

CROPPING SYSTEMS

Cultivar Effects on Oat–Berseem Clover Intercrops

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ABSTRACT

Oat (*Avena sativa* L.) intercropped with berseem clover (*Trifolium alexandrinum* L.), an annual forage legume, has economic and biological advantages for use as a rotation crop in the north-central USA. To investigate the effects of different oat and berseem clover cultivars on the productivity of the intercrop and its components, and to test for interspecific cultivar interactions, we evaluated binary combinations and monocultures of a sample of oat and berseem clover cultivars in three Iowa environments. Oat cultivars varied for oat traits, effects on clover stands and yield, and total intercrop biomass. Berseem clover cultivars varied for forage yield, stand, maturity, damage due to disease and insects, and effects on intercrop biomass. In one environment, only one of seven berseem clover cultivars survived after the first forage harvest. Adding oat to berseem clover reduced total forage and weed yields, clover stands, and relative maturity of clover, but increased total crop biomass and forage plant health. Adding berseem clover to oat did not reduce oat grain or straw yields, and in one year increased oat test weight. Cultivar rankings of each species differed in monoculture vs. intercrop. Interspecific cultivar interactions were not significant for most traits. Greater genetic improvement in the productivity of the oat–berseem clover intercrop will more likely be achieved by improvement of general agronomic productivity of berseem clover than by trying to enhance specific ecological combining ability of particular oat and berseem clover cultivar combinations.

ANNUAL crop production rotations in much of the north-central USA are dominated by corn (*Zea mays* L.) and soybean [*Glycine max* (L.) Merr.]. Crookston et al. (1991) suggested that adding at least a third crop to the corn–soybean rotation could improve the yields of both crops. Problems of pathogens (e.g., soybean cyst nematode, *Heterodera glycines* Ichinohe), weeds, high input costs, soil erosion, and increased economic risk associated with corn–soybean rotations could be alleviated by using more diverse rotations (Liebman and Dyck, 1993; Schmitt, 1991; Wrather et al., 1992).

Forages and oat are important alternative crops in the north-central USA. Despite the benefits of including forages and oat in crop rotations, many farmers are unwilling to plant crop land to perennial forages or to devote large areas to oat because of the low economic value relative to corn and soybean. An intercrop of oat underseeded with an annual forage legume, such as berseem clover, may have potential as an important third rotation crop by fitting in easily with the dominant

cropping pattern and by providing better economic returns than an oat sole crop (Ghaffarzadeh, 1997).

Berseem clover produces excellent quality forage over several harvests in one year. Brink and Fairbrother (1992) demonstrated that the forage quality of berseem clover is at least equal to other clover species such as red clover (*T. pratense* L.), white clover (*T. repens* L.), and subterranean clover (*T. subterraneum* L.). In addition, berseem clover does not induce bloat in animals (Knight, 1985), and it has good late-season vigor. Oat is an excellent companion crop for forage legume establishment (Forsberg and Reeves, 1995), and in the north-central USA most forage legumes are established with an oat companion crop (Simmons et al., 1992; Tesar and Marble, 1988). Oat can be harvested for grain, chopped for green silage, or grazed, providing a multi-purpose crop that offers flexible management alternatives to growers. Ghaffarzadeh (1997) demonstrated that addition of berseem clover to oat increased the total crop biomass without reducing oat grain yield, improved the profitability of the system, contributed N to the succeeding corn crop, and improved the yield of the succeeding corn crop.

An understanding of intraspecific variation for companion cropping performance will help plant breeders improve the components of the oat–berseem intercrop. Different cultivars within the two species vary for gross morphological and growth habit characters such as plant height, leaf size and orientation, tillering or branching habit, and time from planting to flowering, as well as early and late vigor, biomass production, yield potential, grain or forage quality, and disease resistance. Elucidation of interspecific interactions in intercrops, if they exist, could help breeders develop ideotypes of each species to guide future breeding efforts.

Variation among small-grain cultivars for their effects on a common forage legume companion crop has been reported (Collister and Kramer, 1952; Flanagan and Washko, 1950; Nickel et al., 1990; Simmons et al., 1995). The companion cropping performance of small grains may be specific to particular varieties of the legume species, and vice versa. Nielsen et al. (1981) combined five oat and five alfalfa (*Medicago sativa* L.) cultivars in factorial combinations to measure interference of the two crops with each other. They found that specific combinations of oat and alfalfa cultivars caused reductions in oat grain yield or alfalfa yield.

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Abbreviations: DAP, days after planting; GECA, general ecological combining ability; GIA, general intercropping ability; GIR, general intercropping response; GMA, general monoculture ability; SECA, specific ecological combining ability; μ , the mean of all monoculture values.

Plant breeders almost exclusively select for genotypes to be grown as monocultures. If the correlation between the sole crop and the average intercrop performance of a cultivar is sufficiently high, selection under sole-crop conditions will improve cultivars intended for intercrops. If not, the alternative approach of breeding for performance in mixture with other species may be a sensible approach to improving crop plants for use in crop mixtures.

Interactions between the intercrop component species may be general (independent of the cultivars tested) or specific for particular cultivar combinations (Hill, 1996; Zimmermann, 1996). Hill (1990) discussed the issue of cultivar interactions in intercrops in relation to general and specific ecological combining ability (GECA and SECA, respectively), terms coined by Harper (1967) as analogies to general and specific combining ability of hybrid crops (Sprague and Tatum, 1942). If cultivar interactions are important, selection for SECA should be taken into account in the cultivar development process (Hill, 1996), and specific combinations of cultivars should be recommended to farmers. Federer et al. (1982) and Gizlice et al. (1989) developed statistical methodology to partition general combining ability for cultivar blend response into components due to cultivar responses observed in pure stands and additional responses observed in blends that cannot be accounted for by pure-stand responses. Here we extend their model and analysis from diallel treatment designs of cultivar blends to factorial designs of intercrops.

The general intercropping ability (GIA) of a cultivar is similar to its GECA, but also provides information on the mean superiority of intercrops compared with monocultures. Relative differences among cultivars are identical, whether measured in terms of GIA or GECA. GIA can be partitioned into general monoculture ability (GMA), representing cultivar differences observed in monoculture, and general intercropping response (GIR), representing mean cultivar differences observed in intercrops that cannot be accounted for by differences observed in monoculture. Significant GIR differences among cultivars of the same species would indicate that cultivar differences observed in intercrops cannot be predicted from monoculture evaluations.

Our objectives were (i) to determine if variation for intercropping performance exists among oat cultivars and among berseem clover cultivars and (ii) to determine the relative importance of general and specific ecological combining ability effects for oat-berseem clover intercrops.

MATERIALS AND METHODS

1995 Experiment

A field experiment was planted on 2 May at the Agronomy and Agricultural Engineering Research Farm west of Ames, IA, in a Nicollet loam soil (fine-loamy, mixed, superactive, mesic Aquic Hapludolls), following a corn crop from the previous year. Prior to seeding, soil was amended with 45 kg ha⁻¹ P₂O₅ and 134 kg ha⁻¹ K₂O. No herbicide treatments were used. Eight oat cultivars (Bay, Dane, Don, Ogle, Prairie, Sheldon, Starter, and Troy) and seven berseem clover cultivars (Bigbee,

CW8902, CW8903, CW9092, CW9300, Joe Burton, and Multicut) were grown alone and in all possible intercrop combinations. A check entry of 'Vernal' alfalfa monoculture was included, for a total of 72 entries. Entries were arranged in a randomized complete block design with three replications. All oat cultivars were developed in the north-central USA. All berseem clover cultivars were developed in California, except Bigbee, which was developed in Mississippi. Oat seeding was at a rate of 323 seeds m⁻² in plots consisting of four 3.6-m rows spaced 0.3 m apart. Berseem clover was overseeded immediately following oat planting, using a 1.5-m-wide Brillion-type planter at a rate of 10.7 kg ha⁻¹. All plots were bordered on the sides with one row of Ogle oat and on the ends with 1.8-m-wide alleys planted to a mixture of Ogle oat and Bigbee berseem clover.

