REFERENCES


Evaluation of the Afila-Tendrilled Acacia (afaftactac) Pea Foliation 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 tendrilled-acacia (tac) gene restores small leaflets to the tendrils of af plants. The agronomic performance of plants homoyzygous for both af and tac has not been studied. A near-isogenic set of three foliage types: normal (AafTactac), semi-leafless (afaftactac), and afila–tendrilled acacia (afaftactac) 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 afaftactac in comparison with afaftactac and AafTactac at high levels of interplant competition. At the green pea harvest stage, the total foliage area of afaftactac plants was 10% greater than for afaftactac, but not significantly different from AafTactac. Yield of afaftactac averaged 29% lower than AafTactac and 26% lower than afaftactac in the early and mid-season 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 nonseescent foliage were measured in afaftactac over AafTactac and afaftactac in the early and mid-season genetic backgrounds. The addition of leaflets to the tendrils of af plants through incorporation of the tac gene did not result in green pea yield improvement of plants grown at a standard high competition 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 tendril-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 afaftactac phenotype has been described by Marx (1987), but has received no attention from an agronomic standpoint.

The normal pea foliage type (AafTactac) 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 afaftactac, while others have demonstrated its shortcomings. Plants with afaftactac foliage are capable of converting intercepted light radiation into dry matter with the same efficiency as AafTactac foliage plants (Heath and Hebblethwaite, 1985a); however, there are conflicting reports on the yield potential of afaftactac types. Wehner and Gritton

(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). Davison (1977), Snod (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 afifa–tendrilled acacia foliage (afaf-tacTac) near-isogenic lines in three genetic backgrounds: ‘Alswheat 4683’, ‘Frontier’, and ‘Dark Skin Perfection’. Alswheat 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 BC6F1 plants were grown in the greenhouse in the spring. All near-isolines were BC6F2-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-cy-clohexene-1,2-dicarb oximide) 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 $1.34 \times 10^8$ 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 (a-a-a-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 (=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) 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.

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

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 26 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>Variable</th>
<th>Foliage Type</th>
<th>LSD (0.05)†</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>AafA–TacTac</td>
<td>aaf–TacTac</td>
</tr>
<tr>
<td>Foliage area and weight 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>
</tr>
<tr>
<td>Total foliage area at sampling date 2, cm²</td>
<td>295.25</td>
<td>243.74</td>
</tr>
<tr>
<td>Total foliage area at sampling date 3, cm²</td>
<td>226.20</td>
<td>198.33</td>
</tr>
<tr>
<td>Total dry weight at sampling date 1, g</td>
<td>0.19</td>
<td>0.14</td>
</tr>
<tr>
<td>Total dry weight at sampling date 2, g</td>
<td>0.65</td>
<td>1.19</td>
</tr>
<tr>
<td>Relative growth rate 1, cm² d⁻¹</td>
<td>15.72</td>
<td>12.67</td>
</tr>
<tr>
<td>Yield and yield components</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lowest pod-bearing node, no.</td>
<td>13.04</td>
<td>13.28</td>
</tr>
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<td>Pods per node, no.</td>
<td>3.64</td>
<td>3.71</td>
</tr>
<tr>
<td>Peas per plant, no.</td>
<td>6.09</td>
<td>6.81</td>
</tr>
<tr>
<td>Peas per 600 cm² sample, no.</td>
<td>9.18</td>
<td>9.53</td>
</tr>
<tr>
<td>Yield per 10-plant sample, g</td>
<td>3.29</td>
<td>3.48</td>
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<tr>
<td>Yield per 600 cm² sample, g plot⁻¹</td>
<td>77.02</td>
<td>77.31</td>
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<tr>
<td>Agronomic traits</td>
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</tr>
<tr>
<td>Standing ability, %</td>
<td>72.80</td>
<td>69.95</td>
</tr>
<tr>
<td>Canopy height, cm</td>
<td>28.63</td>
<td>31.55</td>
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<tr>
<td>Light interception, %</td>
<td>82.98</td>
<td>75.82</td>
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<tr>
<td>Vine length at sampling date 1, cm</td>
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<td>12.85</td>
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<td>Vine length at sampling date 2, cm</td>
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<td>Vine length at sampling date 3, cm</td>
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<td>65.31</td>
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<tr>
<td>Nodes at sampling date 1, cm</td>
<td>6.96</td>
<td>7.31</td>
</tr>
<tr>
<td>Nodes at sampling date 2, cm</td>
<td>12.26</td>
<td>13.01</td>
</tr>
<tr>
<td>Nodes at sampling date 3, cm</td>
<td>15.92</td>
<td>15.84</td>
</tr>
<tr>
<td>First node with non-senescent foliage, no.</td>
<td>11.67</td>
<td>11.14</td>
</tr>
</tbody>
</table>

