Evaluation of the Aflila-Tendriled Acacia \((a_{af}f-tac_{tac})\) Pea Foliage Type under Minimal Competition

Irwin L. Goldman* and Earl T. Gritton

ABSTRACT

The aflila \((af)\) and tendrilred-acacia \((tac)\) genes condition structural modifications of the pea \((Pisum sativum \text{ L.})\) 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 \((A_{AF}f-A_{TA}c\text{Tac})\), aflila \((a_{af}f-Tac\text{Tac})\), and aflila-tendriled acacia \((a_{af}f-tac_{tac})\) 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 \(a_{af}f-tac_{tac}\) plants over \(a_{af}f-Tac\text{Tac}\) plants by 37%. Green pea yield did not differ significantly among the three foliage types. Dry seed yield of \(a_{af}f-tac_{tac}\) plants was significantly higher than \(a_{af}f-Tac\text{Tac}\) plants and equal to \(A_{AF}f-Tac\text{Tac}\) plants. Expression of the \(tac\) gene varied significantly with genetic background. The \(a_{af}f-tac_{tac}\) combination in the latest-maturing background exhibited the largest increases in yield and yield components over its constituent foliage types.

The AFLILA \((af)\) and tendrilred 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 \(a_{af}f-tac_{tac}\) phenotype under greenhouse conditions is characterized by a proliferation of tendrils that terminate in leaflets similar in shape to those found on normal-foliation plants (Marx, 1987). The \(a_{af}f-tac_{tac}\) foliage type has not previously been studied from an agronomic standpoint.

The normal \((A_{AF}f-Tac\text{Tac})\) 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 \(a_{af}f-Tac\text{Tac}\) (also known as semi-leafless) foliage type in many regions of the world.

Investigations of the predicted advantages of \(a_{af}f-Tac\text{Tac}\) have produced mixed results. Heath and Hebblethwaite (1985a) demonstrated that \(a_{af}f-Tac\text{Tac}\) was able to convert intercepted light radiation into dry matter with the same efficiency as \(A_{AF}f-Tac\text{Tac}\). Reduced lodging (Davies, 1977; Heath and Hebblethwaite, 1985b) and yields similar to \(A_{AF}f-Tac\text{Tac}\) (Davies, 1977; Goldenberg, 1973) have been reported in \(a_{af}f-Tac\text{Tac}\). Wehner and Gritton (1981) showed a superior standing ability and reduced blanding of shelled peas in \(a_{af}f-Tac\text{Tac}\), and no significant yield differences between \(a_{af}f-Tac\text{Tac}\) and \(A_{AF}f-Tac\text{Tac}\). Cardi

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$_5$F$_1$ plants were grown in the greenhouse in the spring of 1987. All near-isolines were BC$_3$F$_{1}$-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.**

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

*** 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.

<table>
<thead>
<tr>
<th>Genetic background and foliage type</th>
<th>Alswet 4683</th>
<th>Frontier</th>
<th>Dark Skin Perfection</th>
<th>LSD (0.05)†</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tendril area, cm²</td>
<td>23.6</td>
<td>62.3</td>
<td>42.5</td>
<td>69.9</td>
</tr>
<tr>
<td>Stem area, cm²</td>
<td>30.9</td>
<td>34.5</td>
<td>37.0</td>
<td>62.3</td>
</tr>
<tr>
<td>Total foliage area, cm²</td>
<td>229.6</td>
<td>204.0</td>
<td>221.8</td>
<td>499.7</td>
</tr>
<tr>
<td>Total pod-bearing nodes, no.</td>
<td>3.8</td>
<td>4.1</td>
<td>3.3</td>
<td>2.9</td>
</tr>
<tr>
<td>Pods, no.</td>
<td>4.0</td>
<td>4.2</td>
<td>3.3</td>
<td>4.7</td>
</tr>
<tr>
<td>Peas, no.</td>
<td>16.2</td>
<td>18.5</td>
<td>12.3</td>
<td>25.6</td>
</tr>
<tr>
<td>Vine length, cm</td>
<td>55.0</td>
<td>61.3</td>
<td>66.6</td>
<td>61.7</td>
</tr>
</tbody>
</table>

† 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 π/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.

