
Density	NS[2]	NS	NS	NS[3]	NS	NS
Crop ratio	NS	NS	NS	NS	NS	NS
Density × crop ratio	NS	NS	NS	NS	NS	NS
CV%[4]	28.0	20.4	15.8	31.6	22.2	17.8

[1] Least significant difference at $P = 0.05$.
[2] NS=not significant at $P \leq 0.05$.
[3] significant at $0.05 < P \leq 0.10$.
[4] CV%= coefficient of variation (%).

two years at Halhale. For Mendefera the treatments with the highest average yields were 25/100 for the barley additive series and 100/50 for the wheat additive series. These yields did not differ significantly from the other yields. Grain yields were closely associated with biomass yield, although at the same grain yield more biomass was regained when crop densities increased (Tables 1 and 2).

The grain yields of all sowing density × crop ratio combinations averaged over the two years are shown in Figure 2. At Halhale, when averaged over the two years, S_2 at 100/25 gave highest grain yields whereas at Mendefera, S_3 at 25/100 showed the best grain yield.

Biomass yield in replacement series

Sowing density had an effect on biomass yield at Halhale in both years with S_1 being significantly lower than the other two densities. The effects of crop ratios and the interaction between sowing density and crop ratio were not significant (in 1997 significant at $P<0.10$; Table 3). At Mendefera, sowing density had a similar effect as at Halhale, but it was only significant when averaged over the two years; the crop ratio had rather consistent significant effects on biomass yield in both years, with 67/33 giving the highest yields (Table 3).

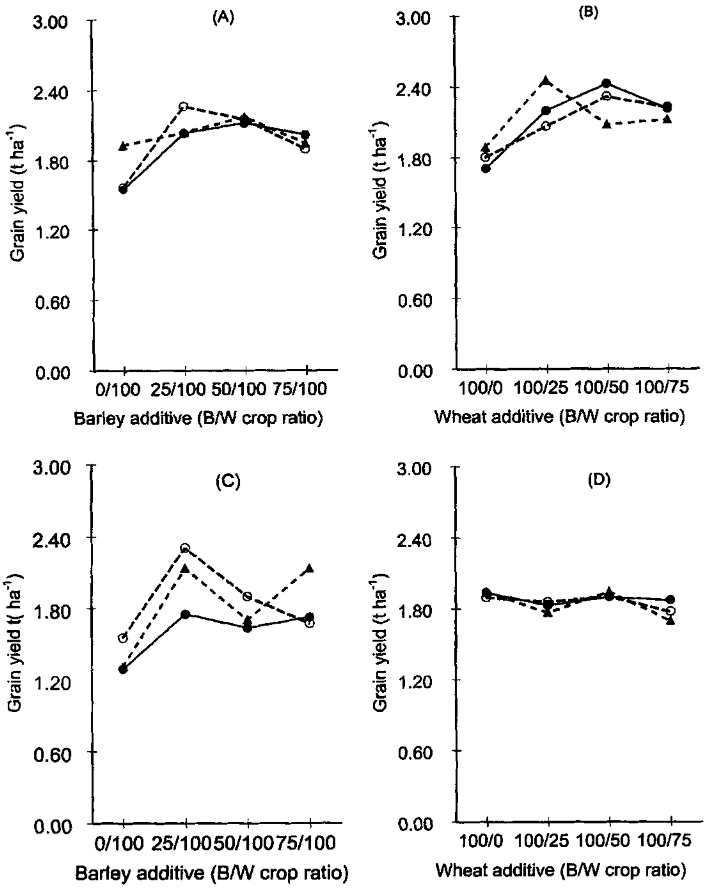

Figure 2. Effect of density and crop ratio (B/W) in the additive series on the mean grain yield of mixed cropping of barley and wheat at two locations. (A) Barley additive, mean of 2 years at Halhale; (B) Wheat additive, mean of 2 years at Halhale; (C) Barley additive, mean of 2 years at Mendefera; (D) Wheat additive, mean of 2 years at Mendefera. ●–S_1 (100%=100 plants m^{-2}), ▲–S_2 (100%=200 plants m^{-2}) and O–S_3 (100%=300 plants m^{-2}).

When averaged over crops/crop ratios and years, a density of 100 plants m^{-2} (S_1) showed reduced biomass yield, whereas 200 plants m^{-2} (S_2) and 300 plants m^{-2} (S_3) gave higher biomass yields. Averaged over densities and years mixtures outyielded the barley and wheat sole crops in biomass yield.