† 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 breeders 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 AafA–TacTac, however at 100% bloom, aaf–TacTac had a total foliage area equal to AafA–TacTac (Table 2). These data show that there is no difference in total foliage area between aaf–tacTac and AafA–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 aaf–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 aaf–tacTac at 28 d after planting, 100% bloom, and green pea harvest, respectively. Plants with aaf–tacTac foliage had 12%, 18%, and 10% more foliage area at 28 d after planting, 100% bloom, and green pea harvest, respectively, than their aaf–TacTac counterparts. The contribution of stipule area to total foliage area at green pea harvest was highest (47%) in aaf–TacTac (data not shown). The AafA–TacTac and aaf–tacTac types had stipule area contributions of 34% and 41%, respectively. An increase in stipule area in aaf–TacTac as compared to AafA–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 AafA 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, AafA–TacTac and aaf–tacTac had significantly higher dry weights than aaf–TacTac. This trend was reversed for total dry weight at the second sampling date, where aaf–TacTac was
highest. The relative growth rate at the second sampling date was highest for \textit{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 \textit{afaf–tactac} type in the Alsweet 4683 background exhibited significantly higher dry weight at the third sampling date than \textit{Afaf–Tactac} and \textit{afaf–Tactac} (Table 3). The \textit{afaf–Tactac} type in the Frontier background had a slightly higher (though non-significant) total dry weight at the third sampling date than \textit{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 \textit{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 \textit{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.

<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–Tact</td>
<td>af–Tact</td>
<td>af–tact</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>Lowest pod-bearing node, no.</td>
<td>9.0</td>
<td>9.5</td>
<td>9.9</td>
</tr>
<tr>
<td>Peas per 600-cm² sample, no.</td>
<td>13.6</td>
<td>14.5</td>
<td>9.5</td>
</tr>
<tr>
<td>Yield per 10-plant sample, g</td>
<td>3.6</td>
<td>3.3</td>
<td>2.7</td>
</tr>
<tr>
<td>Yield per 600-cm² sample, g plot⁻¹</td>
<td>102.1</td>
<td>99.2</td>
<td>74.6</td>
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<td>Canopy height, cm</td>
<td>26.5</td>
<td>29.3</td>
<td>35.4</td>
</tr>
<tr>
<td>Vine length at sampling date 2, cm</td>
<td>43.5</td>
<td>42.3</td>
<td>49.3</td>
</tr>
<tr>
<td>Vine length at sampling date 3, cm</td>
<td>56.1</td>
<td>59.0</td>
<td>75.6</td>
</tr>
<tr>
<td>Nodes at sampling date 1, no.</td>
<td>6.8</td>
<td>7.0</td>
<td>6.8</td>
</tr>
<tr>
<td>Nodes at sampling date 2, no.</td>
<td>10.7</td>
<td>10.7</td>
<td>10.7</td>
</tr>
<tr>
<td>Nodes at sampling date 3, no.</td>
<td>12.2</td>
<td>12.5</td>
<td>14.3</td>
</tr>
<tr>
<td>First node with nonsenescent foliage, no.</td>
<td>8.2</td>
<td>8.3</td>
<td>9.3</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Background and foliage type</th>
<th>LSD (0.05)†</th>
</tr>
</thead>
<tbody>
<tr>
<td>Alsweet</td>
<td>0.5</td>
</tr>
<tr>
<td>Frontier</td>
<td>0.7</td>
</tr>
<tr>
<td>Dark Skin Perfection</td>
<td>0.7</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.
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 nonsense-
escent foliage among afaf–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 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 on ontog-
eny.

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-cm² sample, year
per 10-plant sample, and yield per 600-cm² 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-cm² sample, yield per 10-plant sample,
and yield per 600-cm² sample. In the Frontier back-
ground, afaf–tactac was lowest only for yield per 10-
plant sample and yield per 600-cm² 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 min-
nimal 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 re-
duced fertility. This detrimental effect on reproductive
organs may be further supported by the conclusion
that the unin allele, which is allelic to tac (Marx,
1986) and not present in this study, results in pollen
sterility in unin unin plants. The tac locus may there-
fore exhibit a general pleiotropic effect on Pisum repro-
duction.

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 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 depres-
sions 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 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 afaf–TacTac
and Afaf–TacTac pea foliage types has been thor-
oughly investigated by Gonzalez-Lauck (1990). In a
comparative study of population density and agrono-
mic performance of afaf–TacTac and Afaf–TacTac
cultivars, Gonzalez-Lauck reported that increasing
population densities of afaf–TacTac types was nec-
essary 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 (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. These trends are 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 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 afaf–TacTac or afaf–tactac grown under
minimal competition with support. Compared with their
afaf–TacTac and Afaf–TacTac counterparts, afaf–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 afaf–tactac
type in the late-maturing Dark Skin perfection back-
ground exhibited performance increases over its con-
stituent Afaf–TacTac and afaf–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 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 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 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—TacTact 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


