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Evaluation of the Afila-Tendriled Acacia (*afaf–tactac*) Pea Foliage Type under Minimal Competition

Irwin L. Goldman* and Earl T. Gritton

ABSTRACT

The afila (*af*) and tendriled-acacia (*tac*) genes condition structural modifications of the pea (*Pisum sativum* L.) leaf. The *af* gene replaces leaflets with tendrils and *tac* restores small leaflets to the tendrils of *af* plants. The agronomic performance of plants carrying *tac* in combination with *af* is unknown. Therefore, the objective of this research was to evaluate a near-isogenic set of three foliage types: normal (*AfAf–TacTac*), afila (*afaf–TacTac*), and afila–tendriled acacia (*afaf–tactac*) in three genetic backgrounds. The evaluation was conducted under minimally competitive conditions on widely spaced wire trellises in order to allow for maximal foliage expression. Averaged across genetic backgrounds, *tac* increased the total foliage area of *afaf–tactac* plants over *afaf–TacTac* plants by 37%. Green pea yield did not differ significantly among the three foliage types. Dry seed yield of *afaf–tactac* plants was significantly higher than *afaf–TacTac* plants and equal to *AfAf–TacTac* plants. Expression of the *tac* gene varied significantly with genetic background. The *afaf–tactac* combination in the latest-maturing background exhibited the largest increases in yield and yield components over its constituent foliage types.

THE AFILA (*af*) and tendriled acacia (*tac*) genes condition structural modifications of the pea leaf. The *af* gene, first described by Kujala (1953), when present in the homozygous recessive condition, replaces leaflets with tendrils (Fig. 1). The *tac* gene, first isolated in 1972 following chemical mutagenesis with diethyl sulfate (Sharma, 1972), restores small leaflets to the tendrils of *af* plants when similarly homozygous. The resulting *afaf–tactac* phenotype under greenhouse conditions is characterized by a proliferation of tendrils that terminate in leaflets similar in shape to those found on normal-foliage plants (Marx, 1987). The *afaf–tactac* foliage type has not previously been studied from an agronomic standpoint.

The normal (*AfAf–TacTac*) pea foliage type has several limitations: e.g., a dense canopy that shades lower plant parts, a reduction of light penetration into the understory and corresponding decrease in photosynthetic activity of the lower leaves, a lack of color uniformity of shelled peas due to shading, and a potential buildup of pathogens due to reduced drying in the moist lower-canopy environment. A modification of foliage type with the *af* and *tac* genes has the potential to alleviate these problems. Efforts to remedy these disadvantages have resulted in adoption of the *afaf–TacTac* (also known as semi-leafless) foliage type in many regions of the world.

Investigations of the predicted advantages of *afaf–TacTac* have produced mixed results. Heath and Hebblethwaite (1985a) demonstrated that *afaf–TacTac* was able to convert intercepted light radiation into dry matter with the same efficiency as *AfAf–TacTac*. Reduced lodging (Davies, 1977; Heath and Hebblethwaite, 1985b) and yields similar to *AfAf–TacTac* (Davies, 1977; Goldenberg, 1973) have been reported in *afaf–TacTac*. Wehner and Gritton (1981) showed a superior standing ability and reduced blonding of shelled peas in *afaf–TacTac*, and no significant yield differences between *afaf–TacTac* and *AfAf–TacTac*. Cardi

I.L. Goldman, Dep. of Agronomy, 1102 S. Goodwin Ave., Univ. of Illinois, Urbana, IL 61801; and E.T. Gritton, Dep. of Agronomy, 1575 Linden Dr., Univ. of Wisconsin–Madison, Madison, WI 53706-1597. Research supported by the College of Agric. and Life Sciences, Hatch project 142-2804, and the Midwest Food Processors Assoc. Received 27 Mar. 1991. *Corresponding author.

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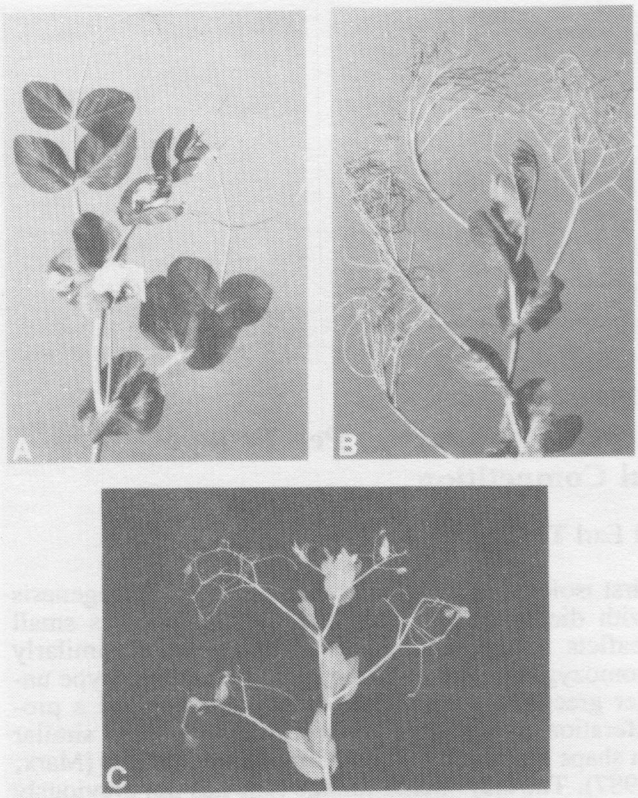


Fig. 1. The three pea foliage types used in this study: (A) normal foliage (*AfAf–TacTac*), (B) semi-leafless foliage (*afaf–TacTac*), and (C) afila–tendriled acacia foliage (*afaf–tactac*).

et al. (1987), on the other hand, measured a yield reduction in *afaf–TacTac* due to decreased number of pods and fertile nodes. The *afaf–TacTac* type had lower yield than *AfAf–TacTac* when planted at similar population densities (Gonzalez-Lauck, 1990). The yield response of *afaf–TacTac* has been shown to be background-specific (Lafond et al., 1981), with yield levels of *afaf–TacTac* lower than *AfAf–TacTac* in some backgrounds.

Despite the potential benefits that *tac* could offer the already-established *afaf–TacTac* foliage type in the form of increased photosynthetic area, there have been no published studies on the performance or potential utility of the *afaf–tactac* combination. In addition, little information is available on the response of altered pea foliage types to varying levels of interplant competition. Widely spaced wire trellises, commonly used in pea breeding nurseries, provide a minimally competitive environment characterized by maximal foliage expression that is ideal for investigation of these questions. Our objective was to evaluate the field performance of *afaf–tactac* in comparison with *afaf–TacTac* and normal foliage (*AfAf–TacTac*) near-isolines in a range of genetic backgrounds in an environment that allowed for minimal interplant competition and maximal foliage expression.