Grain yield in replacement series

The density effects showed the same trends as observed for the biomass yield, but differences were very small in Halhale (Table 4). Crop ratio in the replacement series had a significant effect on grain yield at both locations and in both years. Aver-

Table 3. Biomass yields (kg ha^{-1}) in a replacement series at three sowing densities (S_1–100; S_2–200 and S_3–300 plants m^{-2}) for barley (B) and wheat (W) in mixed cropping at Halhale and Mendefera, Eritrea 1997–1998. The results are averages over the crop ratios or densities.

Treatments	Halhale			Mendefera		
	1997	1998	Mean	1997	1998	Mean
Density						
S_1–100	4653 b[1]	6892 b	5772 b	4499	8174	6337 b
S_2–200	6256 a	7834 a	7045 a	5700	8784	7242 a
S_3–300	6679 a	8336 a	7508 a	6238	8033	7136 a
Mean	5862	7687	6775	5479	8331	6905
Crop ratio B/W						
0/100	4778	8601	6689	4550 b	8286 b	6418 c
33/67	5824	8179	7002	5290 ab	8123 b	6707 bc
50/50	6223	8134	7179	5558 a	8823 ab	7191 ab
67/33	6099	7368	6734	6022 a	9133 a	7578 a
100/0	6388	6156	6272	5976 a	7287 c	6632 bc
Mean	5862	7687	6775	5479	8331	6905
LSD 5%[2]						
Density	962	812	621	NS[4]	NS[3]	547
Crop ratio	NS[4]	NS	NS	770	770	706
Density × crop ratio	NS	NS	NS	NS	NS	NS
CV%[5]	26.3	16.4	14.3	17.1	12.7	12.1

[1] Means within a column followed by the same letter are not significantly different at $P \leq 0.05$.
[2] Least significant difference at $P = 0.05$.
[3] NS=not significant at $P \leq 0.05$.
[4] significant at $0.05 < P \leq 0.10$. [5] CV%= coefficient of variation (%).

aged over sowing densities, mixtures outyielded the barley sole crop in grain yield at both sites in 1998 only, but most mixtures were higher than the wheat sole crop at both sites in both years. Mixtures generally performed better than expected based on their proportions of the two crops, and there was a complementary effect of the barley in the replacement series. When averaged over the two years, a crop ratio of 50/50 showed highest grain yield (1971 kg ha^{-1}) at Halhale, and at Mendefera crop ratios 33/67 (2031 kg ha^{-1}) and 67/33 (2001 kg ha^{-1}) were highest in grain yield, even though these differences were not statistically significant. Grain yield was higher in 1998 than in 1997 due to more rainfall (Table 4).

Yield advantage

The results of the yield advantage analyses in terms of Land Equivalent Ratio and Relative Yield Total are shown in Tables 5 and 6, averaged over the two years.

Land Equivalent Ratio

The LER values based on biomass and grain yield are shown in Table 5. The LER values were always > 1 in both locations and years indicating a yield advantage in

Table 4. Grain yields (kg ha^{-1}) in replacement crop ratios at three sowing densities (S_1–100; S_2–200 and S_3–300 plants m^{-2}) for barley (B) and wheat (W) in mixed cropping at Halhale and Mendefera, Eritrea 1997–1998.

Treatments	Halhale			Mendefera		
	1997	1998	Mean	1997	1998	Mean
Density						
S_1–100	1398	2108	1753	1474 b[1]	1940	1707 b
S_2–200	1697	2084	1891	1801 a	2010	1906 a
S_3–300	1420	2191	1806	1899 a	2031	1965 a
Mean	1505	2128	1817	1725	1994	1859
Crop ratio B/W						
0/100	1281 c	2084 b	1683 b	1261 c	1502 c	1382 b
33/67	1329 bc	2361 a	1846 ab	1605 b	2456 a	2031 a
50/50	1531 abc	2411 a	1971 a	1794 ab	2117 ab	1955 a
67/33	1638 ab	2009 bc	1824 ab	1956 a	2047 ab	2001 a
100/0	1744 a	1773 c	1759 b	2007 a	1848 bc	1928 a
Mean	1505	2128	1817	1725	1994	1859
LSD 5%[2]						
Density	NS[3]	NS[4]	NS	222	NS	196
Crop ratio	359	278	212	286	392	253
Density x crop ratio	NS	NS	NS	NS	NS	NS[4]
CV%[5]	28.1	16.5	14.3	20.1	23.9	16.5