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 Alswet 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 (d) 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 × foliage 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 Alsum 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.
REFERENCES

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/af plants. The agronomic performance of plants homozygous for both afaf 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 afaf 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

*Corresponding author.
(1981) demonstrated that the reduction in leaf area due

to afl had little effect on yield. Yield reduction caused
by decreases in the number of pods and fertile nodes
of afl-TacTac foliage types was documented by Cardi
et al. (1987). Davies (1977), Snod (1974), and Golder
berg (1973) observed that yield of afl-TacTac is simi-
lar to Afl-TacTac, although this effect has been shown
to be genetic background-specific (Lafond et al.,
1981). Those workers observed no significant yield
differences between afl-TacTac and Afl-TacTac in the
‘Century’ background, while yields of afl-TacTac
in the ‘Trapper’ background were significantly lower
than for Afl-TacTac. Plants with afl-TacTac foli-
age lodge less than their Afl-TacTac counterparts
(Heath and Hebblethwaite, 1985b; Davies, 1977;
Wernert and Gritton, 1981). This general conclusion
was also reached by Stelling (1989), although im-
proved standing ability was not always associated
with the afl-TacTac type.

At present, there is no information on the field per-
formance of afl-tactac. The objectives of this study
were to quantify expression of the afl-tactac com-
bination and evaluate the performance of this foliage
type relative to its afl-TacTac and Afl-TacTac
counterparts at a population density that would pro-
vide for a high degree of interplant competition.

MATERIALS AND METHODS

Genetic Material

This study included normal foliage (Afl-TacTac), semi-
leafless foliage (afl-TacTac), and afla—tendril acacia
foliage (afl-tactac) near-isogenic lines in three genetic
backgrounds: ‘Alsweet 4683’, ‘Frontier’, and ‘Dark Skin
Perfection’. Alsweet 4683 is an early-maturing canning
cultivar and Frontier and Dark Skin Perfection are mid-
season and late-maturing cultivars for canning and freezing,
respectively. Foliage types will henceforth be referred
to by their gene symbols. Germplasm containing the tae
gene used in these studies was obtained from B. Sharma (Di-
vision 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
BC3F6 plants were grown in the greenhouse in the spring.
All near-isolines were BC3F6—derived at the beginning of
the study.

Experimental Design

Four replicates of a split-plot arrangement of a ran-
domized complete-block design were planted in 1.26-
m seven-row plots with a row spacing of 18 cm. The ex-
periment was conducted in four environments: the Arlin-
ton 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 Re-
search 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-cy-
cloloxene-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 × 106 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 experi-
ment (Goldman and Gritton, 1992). Trifluralin (α-α-α-tri-
fluoro-2,6-dinitro-N,N-dipropyl-p-toluidine) was incorporat-
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 (=100
tenderometer, the optimal harvest stage for commercial pea
processing). Three 600-cm2 bordered sections of the plot
were delineated after emergence for sampling. Ten-plant
samples composed of randomly chosen plants from separate
600-cm2 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
background were removed simultaneously at each
sampling date. The entire 600-cm2 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 overnigh-
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 tae 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 σ/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 tae leaflet. Total foliage areas were calculated
each at 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 com-
ponents for a given foliage type. Foliage area components
and variables that take foliage area into account were mea-
sured at Arlington in 1989 and 1990 and at West Madison
in 1989. Relative growth rates were calculated as the dif-
ference 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 har-
vest, and 28 d after planting and green pea harvest,
respectively.