Heading dates of oat were estimated as the day after planting (DAP) on which the first node of the rachis was emerged on at least 50% of the plants in the plot. Plant heights of both species in each plot were measured after all oat cultivars had headed completely (72 DAP).

Clover maturity, weed and clover stands, and plant health were rated visually on each plot at 93 DAP, using five-point scales. Clover maturity was scored as 1 = early bud stage; 2 = 10% bloom; 3 = 50% bloom, some seedheads present; 4 = 100% bloom, many seedheads; and 5 = post flowering, seedheads only. Weed and clover stands were scored as 1 = 0–20%, 2 = 21–40%, 3 = 41–60%, 4 = 61–80%, and 5 = 81–100% ground cover. Plant health score of forage plots was based on disease symptoms and potato leafhopper [*Empoasca fabae* (Harris)] feeding damage. Diseases present included fusarium wilt (caused by *Fusarium* spp.), spring blackstem (caused by *Phoma* spp.), and summer blackstem (caused by *Cercospora* spp.). Damage due to disease and insects was not differentiated, because both causal agents were present simultaneously and how much of the damage was due to each one was not clear. Plant health (representing disease symptom incidence and potato leafhopper feeding damage) was scored based on percentage of leaves discolored: 1 = 0–20%, 2 = 21–40%, 3 = 41–60%, 4 = 61–90%, and 5 = 100% (leaves and stems necrotic).

All plots were harvested at 93 DAP, when all oat cultivars had reached grain maturity. Total grain yield and total combined biomass of straw, forage, and weeds were measured from every plot. Forage did not contribute to total biomass of oat sole-crop plots, nor did oat grain and straw contribute to clover sole-crop total biomass. A hand-sample of biomass, excluding grain, was collected from each plot, weighed, dried for 1 wk at 60°C, and separated into straw, clover, and weed components. Each component was weighed separately, to estimate percentage of oat, clover, and weeds in each plot and to calculate the total dry matter yield of each component from each plot. A 0.92-m-wide section through the middle of each forage monoculture plot was harvested with a flail-type harvester. A second forage harvest was made on 3 October.

1996 Experiment

Similar treatment and experimental designs and plot techniques were used as in 1995, except that the poorest performing cultivars from 1995 were replaced with a broader diversity of germplasm. Prairie oat was replaced with 'Pal', and the new forage assortment was six berseem clover entries (Bigbee, CW8902, and Joe Burton as in the previous year, and new entries Exp CB, 'Nilodi', and 'Elite') and one nondormant alfalfa entry ('Mecca II'). Exp CB is a germplasm from Mississippi, Nilodi a cultivar from Italy, and Elite a cultivar from Australia. The experiment was planted on 10 April at the

Agronomy and Agricultural Engineering Research Farm, west of Ames, and on 12 April at the Northeast Research Farm, south of Nashua, IA. At Nashua, the soil type was a Readlyn loam (fine-loamy, mixed, mesic Aquic Hapludolls). Previous crop and fertilizer amendments at Ames were identical to those in 1995. The Nashua experiment was preceded by soybean in the previous year, and no fertilizer amendments were used. No herbicide treatments were used at either location.

At the first grain and forage harvest at both locations, each plot was rated visually for forage and weed stands, forage maturity, and forage plant health using the five-point scales described above. A second forage harvest was taken on 2 October at Ames and on 25 October at Nashua.

Grain harvests were staggered according to grain maturity of oat plots. At Ames, the Dane, Done, Sheldon, Starter, and no-oat plots were harvested at 104 DAP, Ogle and Pal plots at 109 DAP, and Troy and Bay plots at 113 DAP. At Nashua, the Don, Dane, Sheldon, Starter, and no-oat plots were harvested at 105 DAP; other plots were harvested at 112 DAP. Total biomass was dried, weighed, and separated into oat grain, oat straw, forage, and weed components. Forage monoculture plots were harvested with a 0.9-m-wide sickle-bar mower.

Statistical Analyses

We extended the Federer et al. (1982) model for diallel treatment design for pure-line and biblend mixtures of a single crop; that model itself is based on Gardner and Eberhart's (1966) model for analysis of inbred lines of maize and their diallel crosses. Our modification takes into account the factorial (rather than diallel) treatment structure of the intercrops, and the fact that not all variables can be measured on all sole-crop treatments. Phenotypic values of intercrops and sole crops were modeled as follows. For intercrops,

$$Y_{hij} = \mu + \rho_h + \tau_{O_i} + \tau_{F_j} + \delta_{O_i} + \delta_{F_j} - \bar{\delta} + \lambda_{ij} + \epsilon_{hij} \quad [1]$$

For oat monocultures,

$$Y_{hi} = \mu + \rho_h + \tau_{O_i} + \epsilon_{hi} \quad [2]$$

For forage monocultures,

$$Y_{hj} = \mu + \rho_h + \tau_{F_j} + \epsilon_{hj} \quad [3]$$

where terms are defined analogously to Federer et al. (1982): μ is the mean of all monoculture values; ρ_h is the h th environmental effect or the h th block effect; τ_{O_i} is the GMA effect of the i th oat cultivar, which is the deviation of the i th oat cultivar monoculture from the mean of all monocultures; τ_{F_j} is the GMA effect of the j th forage cultivar, which is the deviation of the j th forage cultivar monoculture from the mean of all monocultures; δ_{O_i} is the GIR effect of the i th oat cultivar grown as an intercrop; δ_{F_j} is the GIR effect of the j th forage cultivars grown as an intercrop; $\bar{\delta}$ is the mean GIR effect averaged over all oat cultivars or over all forage cultivars (the mean oat and forage GIR effects are equal and represent the mean difference between monocultures and intercrops); λ_{ij} is the SECA effect of cultivars i and j when grown together in an intercrop; and ϵ_{hij} represents a random error component for analyses conducted on observations within a single environment or a random cultivar \times environment interaction effect for analyses based on treatment means from different environments.

Following from this parameterization, $\bar{\tau}_{O_i}$ and $\bar{\tau}_{F_j}$ are constrained to zero when the trait being considered is measured on only one species—otherwise, they are not; $\bar{\tau}_{O_i}$ necessarily

equals $-\bar{\tau}_{F_j}$ only when the number of forage cultivars equals the number of oat cultivars; and $\bar{\delta}$ is not constrained to zero; however, $\bar{\lambda}_{i..} = \bar{\lambda}_{.j} = \bar{\lambda}_{..} = 0$.

The following mean values are defined.

1. The mean of the i th oat cultivar in monoculture = $\mu + \tau_{O_i}$
2. The mean of the j th forage cultivar in monoculture = $\mu + \tau_{F_j}$
3. The mean of all intercrops with the i th oat cultivar = $\mu + \tau_{O_i} + \bar{\tau}_{F_j} + \delta_{O_i} + \bar{\delta}_{F_j} - \bar{\delta} + \bar{\lambda}_{i..} = \mu + \tau_{O_i} + \bar{\tau}_{F_j} + \delta_{O_i}$
4. The mean of all intercrops containing the j th forage cultivar = $\mu + \bar{\tau}_{O_i} + \tau_{F_j} + \delta_{F_j}$
5. The mean of all intercrops = $\mu + \bar{\tau}_{O_i} + \bar{\tau}_{F_j} + \bar{\delta}$.