[1] Means within a column followed by the same letter are not significantly different at $P \leq 0.05$.
[2] Least significant difference at $P = 0.05$.
[3] NS=not significant at $P \leq 0.05$.
[4] Significant at $0.05 < P \leq 0.10$.
[5] CV%= coefficient of variation (%).

mixtures compared with the sole crops. Higher density in mixtures showed lower yield advantage in terms of land area required for both yield parameters. This was consistent at both locations. There were significant effects of crop ratio on grain yield LER data at both locations averaged over the two years, which were the same as those for each individual year (data not shown). The additional land area required in sole crops to get the same yields as those in mixtures ranged from 23 to 32% when averaged over years, densities and crop ratios. Considering the crop ratios when averaged over the densities, more barley with a fixed quantity of wheat or more wheat with a fixed quantity of barley reduced the (100/25 and 25/100) yield advantage in land area required. Higher additive crop ratio of 75/100 or 100/75 showed the smallest advantage in land area required.

Relative Yield Total

Almost all values in Table 6 are > 1. The RYT > 1 showed that there was a yield advantage of the mixtures in terms of the biomass yield and grain yield for almost all densities and all crop ratios. This was consistent for both locations (Table 6). There was a significant difference in the yield advantage for biomass among the densities but not among the crop ratios. Comparing the densities, the intermediate density (S_2

Table 5. Land Equivalent Ratio (LER) for biomass yield and grain yield in additive crop ratios at three densities (S_1–100%= 100; S_2–100%= 200 and S_3–100%= 300 plants m^{-2}) of barley (B) and wheat (W) mixtures at two locations (Halhale and Mendefera, Eritrea) averaged over two years (1997–1998).

Density / Crop ratio	Biomass yield		Grain yield	
	Halhale	Mendefera	Halhale	Mendefera
Density				
S_1–100	1.40 a[1]	1.18 a	1.37 a	1.45 a
S_2–200	1.22 b	1.06 b	1.20 b	1.29 b
S_3–300	1.20 b	1.11 b	1.11 c	1.21 c
Mean	1.27	1.12	1.23	1.32
Crop ratio B/W				
25/100	1.34	1.17	1.48 a	1.53 a
50/100	1.31	1.13	1.21 b	1.28 b
75/100	1.28	1.11	1.07 c	1.18 c
100/25	1.29	1.12	1.37 a	1.47 a
100/50	1.18	1.10	1.22 b	1.30 b
100/75	1.21	1.07	1.04 c	1.15 c
Mean	1.27	1.12	1.23	1.32
LSD 5%[2]				
Density	0.13	0.08	0.082	0.055
Crop ratio	NS[3]	NS	0.116	0.078
Density × crop ratio	NS	NS	NS	NS
CV%[4]	6.8	12.5	11.6	7.3

[1] Means within a column followed by the same letter are not significantly different at $P \leq 0.05$.
[2] Least significant difference at $P = 0.05$.
[3] NS = not significant at $P \leq 0.05$.
[4] CV% = coefficient of variation (%).

= 200 plants m^{-2}) at Halhale and the highest density (S_3 = 300 plants m^{-2}) at Mendefera gave relatively better yield advantage in biomass yield and grain yield. Considering the crop ratios, 50/50 (Halhale) and 33/67 (Mendefera) seemed to show a slightly higher yield advantage. This was consistent for both biomass yield and grain yield.

Examples of the relative yield total of the component crops in biomass are shown in Figure 3. The relative yield of wheat decreased when the proportion of wheat decreased and that of barley increased when the proportion of barley as a component crop increased. This trend was consistent across the two years. Barley component yields in mixtures were higher than expected on the basis of their proportion, whereas wheat component yields in mixtures were lower than expected. The combined yields of mixtures were generally above the sole crop yields.