Yield and Yield Components

Yield and yield components of the 10-plant sample in-
cluding 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-cm2 section were measured. Green pea yield was mea-
sured on the 10-plant sample and on the 600-cm2 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.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Source of variation</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>G</td>
</tr>
<tr>
<td>df</td>
<td>2</td>
</tr>
<tr>
<td><strong>Foliage area and weight components</strong></td>
<td></td>
</tr>
<tr>
<td>Total foliage area at sampling date 1</td>
<td>NS</td>
</tr>
<tr>
<td>Total foliage area at sampling date 2</td>
<td>NS</td>
</tr>
<tr>
<td>Total foliage area at sampling date 3</td>
<td>NS</td>
</tr>
<tr>
<td>Total plant dry weight at date 1</td>
<td>NS</td>
</tr>
<tr>
<td>Total plant dry weight at date 2</td>
<td>NS</td>
</tr>
<tr>
<td>Total plant dry weight at date 3</td>
<td>NS</td>
</tr>
<tr>
<td>Relative growth rate 1</td>
<td>NS</td>
</tr>
<tr>
<td>Relative growth rate 2</td>
<td>NS</td>
</tr>
<tr>
<td>Relative growth rate 3</td>
<td>NS</td>
</tr>
<tr>
<td><strong>Yield and yield components</strong></td>
<td></td>
</tr>
<tr>
<td>Lowest pod-bearing node</td>
<td>**</td>
</tr>
<tr>
<td>Total pod-bearing nodes</td>
<td>**</td>
</tr>
<tr>
<td>Pods per plant</td>
<td>NS</td>
</tr>
<tr>
<td>Peas per pod</td>
<td>NS</td>
</tr>
<tr>
<td>Peas per node</td>
<td>NS</td>
</tr>
<tr>
<td>Peas per 600-cm² sampling area</td>
<td>NS</td>
</tr>
<tr>
<td>Yield per 10-plant sample</td>
<td>NS</td>
</tr>
<tr>
<td>Yield per 600-cm² sampling area</td>
<td>NS</td>
</tr>
<tr>
<td>Dry seed yield</td>
<td>NS</td>
</tr>
<tr>
<td><strong>Agronomic traits</strong></td>
<td></td>
</tr>
<tr>
<td>Bloom date</td>
<td>NS</td>
</tr>
<tr>
<td>Standing ability</td>
<td>NS</td>
</tr>
<tr>
<td>Canopy height</td>
<td>NS</td>
</tr>
<tr>
<td>Light interception</td>
<td>NS</td>
</tr>
<tr>
<td>Vine length at sampling date 1</td>
<td>NS</td>
</tr>
<tr>
<td>Vine length at sampling date 2</td>
<td>NS</td>
</tr>
<tr>
<td>Vine length at sampling date 3</td>
<td>NS</td>
</tr>
<tr>
<td>Nodes at sampling date 1</td>
<td>NS</td>
</tr>
<tr>
<td>Nodes at sampling date 2</td>
<td>NS</td>
</tr>
<tr>
<td>Nodes at sampling date 3</td>
<td>NS</td>
</tr>
<tr>
<td>First node with non-senescent foliage</td>
<td>NS</td>
</tr>
</tbody>
</table>