We define general intercropping ability (GIA) of the i th oat cultivar as the mean deviation of intercrops containing the i th cultivar from the mean monoculture value:

$$GIA_i = \mu + \tau_{O_i} + \bar{\tau}_{F_j} + \delta_{O_i} - \mu = \tau_{O_i} + \bar{\tau}_{F_j} + \delta_{O_i} \quad [4]$$

Similarly, we define general intercropping ability (GIA) of the j th forage cultivar as the mean deviation of intercrops containing the j th cultivar from the mean monoculture value:

$$GIA_j = \mu + \bar{\tau}_{O_i} + \tau_{F_j} + \delta_{F_j} - \mu = \bar{\tau}_{O_i} + \tau_{F_j} + \delta_{F_j} \quad [5]$$

Thus, GIA includes the cultivar's effect in monoculture, its response to intercropping, and the mean effect of the companion species observed in monoculture.

Statistical analyses were conducted using PROC GLM of SAS (SAS Inst., 1990). Data from 1995 and 1996 were analyzed separately, because different cultivars were tested in each year. The total sum of squares of each variable was partitioned into sources due to the model effects described above. This analysis is a nonorthogonal partitioning of the sums of squares, as is the original Gardner–Eberhart (1966) analysis of diallel crosses, so effects were fitted sequentially, as recommended by Hallauer and Miranda (1988).

Forage and Oat Traits

Forage Traits

The experiment was initially analyzed as a one-way treatment structure of 72 entries to estimate the error variance and the mean difference between forage traits in intercrops and sole crops. Estimates of μ and GMA effects were obtained from analysis of forage sole-crop entries alone. For forage traits (such as forage yield and forage stand score), GMA effects were estimated only for forage cultivars since oat monocultures have zero GMA effects for forage traits. GMA effects from this analysis sum to zero.

A second analysis was conducted to estimate GIR effects of cultivars and SECA effects on intercrops. By subtracting μ and GMA effects from each intercrop value, we obtained residual values of intercrop entries ($\rho_h + \delta_{O_i} + \delta_{F_j} - \bar{\delta} + \lambda_{ij} + \epsilon_{hij}$), which were analyzed as a complete factorial to obtain estimates of GIR and SECA effects of the component cultivars. The mean GIR of all forage cultivars equals the mean GIR of all oat cultivars, and represents the mean difference between intercrops and sole crops. Consequently, it is not constrained to be zero. GIA was calculated by summing GIR and GMA.

Oat Traits

Oat traits (such as grain and straw yield and heading date) were analyzed in a manner analogous to the forage traits (i.e., by switching forage and oat in the description above).

Combined Traits

Traits such as total biomass or weed stand were measured on all entries, including monocultures of both crops. The experiment was first analyzed as a one-way treatment structure to estimate the error variance and the mean differences between (i) forage and oat monocultures, (ii) intercrops and forage monocultures, and (iii) intercrops and oat monocultures. The overall mean, μ , was estimated as the mean of all sole crops of both species. The GMA effect of each forage cultivar was estimated as the deviation of its mean from the overall monoculture mean. The GMA effect of each oat cultivar was estimated as the deviation of its mean from the overall monoculture mean. The mean GMA effect across cultivars of one species is not constrained to equal zero. In a second analysis, the GMA effects of both component cultivars and μ were subtracted from the intercrop entry values to obtain intercrop entry residuals, which were then analyzed to provide estimates of GIR effects of component cultivars and SECA effects of intercrops. Correlations among traits in intercrops were based on entry means from each environment.

RESULTS AND DISCUSSION

Effects of Intercropping

The mean values of oat traits did not differ between sole crops and intercrops, except for test weight in 1996 (Tables 1, 2, and 3). For example, the mean oat grain yield, μ , in 1996 was 2489 kg ha⁻¹ for monocultures and 2456 kg ha⁻¹ ($\mu + \bar{\delta} = 2489 - 33$ kg ha⁻¹) for intercrops, a nonsignificant difference (Table 3). The effect of intercropping on test weight in 1996 was positive: intercrop entries had mean test weights 2% higher than sole crops. Overall, adding berseem clover as a companion crop to oat did not reduce the productivity or value of the oat crop. Intercrop entries had lower weed stand scores than oat sole crops in 1995 ($\mu + \bar{\tau}_O + \bar{\tau}_F + \bar{\delta} = 3.2 - 1.4 = 1.8$ vs. $\mu + \bar{\tau}_O = 3.2 - 1.1 = 2.1$) (Table 2) and than forage sole crops in both years (Tables 4 and 5). Intercrop entries also had higher total biomass than either oat or forage sole crops in both years (Tables 1, 3, 4,

and 5, and data not shown). Adding berseem clover to oat added 501 kg ha⁻¹ total biomass in 1995 ($P < 0.001$; data not shown) and 1049 kg ha⁻¹ ($P < 0.001$) in 1996, as shown by the difference between mean GIA ($\bar{\tau}_O + \bar{\tau}_F + \bar{\delta}$) and GMA effects ($\bar{\tau}_O$): 3180 - 2131 = 1049 kg ha⁻¹ (Table 3). Negative effects of intercropping were observed on some forage traits: forage stands, heights, and yields were lower in intercrops than in sole crops in both years (Tables 4 and 5). In intercrops, total forage yields were reduced about 50%, forage maturity at first harvest was delayed, and mean forage plant health was improved in both years compared with monocultures (Tables 4 and 5). In summary, adding an oat companion crop to berseem clover reduced the productivity of berseem clover, but the intercrops as a whole exhibited higher total productivity (as measured by total biomass) and were more suppressive of weeds than either oat or berseem clover sole crops. These results are generally congruent with those from five years of large-scale evaluations in Iowa by Ghaffarzadeh (1997).

Oat Cultivar Effects

When grown as sole crops, oat cultivars varied for straw yield, test weight, heading date, and height in both years, and for grain yield in 1996 (Tables 1, 2, and 3). After accounting for these differences in monoculture (GMA effects), additional differences were observed in intercrops (GIR effects) for these same variables in both years, except for straw yield in 1995 (Tables 1, 2, and 3). The mean square due to oat cultivars among intercrops for grain yield per se represents GIA variance, while the corresponding mean square calculated based on yield residuals (intercrop values minus GMA effects) represents GIR variance. Because the GIA variance was greater than the GIR variance for grain yield (Table 1), we conclude that GMA effects were more important than GIR effects for grain yield in 1996. Differences among oat cultivars were also observed for GIR effects on forage traits (stand, height, and yield) in both years,