Competition

The results for the estimates of the intraspecific and interspecific competition and niche differentiation indices in mixtures of barley and wheat are shown in Tables 7

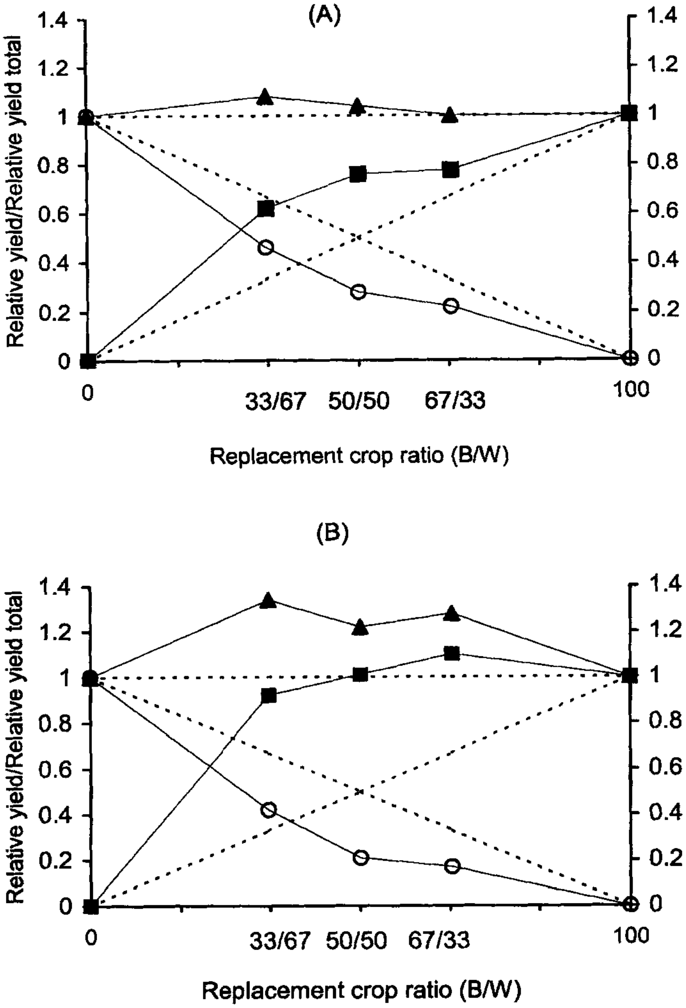

Figure 3. Relative yield in biomass of component crops barley and wheat and of total mixtures in replacement series at Mendefera in 1997 (A) and 1998 (B). Note: ■, Barley as component crop, O, Wheat as component crop and ▲, Mixtures.

and 8. The weight of an isolated plant (g $plant^{-1}$) of barley was not consistently different from that of a wheat plant for total biomass or total grain yield at both locations and years. The maximum attainable yield ($1/b_{11}$, $1/b_{22}$) was often higher for barley as a component crop than for wheat in both years and locations. There was a variation among years and locations in maximum attainable yield for both the component crops (barley and wheat) in total biomass and total grain yield (Table 7).

The relative competitive ability was higher for barley than for wheat in both years and locations. The competition received from barley was relatively greater than from

Table 6. Relative yield total (RYT) for biomass yield and grain yield in a replacement series of crop ratios at three total densities of 100 (S_1), 200 (S_2) and 300 (S_3) plants m^{-2} of barley (B) and wheat (W) mixtures at two locations (Halhale and Mendefera, Eritrea) averaged over two years (1997–1998).

Density / Crop ratio	Biomass yield		Grain yield	
	Halhale	Mendefera	Halhale	Mendefera
Density				
S_1–100	0.90 b[1]	1.08 b	1.18	1.06 b
S_2–200	1.22 a	1.16 ab	1.42	1.20 ab
S_3–300	1.21 a	1.26 a	1.30	1.23 a
Mean	1.12	1.17	1.30	1.16
Crop ratio (B/W)				
33/67	1.10	1.21	1.28	1.27
50/50	1.16	1.12	1.35	1.13
67/33	1.09	1.17	1.27	1.09
Mean	1.12	1.17	1.30	1.16
LSD 5%[2]				
Density	0.18	0.14	NS	0.16
Crop ratio	NS[3]	NS	NS	NS
Density × crop ratio	NS	NS	NS	NS
CV%[4]	18.9	14.6	20.6	16.2

[1] Means within a column followed by the same letter are not significantly different at $P \leq 0.05$.
[2] Least significant difference at $P = 0.05$.
[3] NS = not significant at $P \leq 0.05$.
[4] CV% = coefficient of variation (%).

wheat for total grain yield and total biomass. An example can be taken from the grain yield at Mendefera in 1998 in order to explain the competitive ability of barley in mixtures. For barley, one barley plant was able to compete equally with about eight (7.81) wheat plants. For barley, the presence of one barley plant feels as strong as the presence of eight wheat plants. For wheat, four wheat plants were equal to about one barley plant (0.240; 1/4th). The influence of barley plants relative to the

Table 7. Estimates of parameters b_0 (1/W), b_1 (1/a) and b_2 (c/b_1) for total biomass and grain yields of barley and wheat in both the replacement and additive series (Halhale and Mendefera, Eritrea), 1997–1998.