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

<table>
<thead>
<tr>
<th>Foliage Type</th>
<th>AFAf-TacTac</th>
<th>afaf-TacTac</th>
<th>afaf-tactac</th>
<th>LSD (0.05)†</th>
</tr>
</thead>
<tbody>
<tr>
<td>Variable</td>
<td>Foliage area and weight components</td>
<td>Yield and yield components</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total foliage area at sampling date 1, cm²</td>
<td>53.58</td>
<td>40.92</td>
<td>45.98</td>
<td>2.11</td>
</tr>
<tr>
<td>Total foliage area at sampling date 2, cm²</td>
<td>295.25</td>
<td>243.74</td>
<td>287.24</td>
<td>20.34</td>
</tr>
<tr>
<td>Total foliage area at sampling date 3, cm²</td>
<td>226.20</td>
<td>198.33</td>
<td>218.43</td>
<td>18.41</td>
</tr>
<tr>
<td>Total dry weight at sampling date 1, g</td>
<td>0.19</td>
<td>0.14</td>
<td>0.17</td>
<td>0.010</td>
</tr>
<tr>
<td>Total dry weight at sampling date 2, g</td>
<td>0.65</td>
<td>1.19</td>
<td>1.02</td>
<td>0.12</td>
</tr>
<tr>
<td>Relative growth rate 1, cm² d⁻¹</td>
<td>15.72</td>
<td>12.67</td>
<td>12.42</td>
<td>1.10</td>
</tr>
<tr>
<td>Lowest pod-bearing node, no.</td>
<td>13.04</td>
<td>13.28</td>
<td>14.13</td>
<td>0.33</td>
</tr>
<tr>
<td>Pods per node, no.</td>
<td>3.64</td>
<td>3.71</td>
<td>3.38</td>
<td>0.21</td>
</tr>
<tr>
<td>Peas per plant, no.</td>
<td>6.09</td>
<td>6.81</td>
<td>5.22</td>
<td>0.79</td>
</tr>
<tr>
<td>Peas per 600 cm² sample, no.</td>
<td>9.18</td>
<td>9.53</td>
<td>7.55</td>
<td>1.77</td>
</tr>
<tr>
<td>Yield per 10-plant sample, g.</td>
<td>3.29</td>
<td>3.48</td>
<td>2.90</td>
<td>0.38</td>
</tr>
<tr>
<td>Yield per 600 cm² sample, g plot⁻¹</td>
<td>77.02</td>
<td>77.31</td>
<td>61.31</td>
<td>9.01</td>
</tr>
<tr>
<td>Agronomic traits</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Standing ability, %</td>
<td>72.80</td>
<td>69.95</td>
<td>71.41</td>
<td>1.97</td>
</tr>
<tr>
<td>Canopy height, cm</td>
<td>28.63</td>
<td>31.55</td>
<td>30.42</td>
<td>1.42</td>
</tr>
<tr>
<td>Light interception, %</td>
<td>82.98</td>
<td>75.82</td>
<td>78.29</td>
<td>3.03</td>
</tr>
<tr>
<td>Vine length at sampling date 1, cm</td>
<td>11.75</td>
<td>12.85</td>
<td>12.12</td>
<td>0.59</td>
</tr>
<tr>
<td>Vine length at sampling date 2, cm</td>
<td>46.50</td>
<td>47.22</td>
<td>50.15</td>
<td>1.40</td>
</tr>
<tr>
<td>Vine length at sampling date 3, cm</td>
<td>66.86</td>
<td>65.31</td>
<td>72.04</td>
<td>1.92</td>
</tr>
<tr>
<td>Nodes at sampling date 1, cm</td>
<td>6.96</td>
<td>7.31</td>
<td>7.13</td>
<td>0.40</td>
</tr>
<tr>
<td>Nodes at sampling date 2, cm</td>
<td>12.26</td>
<td>13.01</td>
<td>12.22</td>
<td>0.26</td>
</tr>
<tr>
<td>Nodes at sampling date 3, cm</td>
<td>15.92</td>
<td>15.84</td>
<td>17.24</td>
<td>0.37</td>
</tr>
<tr>
<td>First node with non-senescent foliage, no.</td>
<td>11.07</td>
<td>11.14</td>
<td>12.34</td>
<td>0.37</td>
</tr>
</tbody>
</table>

† Difference of foliages 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 breeders to evaluate and select foliages types for commercial production than other traits that are known to interact strongly with the environment. The genetic background × foliages 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 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 leaves 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.

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–TacTactac 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-cm² 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>
<thead>
<tr>
<th>Variable</th>
<th>Alsweet</th>
<th>Frontier</th>
<th>Dark Skin Perfection</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Af-Tac</td>
<td>af-Tac</td>
<td>af-tac</td>
</tr>
<tr>
<td></td>
<td>Af-Tac</td>
<td>af-Tac</td>
<td>af-tac</td>
</tr>
<tr>
<td>Total dry weight at sampling date 3, g</td>
<td>1.1</td>
<td>1.1</td>
<td>1.6</td>
</tr>
<tr>
<td>Peas per 600-cm² sample, no.</td>
<td>9.0</td>
<td>9.5</td>
<td>9.9</td>
</tr>
<tr>
<td>Yield per 10-plant sample, g</td>
<td>13.6</td>
<td>14.5</td>
<td>9.5</td>
</tr>
<tr>
<td>Yield per 600-cm² sample, g (plot -²)</td>
<td>3.6</td>
<td>3.3</td>
<td>2.7</td>
</tr>
<tr>
<td>Canopy height, cm</td>
<td>102.1</td>
<td>99.2</td>
<td>74.6</td>
</tr>
<tr>
<td>Vine length at sampling date 2, cm</td>
<td>26.5</td>
<td>29.3</td>
<td>35.4</td>
</tr>
<tr>
<td>Vine length at sampling date 3, cm</td>
<td>43.5</td>
<td>42.3</td>
<td>49.3</td>
</tr>
<tr>
<td>Nodes at sampling date 1, no.</td>
<td>56.1</td>
<td>59.0</td>
<td>75.6</td>
</tr>
<tr>
<td>Nodes at sampling date 2, no.</td>
<td>6.8</td>
<td>7.0</td>
<td>6.8</td>
</tr>
<tr>
<td>First node with nonnonescent foliage, no.</td>
<td>10.7</td>
<td>10.7</td>
<td>10.7</td>
</tr>
<tr>
<td>First node with nonnonescent foliage, no.</td>
<td>12.2</td>
<td>12.5</td>
<td>14.3</td>
</tr>
</tbody>
</table>