Table 1. Analysis of variance results for oat grain yield, total legume forage yield, and total biomass in 1996.†

| Source of variation† | df | Grain yield | | df | Forage yield | | df | Biomass | |
|-------------------------------------|----|---------------------|-----------------------|----|---------------------|-----------------------|----|---------------------|-----------------------|
| | | MS _{yield} | MS _{resid} ‡ | | MS _{yield} | MS _{resid} ‡ | | MS _{yield} | MS _{resid} ‡ |
| | | ×10 ³ § | | | ×10 ⁴ § | | | ×10 ⁴ § | |
| Environments | 1 | 191 | | 1 | 1 530 | | 1 | 341 | |
| Oat vs. forage monocultures | 0 | | | 0 | | | 1 | 15 569*** | |
| Oat monocultures vs. intercrops | 1 | 15 | | 0 | | | 1 | 1 541*** | |
| Forage monocultures vs. intercrops | 0 | | | 1 | 1 183*** | | 1 | 39 242*** | |
| Among oat monocultures (GMA) | 7 | 209*** | | 0 | | | 7 | 49 | |
| Among forage monocultures (GMA) | 0 | | | 6 | 72*** | | 6 | 61*** | |
| Among intercrops | 55 | 162*** | 58** | 55 | 34 | 80*** | 55 | 72*** | 137*** |
| Oat (GIA or GIR)¶ | 7 | 1 081*** | 107*** | 7 | 72*** | 72*** | 7 | 217*** | 327*** |
| Forage (GIA or GIR)¶ | 6 | 60*** | 60*** | 6 | 140*** | 323*** | 6 | 96*** | 376*** |
| Oat × Forage (SECA) | 42 | 24 | 24 | 42 | 12 | 12 | 42 | 29 | 29 |
| Genotype × environment interactions | 63 | 31 | | 63 | 26 | | 71 | 33 | |

*** Significant at the 0.05 and 0.001 probability levels, respectively.

† GMA, general monoculture ability; GIA, general intercropping ability; GIR, general intercropping response; SECA, specific ecological combining ability; GECA, general ecological combining ability.

‡ MS_{resid}: mean squares based on intercrop entry residuals remaining after adjustment by subtracting the mean of all monoculture values (μ) and GMA effects.

§ Actual values equal reported values times the indicated factor.

¶ Mean squares for the variable per se correspond to variance due to GIA (or GECA). Mean squares for the intercrop residuals adjusted for GMA effects correspond to variance due to GIR.

Table 2. Oat GMA, GIR, and GIA effects estimated at Ames, IA (1995).†

| Cultivar | Oat traits | | | | | | | | | | | | Forage traits‡ | | | | | | | | | | | |
|------------|-------------|------|------|-------------|------|------|----------|-----|-----|--------------|------|------|----------------|------|------|---------|---------|------|--------|-------|------|------------|------|-----|
| | Grain yield | | | Straw yield | | | Test wt. | | | Heading date | | | Height | | | Stand | | | Yield§ | | | Weed stand | | |
| | GMA | GIR | GIA | GMA | GIR | GIA | GMA | GIR | GIA | GMA | GIR | GIA | GMA | GIR | GIA | GMA | GIR | GIA | GMA | GIR | GIA | GMA | GIR | GIA |
| Bay | -127 | -131 | -258 | 800 | -249 | 552 | -29 | -11 | -40 | 7.0 | 0.1 | 7.1 | 0.9 | 1.0 | 1.8 | -1.1 | -5.4 | -239 | -1.7 | -1.2 | -1.7 | -1.2 | -1.6 | |
| Dane | 33 | -6 | 27 | -132 | -33 | -165 | 7 | -2 | 6 | -4.6 | 0.3 | -4.3 | -6.8 | 1.7 | -5.1 | -0.6 | -7.5 | -168 | -0.5 | -2.0 | -0.5 | -2.0 | -1.2 | |
| Don | 127 | -137 | -9 | -656 | 100 | -555 | 16 | 4 | 20 | -2.6 | 0.2 | -2.4 | -5.8 | 3.9 | -1.9 | -0.5 | -5.4 | -162 | -1.5 | -1.3 | -1.5 | -1.3 | -1.5 | |
| Ogle | 131 | 27 | 158 | 221 | -265 | -44 | -14 | 10 | -4 | 0.4 | 0.0 | 0.4 | 2.6 | 0.3 | 2.9 | -0.8 | -6.7 | -209 | -1.5 | -1.3 | -1.5 | -1.3 | -1.5 | |
| Prairie | -219 | 250 | 32 | 152 | -97 | 55 | -15 | -5 | -20 | 0.7 | -0.3 | 0.4 | -2.1 | 1.6 | -0.5 | -0.9 | -7.1 | -291 | -0.7 | -2.0 | -0.7 | -2.0 | -1.3 | |
| Sheldon | 187 | -92 | 95 | -323 | 56 | -267 | -5 | -3 | -8 | -1.6 | 0.0 | -1.6 | 7.9 | -0.1 | 7.8 | -0.5 | -4.0 | -258 | -0.7 | -2.1 | -0.7 | -2.1 | -1.4 | |
| Starter | -170 | -54 | -223 | -876 | 117 | -759 | 26 | 13 | 39 | -4.2 | 0.4 | -3.8 | -9.9 | 3.8 | -6.1 | -0.2 | -8.4 | -181 | -1.2 | -1.3 | -1.2 | -1.3 | -1.2 | |
| Troy | 37 | 144 | 181 | 714 | -126 | 588 | 13 | -13 | 0 | 5.0 | -0.1 | 4.9 | 13.2 | 2.1 | 15.4 | -1.1 | -3.8 | -277 | -1.3 | -1.4 | -1.3 | -1.4 | -1.4 | |
| Mean | 0 | 0 | 0 | 0 | -65 | -65 | 0 | -1 | -1 | 0.0 | 0.1 | 0.1 | 0.0 | 1.9 | 1.9 | -0.7*** | -6.0*** | -223 | -1.1 | -1.6* | -1.1 | -1.6* | -1.4 | |
| µ±± | 2102 | | | 2227 | | | 475 | | | 56.8 | | 92.0 | | | | | | | | | 3.2 | | | |
| LSD (0.05) | NS | 126 | 126 | 867 | NS | 328 | 25 | 9 | 9 | 0.9 | 0.3 | 0.3 | 7.1 | 2.7 | 2.7 | 0.4 | 2.8 | 99 | NS | NS | 0.4 | 0.4 | 0.4 | |

*, ***, Significant at the 0.05 and 0.001 probability levels, respectively.

† GMA, general monoculture ability; GIR, general intercropping response; GIA, general intercropping ability; GECA, general ecological combining ability.

‡ GMA effects of oat cultivars are zero for all forage traits, so GIR = GIA = GECA for such traits.

§ First-cut forage harvest yield.

¶ Weed stand GIA effects are the sum of cultivar GMA and GIR effects plus the mean GMA effect of forages (+1.3; Table 4).

DAP, days after planting.