Characters or Environments	Barley			Wheat		
	b_{10}	b_{11}	b_{12}	b_{20}	b_{21}	b_{22}
Total biomass yield						
Halhale 1997	0.0610	0.00125	0.00041	0.1560	0.0020	0.00066
Halhale 1998	0.0100	0.00150	0.00076	0.0070	0.0012	0.00120
Mendefera 1997	0.0578	0.00130	0.00044	0.1178	0.0029	0.00100
Mendefera 1998	0.0200	0.00100	0.00015	0.0060	0.0039	0.00110
Total grain yield						
Halhale 1997	0.0891	0.00590	0.00248	0.213	0.0116	0.00630
Halhale 1998	0.0600	0.00580	0.00288	0.130	0.0036	0.00350
Mendefera 1997	0.1400	0.00400	0.00186	0.140	0.0111	0.00550
Mendefera 1998	0.0200	0.00250	0.00032	0.020	0.0304	0.00730

Table 8. Interspecific competition and niche differentiation indices (NDI) in mixtures for barley and wheat mixtures at Halhale and Mendefera, 1997 and 1998. The number of observations for each character / environment is 132 (11 crop combinations, 3 densities, 4 replications).

Characters or Environments	Barley			Wheat			NDI
	b_{11}/b_{12}	SE	r^2	b_{22}/b_{21}	SE	r^2	
Biomass yield							
Halhale 1997	3.049	0.102	0.550**	0.330	0.117	0.699**	1.010
Halhale 1998	1.970	0.290	0.770**	0.998	0.200	0.560**	1.970
Mendefera 1997	2.955	0.377	0.777**	0.345	0.092	0.757**	1.020
Mendefera 1998	6.670	2.100	0.720**	0.282	0.080	0.840**	1.880
Grain yield							
Halhale 1997	2.379	0.228	0.362*	0.543	0.170	0.511**	1.292
Halhale 1998	2.010	0.460	0.460*	0.986	0.250	0.490*	1.990
Mendefera 1997	2.150	0.460	0.580**	0.495	0.130	0.630**	1.060
Mendefera 1998	7.810	2.510	0.310*	0.240	0.110	0.200*	1.880 **

**Significant at $0.05 < P \leq 0.01$; * significant at $P \leq 0.05$. SE = standard error.

influence of wheat was at least four times greater (Table 8).

The relative competitive ability was higher for barley than for wheat. Intraspecific competition was higher than interspecific for barley and interspecific competition was greater than intraspecific for wheat.

Niche differentiation

There was niche differentiation for both total biomass and grain yield at both locations and years. The degree of niche differentiation was nearly the same for grain yield and for biomass at both locations. Niche differentiation greater than 1 for biomass yield and grain yield at both locations and both years suggests that despite the competition in favour of barley, the mixed crop still performed better than the sole crops. This is mainly because the extra growth of barley resulting from the relatively mild competition experienced from wheat more than compensated for the reduced wheat growth. The component crops in mixtures together captured more resources and were utilizing resources probably better than they did as sole crops, which means that the species were not only competing but were also complementary for some of the resources during the growing period. In Table 8 this is reflected in the ratio b_{11}/b_{12} that surpasses the inverse of b_{22}/b_{21} in all cases.

Discussion

Productivity

The total biomass and grain yields were higher in additive series as compared to replacement series at both locations in both years. This is in agreement with several workers who obtained similar results in mixed cropping of other crop species. For example, Banik (1996) confirmed a higher yield potential in the additive series of 100% pigeon pea and 75% sesame.

The total grain yields and total biomass for the mixtures were higher in 1998 than in 1997 at both locations. For barley both the apparent weight of a plant (g $plant^{-1}$) and the maximum attainable yield (g m^{-2}) were consistently higher in 1998 than in 1997. However, for wheat these characters were not consistent because the maximum attainable yield (g m^{-2}) was higher while the weight of an isolated plant was lower (g $plant^{-1}$) in 1997. On the other hand, in the year 1998 the maximum attainable yield was lower while the weight of an isolated plant was higher.