MATERIALS AND METHODS

Genetic Material

Included in the study were normal foliage (*AfAf–TacTac*), semi-leafless foliage (*afaf–TacTac*), and afila–tendriled acacia foliage (*afaf–tactac*) (Fig. 1) near-isogenic lines in three genetic backgrounds: 'Alsweet 4683', 'Frontier', and 'Dark Skin Perfection'. Alsweet 4683 is an early-maturing canning pea cultivar, while Frontier and Dark Skin Perfection represent midseason canning and late-maturing freezing cultivars, respectively. The three foliage types will be referred to by their gene symbols throughout this report. The *tac* gene was obtained from B. Sharma (Division of Genetics, Indian Agricultural Research Institute, New Delhi) and incorporated via the backcross procedure. The sixth backcross was made in the fall of 1986, and the BC_6F_1 plants were grown in the greenhouse in the spring of 1987. All near-isolines were BC_6F_5–derived at the beginning of the study.

Cultural Practices and Experimental Design

Four replicates of a split-plot arrangement of a randomized complete-block design were planted in 3.05-m linear plots along one side of wire trellises in 1988 and 1989 at the Arlington Agricultural Research Station, Arlington, WI, on Plano silt loam soil (fine-silty, mixed, mesic Typic Argiudoll) and in 1989 at the West Madison Agricultural Research Station, Madison, WI, also on Plano silt loam soil. Planting dates were 21 Apr. 1988, and 26 Apr. and 4 May 1989 at Arlington and West Madison, respectively. Seeds were spaced 2.5 cm apart. Genetic background was assigned to the whole plot and foliage type was assigned to the subplot. The wire trellis environment is commonly used by pea breeders as a way to evaluate germplasm (Gritton, 1980). Trellises are characterized by little interplant competition and the absence of lodging, due to the twining of tendrils on wires. Trifluralin (α-α-α-trifluoro-2,6-dinitro-*N*,*N*-dipropyl-*p*-toluidine) was incorporated prior to planting at a rate of 0.17 L ha^{-1} in all environments to control weeds. Supplemental weeding was by hand. On 3 June 1988, 100 cm of irrigation water was applied to the plots.

Table 1. Significance of mean squares from the analysis of variance for 17 pea traits combined across three foliage types, three genetic backgrounds, and three trellis environments.

	Source of variation†					
	G	G×E	F	F×E	G×F	G×F×E
df	2	4	2	4	4	8
Foliage area components						
Stipule area	**	NS	**	NS	NS	NS
Tendril area	**	NS	**	*	*	NS
Stem area	**	NS	*	NS	*	NS
Total foliage area	**	NS	**	NS	**	NS
Yield and yield components						
Lowest pod-bearing node	**	NS	**	*	NS	NS
Pods per node	**	*	NS	NS	NS	NS
Total pod-bearing nodes	NS	NS	NS	NS	**	NS
Pods	*	NS	NS	NS	**	NS
Peas	**	NS	NS	NS	**	NS
Peas per pod	**	NS	NS	NS	NS	NS
Pods per plant	*	NS	NS	NS	NS	NS
Green pea yield	**	NS	NS	NS	NS	NS
Dry seed yield	**	NS	**	NS	NS	NS
Agronomic traits						
Bloom date	*	*	NS	NS	NS	NS
Total plant dry weight	**	NS	*	NS	NS	NS
Vine length	NS	NS	**	NS	*	NS
Nodes	**	NS	*	NS	NS	NS

*,** Significant at the 0.05 and 0.01 probability levels, respectively.
† Sources of variation are G = genetic background, E = environment, F = foliage type.

Table 2. Mean performance of seven traits for three pea foliage types in three genetic backgrounds across three environments grown on wire trellises.

	Genetic background and foliage type									
	Alsweet 4683			Frontier			Dark Skin Perfection			
	Af–Tac	*af–Tac*	*af–tac*	*Af–Tac*	*af–Tac*	*af–tac*	*Af–Tac*	*af–Tac*	*af–tac*	LSD (0.05)†
Tendril area, cm^2	23.6	62.3	42.5	69.9	152.5	134.8	80.1	176.7	188.0	25.4
Stem area, cm^2	30.9	34.5	37.0	62.3	47.3	53.5	40.3	62.2	78.4	10.0
Total foliage area, cm^2	229.6	204.0	221.8	499.7	321.7	414.4	624.7	408.4	667.5	102.9
Total pod-bearing nodes, no.	3.8	4.1	3.3	2.9	2.7	3.4	3.5	3.5	4.9	0.6
Pods, no.	4.0	4.2	3.3	4.7	4.6	5.3	4.8	4.8	6.5	0.9
Peas, no.	16.2	18.5	12.3	25.6	24.7	25.3	26.1	24.4	32.8	4.1
Vine length, cm	55.0	61.3	66.6	61.7	61.8	68.0	59.3	55.7	55.2	6.7

† Difference among genetic background × foliage type means greater than the value in this column indicates significance at the 0.05 level.

Sampling Procedures

A 0.91-m section of plants was removed from the center of each plot at the green pea harvest stage (≈100 tenderometer, the optimal harvest stage for commercially processed peas), placed into an airtight plastic bag, and transported to Madison for analysis. All three foliage types in a given genetic background were removed simultaneously. Since sufficient material for tenderometer evaluation was not available in this study, harvest decisions were based on tenderometer readings of similar cultivars in an adjacent variety trial.

Five plants were chosen randomly from the harvest sample and separated for their constituent foliage and yield components. Areas of stem, stipule, tendril plus petiole, leaflet, and *tac* leaflet were measured on a LI-COR (Lincoln, NE) 3100 leaf area meter for each five-plant bulk. Areas of tendril (plus petiole) and stem were converted by $\pi/2$ (Harvey and Goodwin, 1978) to account for their cylindrical shape. Total foliage area was calculated as the sum of all constituent foliage components for a given foliage type. The lowest pod-bearing node was recorded as the first node at which a fully developed pod appeared.

Yield components measured included pods per node, total pod-bearing nodes, pods per plant, peas per plant, peas per pod, pods per plant, and green pea yield. Dry seed yield was measured at Arlington in 1988 and 1989 as the weight of dry peas from the remainder of the plot. Bloom date was recorded as the date at which 50% of the plants in a plot exhibited exposed petals. Foliage components were dried for 48 h at 56 °C and weighed. Total plant dry weight was calculated as the sum of all dried foliage components for a given foliage type. Vine length and number of nodes per plant were measured on the five-plant sample. One replicate from Arlington in 1989 and two replicates from Madison in 1989 were lost due to spoilage of the samples. Data in this report are thus based on nine replicates.

Table 3. Mean performance of three pea foliage types across three genetic backgrounds and three trellis environments.