** Stand density scores are on a five-point scale: 1 = <20% to 5 = >80% ground cover.

*** µ, the mean of all monoculture values.

Table 3. Oat GMA, GIR, and GIA effects estimated at Ames and Nashua, IA (1996).†

| Cultivar | Oat traits | | | | | | | | | | | | Forage traits‡ | | | | | | | | | | | | | | |
|------------|-------------|------|------|-------------|------|------|----------|-------|-----|--------------|------|------|----------------|------|-------|--------------|---------|---------|----------|---------|---------|---------|------|---------|--------------------|-----|-----|
| | Grain yield | | | Straw yield | | | Test wt. | | | Heading date | | | Height | | | Plant health | | | Maturity | | | Yield§ | | | Total crop biomass | | |
| | GMA | GIR | GIA | GMA | GIR | GIA | GMA | GIR | GIA | GMA | GIR | GIA | GMA | GIR | GIA | GMA | GIR | GIA | GMA | GIR | GIA | GMA | GIR | GIA | GMA | GIR | GIA |
| Bay | -489 | 19 | -470 | 517 | -272 | 245 | -21 | 20 | 0 | 5.9 | 0.0 | 5.9 | 2.5 | -4.4 | -1.9 | -11.7 | -1.7 | -1.1 | -1.2 | -1411 | -1.2 | -1.2 | 2162 | 2855 | 2581 | | |
| Dane | 347 | -167 | 179 | -54 | -225 | -279 | -23 | 16 | -7 | -3.4 | -0.1 | -3.6 | -2.5 | 2.6 | 0.1 | -10.3 | -0.8 | -1.2 | -0.5 | -935 | -0.5 | -0.5 | 2481 | 3172 | 3217 | | |
| Don | 292 | -34 | 258 | -781 | 281 | -499 | 10 | 10 | 20 | -3.8 | -0.1 | -3.8 | -14.5 | 6.0 | -8.5 | -8.4 | -0.9 | -1.3 | -0.6 | -839 | -0.6 | -0.6 | 1591 | 3971 | 3126 | | |
| Ogle | -60 | 7 | -53 | 517 | -8 | 509 | -3 | 15 | 12 | 1.3 | 0.1 | 1.4 | 6.2 | -1.5 | 4.6 | 8.6 | -1.2 | -1.0 | -1.0 | -1006 | -1.0 | -1.0 | 2576 | 3560 | 3699 | | |
| Pall | -68 | -145 | -213 | -455 | -419 | -874 | -53 | 5 | -48 | 1.6 | 0.1 | 1.7 | -10.5 | -1.3 | -11.8 | -5.0 | -0.8 | -0.8 | -0.3 | -763 | -0.3 | -0.3 | 1504 | 3321 | 2389 | | |
| Sheldon | 324 | -42 | 282 | 270 | -98 | 172 | 32 | 11 | 43 | -0.4 | 0.0 | -0.4 | 15.5 | -5.8 | 9.7 | -9.4 | -1.4 | -1.3 | -0.9 | -968 | -0.9 | -0.9 | 2832 | 3335 | 3731 | | |
| Starter | 68 | -2 | 66 | -573 | 246 | -327 | 37 | 1 | 39 | -2.4 | 0.6 | -1.8 | -0.8 | 3.1 | 2.3 | -7.0 | -1.2 | -1.1 | -0.8 | -717 | -0.8 | -0.8 | 1684 | 4006 | 3254 | | |
| Troy | -413 | 100 | -313 | 559 | 85 | 644 | 20 | 12 | 33 | 1.3 | 0.5 | 1.7 | 4.2 | 7.4 | 11.5 | -12.6 | -1.4 | -1.4 | -1.1 | -1162 | -1.1 | -1.1 | 2218 | 3655 | 3438 | | |
| Mean | 0 | -33 | -33 | 0 | -51 | -51 | 0 | 11*** | 11 | 0.0 | 0.1 | 0.1 | 0.0 | 0.8 | 0.8 | -9.1*** | -1.2*** | -1.2*** | -0.8*** | -975*** | -0.8*** | -0.8*** | 2131 | 3485*** | 3180 | | |
| µ±± | 2489 | | | 4015 | | | 534 | | | 77.1 | | 96.8 | | | | | | | | | | | 4415 | | | | |
| LSD (0.05) | 350 | 132 | 132 | 704 | 266 | 266 | 21 | 8 | 8.0 | 1.0 | 0.4 | 0.4 | 13.8 | 5.2 | 5.2 | 4.7 | 0.3 | 0.3 | 0.3 | 384 | 0.3 | 0.3 | NS | 434 | 434 | | |

*, ***, Significant at the 0.001 probability levels; NS, not significant at the 0.05 level.

† GMA, general monoculture ability; GIR, general intercropping response; GIA, general intercropping ability.

‡ GMA effects of oat cultivars are zero for all forage traits, so GIR = GIA for such traits.

§ Total forage yield from two harvests.

¶ Biomass GIA effects are the sum of cultivar GMA and GIR effects plus the mean GMA effect of forages (-2436 kg ha⁻¹; Table 5).

DAP, days after planting.

** Scores are on a five-point scale; stand density, 1 = <20% to 5 = >80% ground cover; plant health, 1 <20% leaves discolored to 5 = stems and leaves necrotic; maturity, 1 = early bud stage to seedhead stage.

*** µ, the mean of all monoculture values.

Table 4. Forage GMA, GIR, and GIA effects estimated at Ames, IA (1995). Except for the check (Vernal alfalfa), the forage entries are berseem clover.

| Cultivar | Forage traits | | | | | | | | | | | | Total crop biomass [‡] | | | | | | Weed yield | | | | | | Weed stand | | | | | | | |
|------------|---------------|------|--------------|------|----------|------|--------|------|-----------------|------|-----------------|------|---------------------------------|------|------|------|-------|-------|------------|-----|------|------|------|------|------------|------|------|------|------|------|------|-----|
| | Stand | | Plant health | | Maturity | | Height | | Yield (1st cut) | | Yield (1st cut) | | GMA | | GIR | | GIA | | GMA | | GIR | | GIA | | GMA | | GIR | | GIA | | | |
| | GMA | GIR | GMA | GIR | GMA | GIR | GMA | GIR | GMA | GIR | GMA | GIR | GMA | GIR | GMA | GIR | GMA | GIR | GMA | GIR | GMA | GIR | GMA | GIR | GMA | GIR | GMA | GIR | GMA | GIR | GIA | |
| Bigbee | 0.4 | 0.4 | 0.8 | -1.4 | -0.1 | -1.5 | -0.8 | -0.4 | -4.8 | 139 | -4 | 135 | 1224 | 1232 | 3072 | 1484 | -1398 | -867 | 1.5 | 2.0 | -1.6 | -1.4 | -1.4 | -1.4 | -1.4 | -1.4 | -1.4 | -1.4 | -1.4 | -1.4 | -1.4 | |
| CW8902 | -0.4 | -0.3 | -0.7 | 0.6 | -1.1 | -0.5 | 0.2 | -0.7 | -7.0 | 101 | -377 | -276 | -912 | 1210 | 914 | 1012 | -1034 | -974 | 0.8 | 1.1 | -1.4 | -1.4 | -1.4 | -1.4 | -1.4 | -1.4 | -1.4 | -1.4 | -1.4 | -1.4 | -1.4 | |
| CW8903 | -0.1 | -0.7 | -0.8 | 0.6 | -1.0 | -0.3 | -0.1 | -0.9 | -4.9 | -20 | -226 | -246 | -1201 | 1312 | 727 | 844 | -628 | -737 | 1.5 | 1.6 | -1.4 | -1.4 | -1.4 | -1.4 | -1.4 | -1.4 | -1.4 | -1.4 | -1.4 | -1.4 | -1.4 | |
| CW9092 | 0.1 | -1.0 | -0.9 | 0.0 | -0.4 | -0.4 | 0.0 | -0.6 | -3.4 | -80 | -190 | -270 | -1153 | 1120 | 583 | 952 | -934 | -935 | 1.3 | 1.8 | -1.4 | -1.4 | -1.4 | -1.4 | -1.4 | -1.4 | -1.4 | -1.4 | -1.4 | -1.4 | -1.4 | |
| CW9300 | 0.6 | -1.6 | -1.0 | -0.5 | -0.1 | -0.7 | -0.1 | -0.6 | -7.1 | 160 | -455 | -295 | -613 | 847 | 850 | 1252 | -1143 | -844 | 1.0 | 1.1 | -1.4 | -1.4 | -1.4 | -1.4 | -1.4 | -1.4 | -1.4 | -1.4 | -1.4 | -1.4 | -1.4 | |
| Joe Burton | -0.2 | -1.0 | -1.3 | 0.1 | -0.5 | -0.4 | 0.7 | -1.6 | -6.0 | -221 | -106 | -327 | -1015 | 1014 | 615 | 1231 | -1131 | -854 | 1.5 | 1.8 | -1.4 | -1.4 | -1.4 | -1.4 | -1.4 | -1.4 | -1.4 | -1.4 | -1.4 | -1.4 | -1.4 | |
| Multicut | -0.4 | -0.6 | -1.0 | 0.6 | -1.0 | -0.4 | 0.0 | -1.3 | -6.0 | -79 | -204 | -283 | -1257 | 1087 | 446 | 848 | -924 | -1029 | 1.2 | 1.5 | -1.4 | -1.4 | -1.4 | -1.4 | -1.4 | -1.4 | -1.4 | -1.4 | -1.4 | -1.4 | -1.4 | |
| Vernal | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| (check)# | -0.4 | 0.3 | 0.3 | -3.3 | -0.6 | -0.9 | 0.0 | -0.9 | -16.0 | -390 | 0 | -223 | -704 | 1117 | 1073 | 1089 | -1027 | -891 | 1.3 | 1.6 | -1.6 | -1.4 | -1.4 | -1.4 | -1.4 | -1.4 | -1.4 | -1.4 | -1.4 | -1.4 | -1.4 | |
| Mean | 0.0 | -0.7 | 0.0 | -0.6 | -0.6 | -0.9 | 0.0 | -0.9 | 33.7 | 402 | 92 | 4065 | 326 | 326 | 1688 | 547 | 1688 | 268 | 3.2 | 3.2 | 3.2 | 3.2 | 3.2 | 3.2 | 3.2 | 3.2 | 3.2 | 3.2 | 3.2 | 3.2 | 3.2 | 3.2 |
| μ | 3.4 | 2.7 | 2.7 | 3.3 | 3.3 | 3.3 | 3.3 | 3.3 | 33.7 | 402 | 92 | 4065 | 326 | 326 | 1688 | 547 | 1688 | 268 | 3.2 | 3.2 | 3.2 | 3.2 | 3.2 | 3.2 | 3.2 | 3.2 | 3.2 | 3.2 | 3.2 | 3.2 | 3.2 | 3.2 |
| LSD (0.05) | NS | 1.2 | 1.2 | 1.2 | 0.4 | 0.4 | NS | 0.3 | NS | 2.6 | 261 | 92 | 1313 | NS | 464 | NS | 268 | 268 | NS | 0.4 | 0.4 | NS | NS | NS | NS | NS | NS | NS | NS | NS | NS | NS |