† 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 nonsen-
scuous foliage among afa-f-tacTac plants (discussed be-
low under Agronomic Traits). These changes were
observed in the Alsweet 4683 and Frontier back-
grounds, but not in Dark Skin Perfection. Increases in
the lowest pod-bearing node and total number of
nodes of afa-f-TacTac types over their AfaF-TacTac
counterparts have also been reported by González-Lauck
(1990). These results suggest that in certain genetic
backgrounds tac has a lengthening effect on ontoge-
y.

Generally, both AfaF-TacTac and afa-f-TacTac had
more peas per pod and peas per plant than afa-f-tacTac
(Table 2). Significant genetic background × foliage
type interaction for peas per 600-cm² sample, yield
per 10-plant sample, and yield per 600-cm² sample
revealed different patterns among foliage types in the
ten genetic backgrounds. The afa-f-tacTac foliage type
in the Alsweet 4683 background had significantly less
peas per 600-cm² sample, yield per 10-plant sample,
and yield per 600-cm² sample. In the Frontier back-
ground, afa-f-tacTac was lowest only for yield per 10-
plant sample and yield per 600-cm² sample; in the
Dark Skin Perfection background, afa-f-tacTac did not
rank lowest for any of these three traits. The fact that
afa-f-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 min-
imal competition. Lower yields in afa-f-tacTac may be
explained by the initial description of tac (Sharma,
1972), which suggested that tac (in an AfaF background)
had a pleiotropic effect on flower structure, rendering
the flowers oblong, slightly deformed and with re-
duced fertility. This detrimental effect on reproductive
organs may be further supported by the conclusion
that the uni° allele, which is allelic to tac (Marx,
1986) and not present in this study, results in pollen
sterility in uni° uni° plants. The tac locus may there-
fore exhibit a general pleiotropic effect on Pisum re-
production.

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 dif-
fences among foliage types that were not apparent
at the green pea harvest stage became evident in com-
paring dry seed yields. Results from the two studies
do, however, agree that yield of afa-f-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 depres-
sions of afa-f-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 previ-
ously 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 afa-f-TacTac
and AfaF-TacTac pea foliage types has been thor-
oughly investigated by González-Lauck (1990). In a
comparative study of population density and agro-
nomic performance of afa-f-TacTac and AfaF-TacTac
cultivars, González-Lauck reported that increasing
population densities of afa-f-TacTac types was neces-
sary 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
afa-f-tacTac is not known.

The yield response of peas to varying population
densities has been discussed by several workers (Grit-
ton 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 trend is especially pronounced in afa-f-
TacTac (González-Lauck, 1990). This result may be
reversed when peas are grown in a widely spaced wire
trellis environment, which eliminates competition be-
tween rows and greatly reduces the competition be-
tween 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 sur-
passed by afa-f-TacTac or afa-f-tacTac grown under
minimal competition with support. Compared with their
afa-f-TacTac and AfaF-TacTac counterparts, afa-f-tac-
Tac types (especially in later-maturing genetic back-
grounds) 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 afa-f-tacTac
type in the late-maturing Dark Skin Perfection back-
ground exhibited performance increases over its con-
stituent AfaF-TacTac and afa-f-TacTac when grown in a
minimally competitive environment, and perform-
ance decreases compared to these two foliage types
when grown in a maximally competitive environment.
Our data suggest that the yield response of afa-f-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 per-
formance increases in the later-maturing lines. In gen-
eral, 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 sam-
ping date. Significant foliage type effects were de-
tected for all agronomic traits with the exception of
bloom date (Table 1). Bloom date of afa-f-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 non-senescent 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 non-senescent 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.

REFERENCES