	Foliage type			
	AfAf-TacTac	*afaf-TacTac*	*afaf-tactac*	LSD (0.05)†
Foliage area components				
Stipule area, cm^2	201.57	197.76	251.52	32.92†
Tendril area, cm^2	57.04	130.48	118.67	14.44
Stem area, cm^2	53.89	47.98	55.52	5.71
Total foliage area, cm^2	484.98	376.22	489.34	48.48
Yield and yield components				
Lowest pod-bearing node, no.	12.95	13.25	13.56	0.37
Dry seed yield, g $plot^{-1}$	223.99	190.77	211.93	20.42
Agronomic traits				
Total plant dry weight, g	6.71	5.91	6.81	0.69
Vine length, cm	58.54	59.60	63.40	3.17
Nodes, no.	16.33	16.66	17.26	0.79

† Difference between foliage type means greater than the value in this column indicates significance at the 0.05 level.

Statistical Analysis

All statistical analyses were performed using the GLM procedure of SAS (SAS Inst., Cary, NC). Each year–location combination was designated an environment. All effects in the analysis, with the exception of environment, were considered fixed. Type III sums of squares were used to calculate mean squares due to the presence of unbalanced data. Comparisons among means were made by least significant difference. Foliage type means within genetic backgrounds across environments were compared when the interaction of genetic background × foliage type was significant. Alternatively, foliage type means across genetic backgrounds and environments were used.

RESULTS AND DISCUSSION

Foliage Area Components

The genetic background × foliage type × environment interaction was not significant for any of the foliage area components (Table 1). A significant interaction of genetic background × foliage type was detected for tendril area, stem area, and total foliage area. The effect of genetic background was significant for stipule, tendril, stem, and total foliage areas. This result is in agreement with other reports (Lafond et al., 1981) suggesting that performance of altered pea foliage types is background-specific. In the Alsweet 4683 background, total foliage area did not differ between the three foliage types, while in the Frontier background, total foliage area was highest for *AfAf–TacTac* (Table 2). In the Dark Skin Perfection background, total foliage area was similar for *AfAf–TacTac* and *afaf–tactac*. Dark Skin Perfection is the latest-maturing of the three backgrounds and, given its slightly longer phenology, *afaf–tactac* in this background may have been capable of adding more *tac* leaflet area. Evidence for this is suggested in results from a companion study that indicate the area due to *tac* leaflets continues to increase throughout the growing season (Goldman et al., 1992).

Stipule area was significantly greater in *afaf–tactac*

than in *AfAf–TacTac* or *afaf–TacTac* (Table 3). Harvey (1976) reported an increase in the stipule area of *afaf–TacTac*; however, in our study no difference in stipule area was detectable between *AfAf–TacTac* and *afaf–TacTac*. Our finding that addition of the *af* gene does not significantly change stipule area in *afaf–TacTac* compared with *AfAf–TacTac* is in agreement with results reported by Wehner and Gritton (1981), although we observed a change in the percentage of total foliage area due to stipules. The percentage of total foliage area due to stipules was 42% in *AfAf–TacTac*, in contrast to 51% in *afaf–tactac* and 53% in *afaf–TacTac*. This difference may be attributed to an epistatic effect between *af* and genes conditioning stipule size (*st*) since both types expressed greater stipule area as a percent of total leaf area. The *Af* locus has been shown to interact with other loci controlling foliage morphology. Cardi et al. (1987) demonstrated that nonallelic interactions of *Af* and *St* significantly affected pea yield components. In addition, *af*, reduced stipule (*st*), and acacia (*tl*) were found to exhibit pleiotropic effects on all traits measured by these investigators.

Significant foliage type × environment interaction was detected for tendril area. Significant foliage-type effects were detected for tendril area, stem area, and total foliage area (Table 1). As expected, based on the presence of *af*, *afaf–TacTac* and *afaf–tactac* were similar for tendril and stem area and had far greater tendril area than *AfAf–TacTac* (Table 3). Stem area of *AfAf–TacTac* and *afaf–tactac* was equal and significantly larger than for *afaf–TacTac*. Increases in plant height and number of nodes (discussed under Agronomic traits, below) support the observation that stem area also increased in *afaf–tactac*. The *AfAf–TacTac* and *afaf–tactac* types had similar total foliage area, and both exceeded *afaf–TacTac*. This result is in agreement with a companion study (Goldman et al., 1992) that demonstrated that *AfAf–TacTac* and *afaf–tactac* had the same total foliage area.

Yield and Yield Components

The genetic background × foliage type × environment interaction was not significant for any of the yield and yield-component traits measured (Table 1). The genetic background × environment interaction was significant only for number of pods per node. The genetic background × foliage-type interaction was significant for total pod-bearing nodes, pods, and peas. For each of these characteristics, *afaf–tactac* in the Dark Skin Perfection background, the latest-maturing of the three backgrounds, was superior to its *afaf–TacTac* and *AfAf–TacTac* counterparts (Table 2). Most of the foliage type × environment interactions were nonsignificant. As with foliage traits, the effect of genetic background was significant for most traits, suggesting a similar pattern of background specificity for yield and yield components that was measured with identical genetic material grown under high levels of interplant competition in row plots (Goldman et al., 1992). With the exception of lowest pod-bearing node and dry seed yield, no significant differences between foliage types were detected for any of the yield components measured (Table 1).

The lowest pod-bearing node was significantly higher in *afaf–tactac* than in *AfAf–TacTac* (Table 3). The lowest pod-bearing node is a varietal characteristic and remains relatively constant for a given genotype. The higher lowest pod-bearing node measured in *afaf–tactac* suggests that *tac* may interact with genes affecting flower initiation. Evidence for this observation may be found in the slightly later (1 d) bloom dates of *afaf–tactac* in the Frontier background (data not shown). Dry seed yield of *afaf–tactac* and *AfAf–TacTac* were superior to *afaf–TacTac*. Thus, yield differences not present at the processing stage became evident later in the growing season. This finding is supported in part by the fact that *tac* leaflet area continues to increase throughout the season (Goldman et al., 1992), and thus may make a larger contribution toward dry seed yield than toward green pea yield. This would indicate that field pea cultivars and other *Pisum* genotypes grown for their dry seed may be able to take full advantage of the *afaf–tactac* foliage type.

Agronomic Traits

No significant genetic background × folige type × environment interaction was detected for the agronomic traits measured (Table 1). The genetic background × environment interaction was significant for bloom date, and the effect of genetic background was significant for all agronomic traits except vine length. Nonsignificant foliage type × environment interaction and significant foliage-type effects were detected for three out of four agronomic traits. Total dry weight of *AfAf–TacTac* and *afaf–tactac* was significantly greater than that observed for *afaf–TacTac*. The *afaf–tactac* type had greater vine length and more nodes than its *AfAf–TacTac* counterpart in the Alsweet and Frontier backgrounds, but not in Dark Skin Perfection (Table 3). This result was also noted under high levels of interplant competition in row plots in a separate study (Goldman et al., 1992).