*** Significant at the 0.05 and 0.001 probability levels, respectively.
 † GMA, general monoculture ability; GIR, general intercropping response; GIA, general intercropping ability.
 ‡ Total crop biomass includes second-cut forage yields, which were taken only on Bigbee berseem clover due to complete stand loss of other cultivars.
 § Biomass, weed yield, and weed score GIA effects are the sum of cultivar GMA and GIR effects plus the mean GMA effect of oat cultivars (660 kg ha⁻¹ biomass, -953 kg ha⁻¹ weed yield, and -1.1 weed stand).
 ¶ Scores are on a five-point scale: stand density, 1 = <20% to 5 = >80% ground cover; plant health, 1 <20% leaves discolored to 5 = stems and leaves necrotic; maturity, 1 = early bud stage to 5 = seedhead stage.
 # Vernal (check) effect is not included in overall effects mean; it is computed as a deviation from μ (the mean of all monoculture effects).

Table 5. Forage GMA, GIR, and GIA effects estimated at Ames and Nashua, IA (1996). Except for Mecca II alfalfa and the check (Vernal alfalfa), the forage entries are berseem clover.

| Cultivar | Forage traits | | | | | | | | | | | | Total crop biomass [‡] | | | | | | Weed yield | | | | | | Weed stand | | | | | | | |
|-----------------|---------------|------|--------------|------|----------|------|--------|------|-----------------|-------|-----------------|-------|---------------------------------|-------|------|------|-------|-------|------------|-----|------|------|------|------|------------|------|------|------|------|------|------|----|
| | Stand | | Plant health | | Maturity | | Height | | Yield (1st cut) | | Yield (1st cut) | | GMA | | GIR | | GIA | | GMA | | GIR | | GIA | | GMA | | GIR | | GIA | | | |
| | GMA | GIR | GMA | GIR | GMA | GIR | GMA | GIR | GMA | GIR | GMA | GIR | GMA | GIR | GMA | GIR | GMA | GIR | GMA | GIR | GMA | GIR | GMA | GIR | GMA | GIR | GMA | GIR | GMA | GIR | GIA | |
| Bigbee | 0.4 | -1.1 | -0.7 | -0.6 | -0.7 | -1.3 | 0.1 | -0.6 | -4.0 | 741 | -1263 | -522 | -96 | -1536 | 2999 | 3594 | -1558 | -1684 | 1.1 | 1.2 | -1.2 | -1.2 | -1.2 | -1.2 | -1.2 | -1.2 | -1.2 | -1.2 | -1.2 | -1.2 | -1.2 | |
| Exp. CB | -0.1 | -1.2 | -1.3 | -0.7 | -0.6 | -1.4 | 0.2 | -0.9 | -11.7 | -37 | -8.0 | -1089 | -8 | -3191 | 4213 | 3153 | -2752 | -1693 | 1.5 | 1.6 | -1.2 | -1.2 | -1.2 | -1.2 | -1.2 | -1.2 | -1.2 | -1.2 | -1.2 | -1.2 | -1.2 | |
| CW8902 | 0.6 | -1.5 | -0.8 | -0.2 | -1.0 | -1.2 | 1.0 | -1.3 | -5.3 | 916 | -1671 | -755 | -100 | -2014 | 3079 | 3196 | -1633 | -1676 | 1.6 | 1.7 | -1.2 | -1.2 | -1.2 | -1.2 | -1.2 | -1.2 | -1.2 | -1.2 | -1.2 | -1.2 | -1.2 | |
| Elite | 0.3 | -1.5 | -1.2 | -0.5 | -0.9 | -1.4 | 0.3 | -0.8 | -8.3 | -431 | -676 | -1107 | 29 | -2504 | 3549 | 3176 | -1872 | -1689 | 1.3 | 1.3 | -1.1 | -1.1 | -1.1 | -1.1 | -1.1 | -1.1 | -1.1 | -1.1 | -1.1 | -1.1 | -1.1 | |
| Joe Burton | -0.7 | -0.8 | -1.6 | 0.5 | -2.0 | -1.5 | -0.4 | -0.8 | -1.2 | -2.7 | -5.3 | -1072 | 2 | -2946 | 3947 | 3132 | -2585 | -1687 | 1.2 | 1.1 | -1.0 | -1.0 | -1.0 | -1.0 | -1.0 | -1.0 | -1.0 | -1.0 | -1.0 | -1.0 | -1.0 | |
| Mecca II | -0.8 | -0.5 | -1.3 | 1.5 | -1.5 | 0.0 | -2.0 | 0.1 | -1.9 | -13.7 | -3.2 | -844 | 71 | -2491 | 3614 | 3254 | -1521 | -1670 | 1.0 | 0.9 | -1.0 | -1.0 | -1.0 | -1.0 | -1.0 | -1.0 | -1.0 | -1.0 | -1.0 | -1.0 | -1.0 | |
| Nilodi | 0.2 | -1.6 | -1.4 | 0.2 | -1.5 | -1.3 | 0.8 | -1.4 | -9.7 | -99 | -1339 | -1437 | -71 | -2365 | 2990 | 2757 | -1571 | -1674 | 1.2 | 1.2 | -1.2 | -1.2 | -1.2 | -1.2 | -1.2 | -1.2 | -1.2 | -1.2 | -1.2 | -1.2 | -1.2 | |
| Vernal (check)# | -0.2 | 0.8 | 0.8 | -1.3 | -10.6 | -0.6 | -0.8 | -0.8 | -9.1 | 334 | 0 | -975 | -33 | -2436 | 3485 | 3180 | -1928 | -1682 | 1.3 | 1.3 | -1.3 | -1.1 | -1.1 | -1.1 | -1.1 | -1.1 | -1.1 | -1.1 | -1.1 | -1.1 | -1.1 | |
| Mean | 0.0 | -1.2 | -1.2 | 0.0 | -1.2 | -1.2 | 0.0 | -0.8 | 36.4 | 2156 | 359 | 4415 | 1925 | 1925 | 3180 | 1966 | 1966 | 537 | 2.8 | 2.8 | 2.8 | 2.8 | 2.8 | 2.8 | 2.8 | 2.8 | 2.8 | 2.8 | 2.8 | 2.8 | 2.8 | |
| μ | 4.1 | 3.1 | 3.1 | 3.1 | 3.1 | 3.1 | 3.1 | 3.1 | 36.4 | 2156 | 359 | 4415 | 1925 | 1925 | 3180 | 1966 | 1966 | 537 | 2.8 | 2.8 | 2.8 | 2.8 | 2.8 | 2.8 | 2.8 | 2.8 | 2.8 | 2.8 | 2.8 | 2.8 | 2.8 | |
| LSD (5%) | 0.9 | 0.3 | 0.3 | 0.8 | 0.3 | 0.3 | 0.9 | 0.3 | 12.5 | 4.4 | 1015 | 124 | 406 | 406 | 406 | 1517 | 537 | NS | NS | NS | NS | NS | NS | NS | NS | NS | NS | NS | NS | NS | NS | NS |