Yield advantage analysis

Land equivalent ratio and relative yield total do not describe the nature of intraspecific and interspecific competition. Furthermore, these parameters do not quantify the relative competitive ability of the crop species but only show the extent of yield advantage, which could be the result of resource complementarity. It is believed that yield advantage analysis together with the nonlinear regression approach can describe what is happening in a mixed cropping experiment. In this study the nature of the conclusions based on LER or RYT corresponded with the results of niche differentiation index in most of the situations.

The analysis also showed that it was advantageous to grow barley and wheat in mixtures because more land area was required to obtain a yield in sole crops similar to that in mixtures. The yield advantage could be because the two crop species are complementary in resource use or could be caused by the density effect. The analysis in the additive design showed that the yield advantage of the mixtures could also be due to increased total plant density, which was evident from Table 5. The question is why not achieve a benefit of higher yield in the sole crop by using higher density rather than growing mixtures. Indeed, part of the benefit of higher total yield might be achieved by growing the sole crop at higher density but this is not always true.

The replacement approach is more suitable in order to address the issue of yield advantage of mixed cropping. In this approach the ratios vary but the total densities are the same in mixtures as in sole crops. In Eritrea, mixed cropping is practised as an insurance mechanism in case of drought, so growing sole crops of wheat means facing a risk of stress especially if a high density is used in sole crops. However, the hyperbolic regression approach has confirmed that barley and wheat grown together in mixtures have promoted each other so that yield advantage was at least to some extent the result of complementary use of resources. It is important to note that barley and wheat mixtures have other advantages and benefits apart from higher total yield like preferred diet (*kicha*, local bread) and need for animal feed.

Competitive ability

Any wheat plant suffered less competition from other wheat plants than from the barley plant while barley plants suffered more from barley than from wheat. Willey

& Osiru (1972) have mentioned that, in a mixture, the more competitive species will actually utilize a greater proportion of the environment than is allocated to it at sowing time. Thus if the more competitive species has a higher yield potential, the comparison of a mixture with pure stands will be in favour of the mixtures. In addition, it was observed that on a plant basis and compared with their respective sole crops, the relief in competition experienced by barley plants was stronger than the increase in competition experienced by wheat plants. Moreover, the fact that competition among the same plant species in monocropping was higher for barley than for wheat suggests that the density for barley should be relatively less than that of wheat due to higher competitive ability among the barley plants.

Niche differentiation

The NDI > 1 was related to RYT > 1 showing that the yield advantage was due to complementary use of resources. In general, the niche differentiation in barley and wheat mixtures can be explained in terms of time and resource use. Barley is early maturing and can escape periods of moisture deficit by maturing before the onset of the period with low rainfall. Difference in plant height could help the crops to utilize resources at different times in a better way. A rapid increase in plant height of barley was observed during early stage of plant growth. Wheat plants in mixture were first suppressed but later on grew taller than barley. Furthermore, barley is sensitive to lodging under sole cropping but in mixtures it is physically supported by the more robust wheat allowing it to get enough solar resources.

Descriptive model

The nonlinear regression approach proved a useful tool in estimating the yield density relationship in mixed cropping because it described the interaction between the two crop species accurately. The product of the competitive ability of the crop species helps to estimate the niche differentiation among crop species, explaining whether the two crop species when grown together are maximizing soil resources for optimum productivity in mixtures. Such description is much more difficult to get using only LER or RYT values. However, it should be noted also that the hyperbolic regression approach is a descriptive one and explains what is happening in a particular location during that specific season by describing the competitive interactions between species in mixed cropping.

The model is applicable to any data set of populations varying in crop ratio and total density. The descriptive regression approach is very suitable when a range of densities are used, as it is the case in this study. It has been used in intercropping experiments regardless of the density design (i.e. whether it is an additive or a replacement design) (Spitters *et al.*, 1989). The time course of competition can be described by the help of this model in experiments where both sole crops and mixed crops are harvested at intervals. For each harvest the competition parameters can be estimated as well.

Conclusion

Mixed cropping of barley and wheat showed a yield advantage compared to the sole crops. The relative competitive ability of barley was higher than for wheat. Despite the competition in favour of barley the component crops did not inhibit each other from sharing resources. They were able to capture and utilize more resources probably better than do the sole crops which was the main reason for the yield advantage.

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