CONCLUSIONS

The minimally competitive environment of this study allowed for maximal vegetative growth. *AfAf–TacTac* and *afaf–tactac* had equal total foliage area. Although differences among the three foliage types were detected for a number of performance traits, no significant green pea yield advantage was measured for *afaf–tactac*. However, *afaf–tactac* had a significantly greater dry seed yield than *afaf–TacTac*. In addition, several foliage and yield-component traits of *afaf–tactac* in the later-maturing genetic background were significantly greater than those measured in *afaf–TacTac*. At present, only *afaf–tactac* lines in later-maturing genetic backgrounds should be able to capitalize on whatever agronomic benefits may be obtained from *tac* in a minimally competitive environment.

When grown on wire trellises, *afaf–tactac* plants exhibit larger values for all aspects of plant stature than their *AfAf–TacTac* and *afaf–TacTac* counterparts. Plant height, number of nodes, stem area, and lowest-pod bearing node were all significantly higher for *afaf–tactac* plants than for the other foliage types. Despite these increases, *afaf–tactac* did not exhibit a yield advantage over semi-leafless peas when grown on wire trellises.

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Evaluation of the Afila-Tendriled Acacia (*afaf–tactac*) Pea Foliage Type under High Competition

Irwin L. Goldman,* Earl T. Gritton, and Patrick J. Flannery

ABSTRACT

The afila (*af*) gene replaces pea (*Pisum sativum* L.) leaflets with tendrils, and the tendriled-acacia (*tac*) gene restores small leaflets to the tendrils of *af* plants. The agronomic performance of plants homozygous for both *af* and *tac* has not been studied. A near-isogenic set of three foliage types: normal (*AfAf–TacTac*), semi-leafless (*afaf–TacTac*), and afila–tendriled acacia (*afaf–tactac*) in three genetic backgrounds was evaluated for 2 yr in two locations using a normal plant population for pea grown for processing. The objective of the study was to measure performance of *afaf–tactac* in comparison with *afaf–TacTac* and *AfAf–TacTac* at high levels of interplant competition. At the green pea harvest stage, the total foliage area of *afaf–tactac* plants was 10% greater than for *afaf–TacTac*, but not significantly different from *AfAf–TacTac*. Yield of *afaf–tactac* averaged 29% lower than *AfAf–TacTac* and 26% lower than *afaf–TacTac* in the early and midseason genetic backgrounds, but did not differ significantly in the late genetic background. Significant increases in vine length, number of nodes, lowest pod-bearing node, and first node with nonsenescent foliage were measured in *afaf–tactac* over *AfAf–TacTac* and *afaf–TacTac* in the early and midseason genetic backgrounds. The addition of leaflets to the tendrils of *afaf* plants through incorporation of the *tac* gene did not result in green pea yield improvement of plants grown at a standard highly competitive population density.

THE GARDEN PEA is unique among crop plants for its vast array of single genes that condition major changes in leaf morphology. Since the discovery of the *af* gene (Kujala, 1953; Goldenberg, 1965), which replaces leaflets with tendrils, foliage mutants have held promise for restructuring pea canopy architecture. Cultivars homozygous for *af*, which are also known as semi-leafless, have been released throughout the world. The tendriled-acacia gene, (hereafter referred to as *tac*), was discovered by Sharma (1972) following chemical mutagenesis with diethyl sulfate. When present in the homozygous recessive condition in conjunction with the homozygous *af* gene, *tac* restores small leaflets to the tendrils of *af* plants. Both *af* and *tac* are considered to be homeotic mutants. Tissues from one segment of the leaf are transformed into tissues of another (small leaflets restored to tendrils) (Marx, 1987). These homeotic mutants present novel phenotypes that may enhance pea improvement efforts. The *afaf–tactac* phenotype has been described by Marx (1987), but has received no attention from an agronomic standpoint.

The normal pea foliage type (*AfAf–TacTac*) has several disadvantages. Large amounts of foliage result in a dense canopy that shades lower plant parts. This in turn results in reduction of light penetration into the understory, a corresponding decrease in photosynthetic activity of the lower leaves, a lack of color uniformity of shelled peas due to shading, and a potential buildup of pathogens due to the moist lower-canopy environment.

Several reports have confirmed the predicted advantages of *afaf–TacTac*, while others have demonstrated its shortcomings. Plants with *afaf–TacTac* foliage are capable of converting intercepted light radiation into dry matter with the same efficiency as *AfAf–TacTac* foliage plants (Heath and Hebblethwaite, 1985a); however, there are conflicting reports on the yield potential of *afaf–TacTac* types. Wehner and Gritton

I.L. Goldman, Dep. of Agronomy, 1102 S. Goodwin Ave., Univ. of Illinois, Urbana, IL 61801; E.T. Gritton and P.J. Flannery, Dep. of Agronomy, 1575 Linden Dr., University of Wisconsin, Madison, WI 53706-1597. Research Supported by the Univ. of Wis. College of Agricultural and Life Sciences project 142-2804 and the Midwest Food Processors Assoc. Received 27 Mar. 1991. *Corresponding author.

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(1981) demonstrated that the reduction in leaf area due to *af* had little effect on yield. Yield reduction caused by decreases in the number of pods and fertile nodes of *afaf–TacTac* foliage types was documented by Cardi et al. (1987). Davies (1977), Snoad (1974), and Goldenberg (1973) observed that yield of *afaf–TacTac* is similar to *AfAf–TacTac*, although this effect has been shown to be genetic background-specific (Lafond et al., 1981). Those workers observed no significant yield differences between *afaf–TacTac* and *AfAf–TacTac* in the 'Century' background, while yields of *afaf–TacTac* in the 'Trapper' background were significantly lower than for *AfAf–TacTac*. Plants with *afaf–TacTac* foliage lodge less than their *AfAf–TacTac* counterparts (Heath and Hebblethwaite, 1985b; Davies, 1977; Wehner and Gritton, 1981). This general conclusion was also reached by Stelling (1989), although improved standing ability was not always associated with the *afaf–TacTac* type.

At present, there is no information on the field performance of *afaf–tactac*. The objectives of this study were to quantify expression of the *afaf–tactac* combination and evaluate the performance of this foliage type relative to its *afaf–TacTac* and *AfAf–TacTac* counterparts at a population density that would provide for a high degree of interplant competition.

MATERIALS AND METHODS

Genetic Material

This study included normal foliage (*AfAf–TacTac*), semi-leafless foliage (*afaf–TacTac*), and afila–tendriled acacia foliage (*afaf–tactac*) near-isogenic lines in three genetic backgrounds: 'Alsweet 4683', 'Frontier', and 'Dark Skin Perfection'. Alsweet 4683 is an early-maturing canning pea cultivar and Frontier and Dark Skin Perfection are midseason and late-maturing cultivars for canning and freezing, respectively. Foliage types will henceforth be referred to by their gene symbols. Germplasm containing the *tac* gene used in these studies was obtained from B. Sharma (Division of Genetics, Indian Agricultural Research Institute, New Delhi) and incorporated via the backcross procedure. The sixth backcross was made in the fall of 1986 and the BC_6F_1 plants were grown in the greenhouse in the spring. All near-isolines were BC_6F_6–derived at the beginning of the study.