*** Significant at the 0.001 probability level; NS, not significant at the 0.05 level.
 † GMA, general monoculture ability; GIR, general intercropping response; GIA, general intercropping ability.
 ‡ Total crop biomass includes second-cut forage yields, which were taken only on Bigbee berseem clover due to complete stand loss of other cultivars.
 § Biomass, weed yield, and weed score GIA effects are the sum of cultivar GMA and GIR effects plus the mean GMA effect of oat cultivars (2131 kg ha⁻¹ biomass, -1720 kg ha⁻¹ weed yield, and -1.1 weed stand).
 ¶ Scores are on a five-point scale: stand density, 1 = <20% to 5 = >80% ground cover; plant health, 1 <20% leaves discolored to 5 = stems and leaves necrotic; maturity, 1 = early bud stage to 5 = seedhead stage.
 # Vernal (check) effect is not included in overall effects mean; it is computed as a deviation from μ (the mean of all monoculture effects).

on weeds in 1995, and on plant health and total biomass in 1996 (Tables 2 and 3). If oat cultivars all responded similarly to intercrops and monocultures, all GIR effects would be zero. Oat cultivars differed for GIR effects for most traits, indicating that intercrop performance cannot be predicted based on monoculture results. The large contribution to GIA by GMA effects for most traits, however, implies that the differences between monoculture and intercrop performance for such traits are relatively small.

Correlation analysis identified characteristics of oat cultivars associated with companion cropping ability. Grain yield was not correlated with forage yield, but straw yield was negatively correlated with forage yield in 1996 ($r = -0.55$, $P = 0.0001$). These results suggest that oat cultivars with high yield and high harvest index would be best for both grain production and companion cropping performance. Oat height at grain maturity was negatively correlated with forage maturity ($r = -0.39$, $P = 0.003$ for 1995; $r = -0.31$, $P = 0.02$ for 1996), but not with total forage yield. Oat heading date, however, was negatively correlated with forage stand in both years ($r = -0.35$, $P = 0.008$ for 1995; $r = -0.28$, $P = 0.04$ for 1996) and with total forage yield in 1996 ($r = -0.43$, $P = 0.001$).

Bay, the latest-heading but not the tallest oat cultivar tested, had the most severe effects on total forage yields in 1996 and forage stand scores in both years (as seen by its large, negative GIR effect), indicating that it was highly competitive with its forage companion (Tables 2 and 3). Additionally, Bay had the lowest weed score GIA in 1995, and the lowest grain yield GIA in both years. In contrast, Starter was both earlier heading and shorter than average and had the smallest negative GIA (and GIR) effect on forage yield in 1996, indicating that it provided less intercropping competition than other oat cultivars.

Our results suggest that heading date rather than oat height may be more strongly associated with the competitiveness of oat on a forage companion crop. Previous experiments on the effects of small-grain height on companion crops have produced inconsistent results. Flanagan and Washko (1950), Collister and Kramer (1952), and Nickel et al. (1990) reported that taller small-grain cultivars were associated with lower companion forage stands. Simmons et al. (1995), however, reported no overall differences between companion crop performance of conventional and semidwarf small-grain cultivars. Late-maturing oat cultivars often tiller excessively during their extended vegetative growth phase, which might explain the clover and weed growth suppression observed with Bay in our study.

Berseem Clover Effects

A long period of extremely hot, humid weather in 1995 killed most plants of berseem clover cultivars other than Bigbee. In this environment, second-cut forage yield data were made taken only for Bigbee berseem clover plots.

Forage cultivars varied for GMA effects on plant

health and forage yield in both years, while variation for GMA for stand, maturity, height, and total biomass was observed in 1996 only (Tables 1, 4, and 5). Forage cultivars did not differentially affect oat straw yield or test weight in either year, but small differences ($P < 0.10$) existed among forage cultivar GIR effects on oat grain yield in 1996 (Table 5). GIR effects were more important than GMA effects for forage yield in 1996, as indicated by the larger mean square due to forage cultivars among intercrops based on GIR residuals compared with that based on forage yield per se (Table 1). Forage cultivars varied for GIR effects on forage stand, plant health, maturity, height, and yield, and weeds in both years, and on total biomass in 1996 (Tables 4 and 5). These results suggest that the considerable variability among berseem clover cultivars observed in intercrops for important agronomic traits may be missed (neither observed nor predicted) in monoculture evaluations.

Bigbee was the most consistently high-performing berseem clover cultivar across environments. Bigbee ranked first for forage yield and stand GIA in both years (Tables 4 and 5). Importantly, as Bigbee was the only berseem clover cultivar to survive beyond the first harvest in 1995, this trial proved valuable for identifying berseem clover cultivars with unstable yield potential in Iowa. Bigbee had higher forage yield in monoculture than the Vernal alfalfa monoculture check in both years and outyielded Mecca II nondormant alfalfa in both monoculture and intercrops (Table 5). Given that berseem clover forage quality is at least equal to alfalfa (Knight, 1985), and that berseem clover has superior tolerance to potato leafhoppers, Bigbee is a logical choice for annual forage production in the north-central USA. In general, most of the berseem clover cultivars, with the exception of Bigbee and possibly CW8902, appeared to be poorly adapted to Iowa conditions and produced suboptimal forage yields.

General Ecological Combining Ability

Hill (1996) defined GECA as the deviation in performance of a cultivar (or species) from the mean of all mixtures. In terms of our model, $GECA_i = \tau_{oi} - \bar{\tau}_o + \delta_{oi} - \bar{\delta}$ for the i th oat cultivar. We define GIA in terms of the monoculture mean, μ , and GIA can be converted to Hill's GECA by subtracting the sum of the mean GMA values for both species and the mean GIR value from the GIA value: $GECA_i = GIA_i - (\bar{\tau}_o + \bar{\tau}_f + \bar{\delta})$. When the trait under consideration is measured on only one of the component species, both $\bar{\tau}_o$ and $\bar{\tau}_f$ equal zero, and $GECA_i = GIA_i - \bar{\delta}$. Cultivar differences are identical whether measured in terms of GIA or GECA, because the two parameters differ only by a constant value. Here, we computed GIA values, because they provide information on the general superiority or inferiority of intercrops compared with monocultures as well as on differences among cultivars in mixtures but GECA provides only the latter.