Experimental Design

Four replicates of a split-plot arrangement of a randomized complete-block design were planted in 1.26-m by 1.52-m seven-row plots with a row spacing of 18 cm. The experiment was conducted in four environments: the Arlington Agricultural Research Station, Arlington, WI, in 1989 and 1990 on Plano silt loam soil (fine-silty, mixed, mesic Typic Argiudoll), and the West Madison Agricultural Research Station, Madison, WI in 1989 and 1990 on Plano silt loam soil. In each experiment, genetic background was assigned to the whole plot, and foliage type was assigned to the sub-plot.

Cultural Practices

Planting dates at Arlington were 27 Apr. and 1 May in 1989 and 1990, respectively, and 3 May and 2 May at West Madison in 1989 and 1990, respectively. Seeds were treated with the fungicide Captan (cis-*N*-trichloromethylthio-4-cyclohexene-1,2-dicarboximide) prior to planting by hand in 7.6 cm-deep furrows. Seeds were spaced 2.5 cm apart in the row. Plots were sown to a density of 1.34×10^6 plants per hectare. This density is representative of the population density used by the commercial pea processing industry. The high degree of interplant competition was designed to contrast with a minimally competitive wire trellis experiment (Goldman and Gritton, 1992). Trifluralin (α-α-α-trifluoro-2,6-dinitro-*N*,*N*-dipropyl-*p*-toluidine) was incorporated prior to planting at a rate of 0.17 L ha^{-1} in all trials to control weeds. Supplemental weeding was by hand.

Sampling Practices

Plant samples were removed from interior sections of the plots three times during the growing season: 28 d after planting, 100% bloom stage, and at green pea harvest ($\approx$100 tenderometer, the optimal harvest stage for commercial pea processing). Three 600-cm^2 bordered sections of the plot were delineated after emergence for sampling. Ten-plant samples composed of randomly chosen plants from separate 600-cm^2 bordered sections of the plot were removed at 28 d after planting and 100% bloom. The decision to sample 10 plants was based on sample size estimates reported by Gritton and Chi (1972). All three foliage types in a given genetic background were removed simultaneously at each sampling date. The entire 600-cm^2 section was removed at green pea harvest and transported to Madison, where the 10-plant sample was randomly chosen. Each of the samples was placed in an airtight plastic bag, refrigerated overnight, and analyzed within 48 h.

Foliage Components

The 10-plant sample was separated for its constituent foliage components (and yield components at green pea harvest). Foliage components from the sample including stipule, leaflet, tendril plus petiole, stem, and *tac* leaflet were bulked and their area measured on a LI-COR 3100 (LI-COR, Lincoln, NE) leaf area meter. The area of the tendrils plus petioles and stems were corrected by $\pi/2$ (Harvey and Goodwin, 1978) to account for their cylindrical shape. Total foliage area for each sampling date was calculated as the sum of the area of stem, tendril plus petiole, stipule, and leaflet or *tac* leaflet. Total foliage areas were calculated at each of the three sampling dates. Foliage components were dried for 48 h at 56 °C and weighed. Total plant dry weight was calculated as the sum of all dried foliage components for a given foliage type. Foliage area components and variables that take foliage area into account were measured at Arlington in 1989 and 1990 and at West Madison in 1989. Relative growth rates were calculated as the difference in foliage area between two sampling dates divided by the number of days between those dates. Relative growth rate at the first through third sampling dates refer to the growth in total foliage area per day between 28 d after planting and 100% bloom, 100% bloom and green pea harvest, and 28 d after planting and green pea harvest, respectively.

Yield and Yield Components

Yield and yield components of the 10-plant sample including lowest pod-bearing node, number of pod-bearing nodes per plant, pods per plant, peas per pod, pods per node, peas per plant, and total number of peas from the 600-cm^2 section were measured. Green pea yield was measured on the 10-plant sample and on the 600-cm^2 sampling area. Dry seed yield was measured on the remainder of the plot in 1989 at Arlington and in 1989 and 1990 at West Madison.

Agronomic Data

Plant counts (data not shown) were determined three weeks after planting by the average of three counts, each taken in

Table 1. Significance levels of mean squares from the combined analysis of variance for 31 pea foliage area, yield component, and agronomic variables over four environments.

Variable	Source of variation†					
	G	G × E	F	F × E	G × F	G × F × E
df	2	6	2	6	4	12
		Foliage area and weight components				
Total foliage area at sampling date 1	*	NS	**	NS	NS	NS
Total foliage area at sampling date 2	**	**	**	NS	NS	NS
Total foliage area at sampling date 3	**	NS	*	**	NS	NS
Total plant dry weight at date 1	NS	NS	**	NS	NS	NS
Total plant dry weight at date 2	**	NS	*	NS	NS	NS
Total plant dry weight at date 3	**	NS	NS	NS	*	*
Total dry weight of 600-cm² sample	*	NS	NS	NS	NS	NS
Relative growth rate 1	**	NS	**	NS	NS	NS
Relative growth rate 2	**	NS	NS	NS	NS	NS
Relative growth rate 3	**	NS	NS	**	NS	NS
		Yield and yield components				
Lowest pod-bearing node	**	NS	*	**	*	NS
Total pod-bearing nodes	**	*	NS	NS	NS	NS
Pods per plant	**	**	NS	NS	NS	NS
Peas per pod	NS	**	*	NS	NS	NS
Pods per node	**	*	NS	NS	NS	NS
Peas per plant	*	**	*	*	NS	NS
Peas per 600-cm² sampling area	*	NS	*	NS	*	*
Yield per 10-plant sample	NS	NS	*	NS	*	*
Yield per 600-cm² sampling area	**	NS	**	NS	*	*
Dry seed yield	*	**	NS	NS	NS	NS
		Agronomic traits				
Bloom date	**	NS	NS	NS	NS	NS
Standing ability	**	NS	**	**	NS	NS
Canopy height	**	NS	**	NS	**	NS
Light interception	NS	NS	**	NS	NS	NS
Vine length at sampling date 1	**	NS	**	**	NS	**
Vine length at sampling date 2	**	NS	**	NS	**	NS
Vine length at sampling date 3	**	NS	**	NS	**	NS
Nodes at sampling date 1	**	NS	**	NS	*	NS
Nodes at sampling date 2	**	NS	**	NS	**	NS
Nodes at sampling date 3	**	NS	**	**	**	NS
First node with non-senescent foliage	**	NS	*	NS	*	NS

*,** Significant at the 0.05 and 0.01 probability levels, respectively.
† Sources of variation are: G = genetic background, E = environment, F = foliage type.

separate 1.2-m sections of row. Bloom date was recorded when 50% of the plants in a plot had open flowers. Standing ability, or the proportion of the plants erect at green pea harvest in each plot was calculated based on the following measurements: (total nodes per plant / number of first node with nonsenescent foliage per plant) × 100. This formula was used to model the observed situation where the amount of stem lying on the ground at harvest is related to the number of nodes with senescent foliage below the first node with nonsenescent foliage. The first node with nonsenescent foliage was measured on the 10-plant sample and tabulated as the lowest node in which dead foliage was not present. Canopy height was measured just prior to green pea harvest. Light interception was measured with a LI-COR line quantum sensor once during the growing season at Arlington in 1989 and 1990 at ≈2 wk prior to green pea harvest.

Six readings were taken in each plot. One reading was taken just above ground level on exposed soil adjacent to each plot to determine the maximum amount of solar radiation reaching the soil surface. Data are expressed as % light intercepted by foliage relative to that reaching the soil surface. Vine length was measured 28 d after planting, at 100% bloom, and at green pea harvest. The number of nodes per plant were tabulated on the sample at each sampling date.

Statistical Analyses

Data were analyzed by analysis of variance using the GLM procedure of SAS (Statistical Analysis Systems, Cary, NC). Each year–location combination was considered an environment, and a combined analysis of variance was performed across all environments. All effects in the analysis, with the exception of environments and replicates, were treated as fixed. Type III sums of squares were used to compute mean squares due to missing data. Comparisons among means were made by least significant difference. Foliage type means within genetic backgrounds across environments were compared when genetic background × foliage type was significant. When this interaction was not significant, foliage type means across genetic backgrounds and environments were used.

RESULTS AND DISCUSSION

Foliage Area and Weight Components

Genetic background × environment interactions were nonsignificant for all but one foliage component trait. This is in agreement with the pattern of environmental interactions measured in a minimally competitive environment (Goldman and Gritton, 1992). Significant differences for genetic background were observed for most traits (Table 1), which is consistent with results reported by LaFond et al. (1981), who concluded that the performance of altered leaf types in pea was background-specific. In general, the significance of the genetic background effect seems to be related to the maturity of the lines.

Table 2. Means per plant of foliage area component, yield and yield component, and agronomic variables of pea measured under high levels of interplant competition across three genetic backgrounds and four environments.

Variable	Foliage Type			LSD (0.05)†
	AfAf–TacTac	*afaf–TacTac*	*afaf–tactac*	
Foliage area and weight components				
Total foliage area at sampling date 1, cm^2	53.58	40.92	45.98	2.11
Total foliage area at sampling date 2, cm^2	295.25	243.74	287.24	20.34
Total foliage area at sampling date 3, cm^2	226.20	198.33	218.43	18.41
Total dry weight at sampling date 1, g	0.19	0.14	0.17	0.010
Total dry weight at sampling date 2, g	0.65	1.19	1.02	0.12
Relative growth rate 1, $cm^2\ d^{-1}$	15.72	12.67	12.42	1.10
Yield and yield components				
Lowest pod-bearing node, no.	13.04	13.28	14.13	0.33
Pods per node, no.	3.64	3.71	3.38	0.21
Peas per plant, no.	6.09	6.81	5.22	0.79
Peas per 600 cm^2 sample, no.	9.18	9.53	7.55	1.77
Yield per 10-plant sample, g.	3.29	3.48	2.90	0.38
Yield per 600 cm^2 sample, g $plot^{-1}$	77.02	77.31	61.31	9.01
Agronomic traits				
Standing ability, %	72.80	69.95	71.41	1.97
Canopy height, cm	28.63	31.55	30.42	1.42
Light interception, %	82.98	75.82	78.29	3.03
Vine length at sampling date 1, cm	11.75	12.85	12.12	0.59
Vine length at sampling date 2, cm	46.50	47.22	50.15	1.40
Vine length at sampling date 3, cm	66.86	65.31	72.04	1.92
Nodes at sampling date 1, cm	6.96	7.31	7.13	0.40
Nodes at sampling date 2, cm	12.26	13.01	13.22	0.26
Nodes at sampling date 3, cm	15.92	15.84	17.24	0.37
First node with non-senescent foliage, no.	11.67	11.14	12.34	0.37

† Difference of foliage type means greater than the value in this column indicates significance at the 0.05 level.

Foliage type × environment mean squares were significant only for total foliage area at green pea harvest and relative growth rate between 28 d after planting and green pea harvest. The lack of significant foliage type × environment interaction suggests that it may be more efficient for pea breaders to evaluate and select foliage types for commercial production than other traits that are known to interact strongly with the environment. The genetic background × foliage type and genetic background × foliage type × environment interactions were nonsignificant for all foliage area and weight components except total plant dry weight at the third sampling date.

The combined analysis of variance across environments revealed significant foliage type effects for total foliage area at each of the three sampling dates, total plant dry weight at sampling dates one and two, and relative growth rate at the first sampling date (Table 1). Foliage Areas at 28 d after planting were highest for *AfAf–TacTac*, however at 100% bloom, *afaf–tactac* had a total foliage area equal to *AfAf–TacTac* (Table 2). These data show that there is no difference in total foliage area between *afaf–tactac* and *AfAf–TacTac* after the 100% bloom stage. Results from experiments conducted under minimal competition (Goldman and Gritton, 1992) are in agreement with this finding. Foliage area of *afaf–TacTac* was always significantly less than the other foliage types. Area measurements of stem, stipule, tendril plus petiole, leaflet, and *tac* leaflet (data not shown) indicated that *tac* leaflets comprised 30, 12, and 20% of the total foliage area of *afaf–tactac* at 28 d after planting, 100% bloom, and green pea harvest, respectively. Plants with *afaf–tactac* foliage had 12%, 18%, and 10% more foliage area at 28 d after planting, 100% bloom, and green pea harvest, respectively, than their *afaf–TacTac* counterparts. The contribution of stipule area to total foliage area at green pea harvest was highest (47%) in *afaf–TacTac* (data not shown). The *AfAf–TacTac* and *afaf–tactac* types had stipule area contributions of 34% and 41%, respectively. An increase in stipule area in *afaf–TacTac* as compared to *AfAf–TacTac* has been noted by Harvey (1976).

An unexpected finding of this study was the apparent tendency of the foliage area of *tac* leaflets to increase with ontogeny in all three genetic backgrounds. Area of foliage components was averaged across genetic backgrounds and plotted by sampling date. While the area of other laminar foliage components (stipule, leaflet) reached a peak at 100% bloom and decreased throughout the remainder of the season, due to senescence in the crop canopy (Fig. 1), *tac* leaflet and stem continued to increase in foliage area from 100% bloom to green pea harvest. Amplification of leaf components is common in *Pisum* (Marx, 1987). Leaflets in *AfAf* plants commonly increase in size and number as development progresses. These data suggest that amplification may occur in *tac* leaflets as well. In general, the greatest benefit in terms of photosynthetic surfaces from the *tac* leaflets comes later in the growing season.