GECA can be estimated even if no monoculture entries are present in an experiment. However, if monoculture entries are included, GMA, GIR, and GIA can be

Table 6. Correlations between mean GMA (general monoculture ability) and GIA (general intercropping ability) estimates of oat cultivars and forage cultivars.

| Oat cultivars | | Forage cultivars | |
|---------------|-------------|------------------|-------------|
| Trait | Correlation | Trait | Correlation |
| Grain yield | 0.89*** | Forage yield | NS |
| Height | 0.99*** | Height | 0.71** |
| Heading date | 0.99*** | Maturity | 0.85*** |
| Straw yield | 0.98*** | Plant health | 0.69** |
| Test weight | 0.93*** | Stand | NS |
| Biomass | 0.82*** | Biomass | NS |
| Weed stand | 0.72* | Weed stand | NS |
| | | Weed yield | NS |

*, **, *** Significant at the 0.05, 0.01, and 0.001 probability levels, respectively.

estimated also. Because cultivar variation for GIA is identical to variation for GECA, we conclude that there was significant variation for GECA among cultivars of both species for most traits measured. Partitioning GIA into GMA and GIR provided further insight into the nature of cultivar variation for intercropping performance. For most oat traits, GECA differences among oat cultivars could be explained in large part by responses observed in monoculture (GMA effects). Conversely, we found that, although forage cultivars differed for GECA for many traits, these differences generally could not be explained by GMA effects.

Specific Ecological Combining Ability

Specific ecological combining ability was a significant source of variation only for oat heading date in 1995. Our results differ from Nielsen et al. (1981), who reported interactions among oat and alfalfa cultivars for grain and forage yield, suggesting that companion cropping performance is specific to particular cultivar combinations.

The effort required to conduct factorial intercropping experiments to identify superior specific combinations of oat and berseem clover cultivars from among many possible combinations increases dramatically as the number of cultivars or genotypes of the two species increases. Since SECA was not significant for any yield components in our study, SECA experiments are not warranted. The major limitation to the improvement of oat-berseem clover intercrops in the north-central USA is the limited agronomic variability among berseem clover cultivars in this region. All cultivars except Bigbee died after the first harvest in 1995, due to the combined effects of disease, potato leafhopper damage, and heat.

A breeding program designed to improve the general agronomic characters of berseem clover, such as disease resistance and environmental adaptation, would (for now) be more profitable than evaluating specific ecological combining ability. If a greater variety of well-adapted cultivars or populations were available, SECA might become a more important source of variation for yield components of the intercrop. Thus, the importance of oat-berseem clover interactions needs to be reconsidered if a number of agronomically suitable berseem clover cultivars become available.

Breeding for Intercrops

Correlations between GMA and GIA effects of oat cultivars for various oat traits were high, indicating that monoculture evaluations can be used to predict intercrop performance of oat for such traits (Table 6). Conversely, low, nonsignificant correlations were noted for forage cultivars, with the exception of height, maturity, and plant health. For the agronomically important traits of forage yield and stand, monoculture evaluations of forages do not predict intercrop performance. Similarly, oat cultivar effects on forage yield of companion crops cannot be reliably predicted based on monoculture performance. Thus, selection and evaluation of cultivars intended for intercropping systems must be practiced in conjunction with the companion crop. Because SECA effects were not present in this study, GECA could be evaluated by growing various cultivars or breeding lines of one species with one or a few testers of the other species. A selected set of tester lines or cultivars, representing extreme phenotypes with which the companion species would need to interact, could be used during selection without necessitating evaluation of all possible cultivar combinations of the two species.

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Estimation of Nitrogen Fixed by Legumes in Long-Term vs. Short-Term Cropping Systems

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ABSTRACT

A critical evaluation of legumes should consider both the above- and belowground contribution to N₂ fixation. Based on the amount of N in crops and correcting for the changes of soil N as a result of cropping, 15 equations are presented for estimation of the apparent net amount of atmospheric N₂ fixed by legumes grown in short- and long-term cropping systems. In the final equation, all components of a legume-cereal rotation system were considered. In estimating N₂ fixation, including in the equation the non-N₂-fixing crop that follows the legume in the rotation is an innovation of the method, in addition to the system approach concept. The validity and accuracy of each equation in estimating N₂ fixation by legumes is discussed. An example is provided using data from long-term vetch-barley (*Vicia sativa* L.–*Hordeum vulgare* L.) rotation studies in Cyprus. The estimated amount of apparent net N₂ fixation by vetch was 184 kg N ha⁻¹, a quantity twice that usually estimated using only the aboveground vetch production. This result shows the importance of calculating apparent net N₂ fixation by considering above- and belowground system components.

COMPREHENSION of the true value of legumes for increased productivity, as well as a source of N, will encourage the use of legumes and thus a sustainable farming practice. These values have been demonstrated with rotation studies in many countries (e.g., Clarke and Russell, 1977; Heichel, 1987). In long-term rotation studies in Cyprus, research has proven consistently that legumes lead to an environmentally correct cropping system, with higher productivity (Papastylianou, 1993b), greater income for farmers (Papastylianou and Panayiotou, 1993), and lower N fertilizer requirements (Papastylianou, 1993b). As use of chemicals becomes both an environmental and food quality problem, and the world searches and emphasizes sustainability (NRC, 1991; FAO, 1994), now is the time to reevaluate the rotation approach suggested by Theophrastus (Enquiry into Plants, ix.1) in the 4th century BCE, when chemicals were not available: κύαμος ... οὐ βαρὺ καὶ ἔτι κοπρῖζειν

δοκεῖ τῆν γῆν... “Beans ... [are] not a burdensome crop to the ground, they even seem to manure it...” (Theophrastus, 1932, p. 198–199). Adoption of that classical approach requires adjustments for minimum inputs based on innovations that have occurred in the many centuries since, such as varieties, insect control, or intensified production.

Farming systems based on legumes maintain productivity of the land for many generations. Since the development of N fertilizer technology, monoculture of non-N₂-fixing crops has been the dominant practice. The N₂ previously provided by legumes has been replaced by N fertilizer produced with an energy cost. The proposals of the LISA program (Low-Input Sustainable Agriculture) to minimize chemical input (Schaller, 1991) seem to be forgotten. Examples that indicate the values of legumes could encourage reevaluation of what a low-input sustainable farming system actually means, while demonstrating increased productivity and maintenance of natural resources.

The major advantage derived from using legumes in rotation with other crops is atmospheric N₂ fixation. The legume-bacteria symbiosis provides legumes with N for growth and metabolism and there is an increase of soil N following the legumes (e.g., Heichel, 1987). Several methods for calculating the N₂ fixed by legumes have been proposed. The most widely used methods are the difference method, N accumulation, the acetylene reduction technique, and ¹⁵N methodology. For detailed reviews of these methods, see La Rue and Patterson (1981) and Danso (1995). The difference and accumulation methods are based on the standard N analysis by the Kjeldahl determination and can be applied without any other equipment. Their simplicity and low cost make these methods attractive, especially where extensive laboratory facilities are not available.

The N accumulation method assumes that the total N produced by a legume is fixed from the atmosphere. The difference method is based on the amount of N produced by a legume and a reference non-N₂-fixing crop. One of the major criticisms for the difference method is that it does not consider soil N changes under

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