Significant differences among foliage types were detected for total dry weight at the first and second sampling dates, but not at the third sampling date (Table 1). At 28 d after planting, *AfAf–TacTac* and *afaf–tactac* had significantly higher dry weights than *afaf–TacTac*. This trend was reversed for total dry weight at the second sampling date, where *afaf–TacTac* was

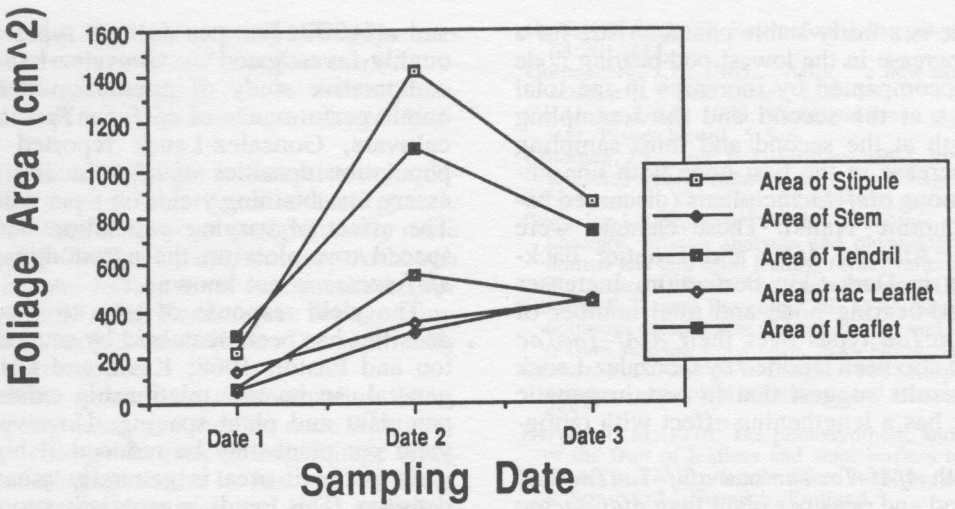


Fig. 1. Foliage area components of pea at three sampling dates averaged across three genetic backgrounds and four environments. The three sampling dates are 28 d after planting, 100% bloom, and green pea harvest. Each mean, with the exception of *tac* leaflet and leaflet, is averaged across all three foliage types.

highest. The relative growth rate at the second sampling date was highest for *AfAf–TacTac*. No significant differences among foliage types were detected for relative growth rates at the third sampling date and over the entire season, suggesting that both mutant foliage types had growth rates equal to that of the normal foliage type as the season progressed.

The *afaf–tactac* type in the Alsweet 4683 background exhibited significantly higher dry weight at the third sampling date than *AfAf–TacTac* and *afaf–TacTac* (Table 3). The *afaf–TacTac* type in the Frontier background had a slightly higher (though non significant) total dry weight at the third sampling date than *afaf–tactac*.

Yield and Yield Components

The genetic background × environment interaction, the genetic background × foliage type interaction, and the effect of genetic background were significant for many yield component traits. In contrast to foliage area and weight components in these backgrounds, Alsweet 4683 had higher values than Frontier or Dark Skin Perfection for some yield components (Table 3). This result is in part due to the detrimental effects of excessive soil moisture on late-maturing lines during the 1990 growing season. Generally, later-maturing cultivars are superior in yield to early-maturing cultivars. In 1990, however, excessive soil moisture enhanced disease development, and this problem worsened as the season progressed and became especially acute in the later-maturing material. The largest decreases in yield performance (yield of the 10-plant sample and yield of the 600-cm^2 section) in *afaf–tactac* were observed for Alsweet 4683 and Frontier. In contrast, no significant yield differences were observed between foliage types in the later-maturing Dark Skin Perfection background. This similarity in performance of foliage types in later-maturing genetic backgrounds is in agreement with results of our observations from material grown under minimal competition (Goldman and Gritton, 1992).

Significant genetic background × foliage type interaction revealed that the lowest pod-bearing node of *afaf–tactac* was slightly higher than the other two foliage types in Alsweet 4683 and Frontier, and slightly lower in Dark Skin Perfection (Table 3). The lowest

Table 3. Background means per plant of selected foliage area component, yield component, and agronomic variables of pea measured under high levels of interplant competition across four environments.

Variable	Background and foliage type									LSD (0.05)†
	Alsweet			Frontier			Dark Skin Perfection			
	Af–Tac	*af–Tac*	*af–tac*	*Af–Tac*	*af–Tac*	*af–tac*	*Af–Tac*	*af–Tac*	*af–tac*	
Total dry weight at sampling date 3, g	1.1	1.1	1.6	2.0	2.0	1.7	2.2	1.9	2.1	0.5
Lowest pod-bearing node, no.	9.0	9.5	9.9	15.4	15.9	16.3	14.5	14.5	14.1	0.7
Peas per 600-cm^2 sample, no.	13.6	14.5	9.5	7.4	5.5	6.9	6.5	8.6	7.0	3.4
Yield per 10-plant sample, g	3.6	3.3	2.7	2.9	3.7	2.4	3.3	3.4	3.4	0.7
Yield per 600-cm^2 sample, g plot^{-1}	102.1	99.2	74.6	64.6	60.3	44.3	65.1	72.4	69.9	22.2
Canopy height, cm	26.5	29.3	35.4	29.7	34.3	30.8	29.7	31.1	27.0	2.4
Vine length at sampling date 2, cm	43.5	42.3	49.3	47.6	52.4	53.2	48.3	47.0	47.6	2.3
Vine length at sampling date 3, cm	56.1	59.0	75.6	70.7	71.7	76.5	73.4	65.2	65.3	3.8
Nodes at sampling date 1, no.	6.8	7.0	6.8	6.9	7.4	7.3	7.2	7.5	7.2	0.2
Nodes at sampling date 2, no.	10.7	10.7	10.7	13.9	15.1	14.8	12.2	13.3	12.9	0.4
Nodes at sampling date 3, no.	12.2	12.5	14.3	18.5	18.5	19.4	16.9	16.6	16.5	0.7
First node with nonsenescent foliage, no.	8.2	8.3	9.3	14.1	13.3	14.3	12.5	11.8	11.9	0.7

† Difference among genetic background × foliage type means greater than the value in this column indicates significance at the 0.05 level.

pod-bearing node is a fairly stable characteristic for a given cultivar. Increase in the lowest pod-bearing node was generally accompanied by increases in the total number of nodes at the second and third sampling dates, vine length at the second and third sampling dates, and an increase in the first node with nonsenescent foliage among *afaf–tactac* plants (discussed below under Agronomic Traits). These changes were observed in the Alsweet 4683 and Frontier backgrounds, but not in Dark Skin Perfection. Increases in the lowest pod-bearing node and total number of nodes of *afaf–TacTac* types over their *AfAf–TacTac* counterparts have also been reported by Gonzalez-Lauck (1990). These results suggest that in certain genetic backgrounds *tac* has a lengthening effect with ontogeny.

Generally, both *AfAf–TacTac* and *afaf–TacTac* had more peas per pod and peas per plant than *afaf–tactac* (Table 2). Significant genetic background × foliage type interaction for peas per 600-cm^2 sample, yield per 10-plant sample, and yield per 600-cm^2 sample revealed different patterns among foliage types in the three genetic backgrounds. The *afaf–tactac* foliage type in the Alsweet 4683 background had significantly less peas per 600-cm^2 sample, yield per 10-plant sample, and yield per 600-cm^2 sample. In the Frontier background, *afaf–tactac* was lowest only for yield per 10-plant sample and yield per 600-cm^2 sample; in the Dark Skin Perfection background, *afaf–tactac* did not rank lowest for any of these three traits. The fact that *afaf–tactac* in the Dark Skin Perfection background did not show decreases in these yield components compared with the other foliage types is consistent with findings from similar material grown under minimal competition. Lower yields in *afaf–tactac* may be explained by the initial description of *tac* (Sharma, 1972), which suggested that *tac* (in an *Af* background) had a pleiotropic effect on flower structure, rendering the flowers oblong, slightly deformed and with reduced fertility. This detrimental effect on reproductive organs may be further supported by the conclusion that the *uni^{tac}* allele, which is allelic to *tac* (Marx, 1986) and not present in this study, results in pollen sterility in *uni^{tac}uni^{tac}* plants. The *tac* locus may therefore exhibit a general pleiotropic effect on *Pisum* reproduction.

No significant foliage type effects were measured for dry seed yield. This is in contrast to results with similar material grown under minimal competition (Goldman and Gritton, 1992). In that study, yield differences among foliage types that were not apparent at the green pea harvest stage became evident in comparing dry seed yields. Results from the two studies do, however, agree that yield of *afaf–tactac* relative to yield of the other two foliage types is higher at the dry seed stage than at the green pea stage. Under these high levels of interplant competition, yield depressions of *afaf–tactac* at the green pea harvest stage were no longer present at the dry seed stage. The operative mechanism in this case may be the previously mentioned developmental increase in *tac* leaflet area, causing a larger contribution to dry seed yield than to green pea yield.

The effect of population density on *afaf–TacTac* and *AfAf–TacTac* pea foliage types has been thoroughly investigated by Gonzalez-Lauck (1990). In a comparative study of population density and agronomic performance of *afaf–TacTac* and *AfAf–TacTac* cultivars, Gonzalez-Lauck reported that increasing population densities of *afaf–TacTac* types was necessary for obtaining yields on a par with *AfAf–TacTac*. The effect of varying population density in closely spaced row plots on the agronomic performance of *afaf–tactac* is not known.

The yield response of peas to varying population densities has been discussed by several workers (Gritton and Eastin, 1968; Kaatz and Gritton, 1975). In general, an inverse relationship exists between yield per plant and plant spacing. However, even though yield per plant may be reduced at high populations, yield per unit area is generally greater than at low densities. This trends is especially pronounced in *afaf–TacTac* (Gonzalez-Lauck, 1990). This result may be reversed when peas are grown in a widely spaced wire trellis environment, which eliminates competition between rows and greatly reduces the competition between plants within a row. Yields of plants supported and kept from lodging have been greater than from unsupported plants (Kaatz and Gritton, 1975). Results from a separate study (Goldman and Gritton, 1992) demonstrate that yields of *AfAf–TacTac* may be surpassed by *afaf–TacTac* or *afaf–tactac* grown under minimal competition with support. Compared with their *afaf–TacTac* and *AfAf–TacTac* counterparts, *afaf–tactac* types (especially in later-maturing genetic backgrounds) achieve optimal yields when grown in a minimally competitive environment (Goldman and Gritton, 1992) and poorer yields when grown in a maximally competitive environment. The *afaf–tactac* type in the late-maturing Dark Skin Perfection background exhibited performance increases over its constituent *AfAf–TacTac* and *afaf–TacTac* when grown in a minimally competitive environment, and performance decreases compared to these two foliage types when grown in a maximally competitive environment. Our data suggest that the yield response of *afaf–tactac* is influenced by both population density and genetic background.

Agronomic Traits

The interaction of genetic background × foliage type × environment was significant for vine length at the first sampling date. The interaction of genetic background × environment was nonsignificant and the effect of genetic background was significant for most traits. As with the foliage components, most of the differences between backgrounds were due to performance increases in the later-maturing lines. In general, Alsweet 4683 types had fewer nodes and were not as tall as Frontier and Dark Skin Perfection (Table 3).

The foliage type × environment interaction was significant for standing ability, vine length at the first sampling date, and number of nodes at the third sampling date. Significant foliage type effects were detected for all agronomic traits with the exception of bloom date (Table 1). Bloom date of *afaf–tactac* tended to be slightly later (data not shown) than *AfAf–TacTac*

or *afaf–TacTac*. Standing ability of *AfAf–TacTac* was significantly greater than for *afaf–TacTac* or *afaf–tactac* (Table 2). In this study, *afaf–TacTac* did not demonstrate its usual superiority in standing ability to *AfAf–TacTac*.

Significant differences in light interception were detected among the three foliage types in each genetic background. *AfAf–TacTac* intercepted significantly more radiation than *afaf–TacTac* or *afaf–tactac*. Although no differences in total foliage area were measured between *afaf–tactac* and *AfAf–TacTac* (see foliage components), the large leaflets of *AfAf–TacTac* apparently maximize light interception.

Vine length at the second and third sampling dates, nodes at all sampling dates, and the first node with nonsenescent foliage changed in rank among foliage types in the three genetic backgrounds. In Alsweet 4683 and Frontier, vine length at the second and third sampling dates and the first node with nonsenescent foliage was greatest in *afaf–tactac* types, while in Dark Skin Perfection, *afaf–tactac* was intermediate. The first node with non-senescent foliage was approximately one node higher for *afaf–tactac* than for *AfAf–TacTac* or *afaf–TacTac* in the Alsweet 4683 and Frontier backgrounds. No clear trend was detected among the genetic backgrounds and foliage types for number of nodes.

CONCLUSIONS

Based on the results of this investigation, *afaf–tactac* does not seem to offer any advantages for field-scale green pea production over AfAf–TacTac or *afaf–TacTac*. In fact, shelled pea yields were less than from the two other types, and there were no other advantages demonstrated. There were, however, some significant foliage type × genetic background interactions, which points out that expression can differ depending on the background genotype. The *afaf–tactac* foliage type performed best in the late-maturing Dark Skin Perfection background and it may well be worthwhile to continue such research with other late-maturing genotypes.

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