

Increased Herbage Yield in Alfalfa Associated with Selection for Fibrous and Lateral Roots

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ABSTRACT

A positive association between root morphology and herbage yield in alfalfa (*Medicago sativa* L.) has been reported previously. To further investigate this association, we created populations that differ in root morphology within four unrelated experimental germplasm sources. Two germplasm sources were divergently selected for lateral root number, and two sources underwent divergent selection for fibrous root mass followed by divergent selection for lateral root number. Selected and unselected populations from all germplasm sources were evaluated for herbage yield, root morphology, fall dormancy response, and disease resistance. Herbage yield was evaluated using eight replicates of a randomized complete block design with a split-plot arrangement of fertilizer rates (0 and 200 kg N ha⁻¹) as whole plots and alfalfa populations as subplots. Experiments were established twice at each of two locations in May 1994. Two herbage yield harvests were recorded from one experiment at each location, and plots were dug and evaluated for root traits in fall 1994. Herbage yields were taken from the other experiment at each location twice in 1994 and four times in 1995, and again plots were dug and evaluated for root traits in fall 1995. All populations were evaluated for fall dormancy response in 1994 and disease resistance in 1995 according to standard protocols. Populations selected for more fibrous or lateral roots had greater herbage yield than populations selected for no or few fibrous or lateral roots in all four germplasm sources. No differences in root size or weight, dormancy, or disease resistance were found between fibrous or branch-rooted vs. taprooted populations. Selection for fibrous and lateral roots within these alfalfa germplasms increased herbage yield in the tested environments.

A MAJOR GOAL of most plant breeding programs is to increase yield. In alfalfa, forage yield increases have been mostly credited to improved disease and pest resistance. Changing root growth patterns in alfalfa could possibly increase forage yield by affecting water and nutrient-uptake capacities. Several researchers have investigated the association between herbage yield and root morphology in alfalfa. Burton (1937) reported a low correlation ($r = 0.30$) between branched-root type and yield for individual plants grown in pots in a greenhouse and in a space-planted field. McIntosh and Miller (1980) evaluated three alfalfa cultivars in space-planted field conditions and found that correlations between root branching habit and shoot weight varied from 0.27 to 0.52. They also found that the association between root branching and plant weight when evaluated in

greenhouse pots was higher ($r = 0.60$) under water stress than under non-stress conditions ($r = 0.49$) (McIntosh and Miller, 1981). Peterson (1982) reported that lateral root number and total forage yield were moderately correlated in space-planted field studies at two locations ($r = 0.48$ and 0.51), while a weaker relationship was found between fibrous root mass and total forage yield ($r = 0.25$ and 0.34). Pederson et al. (1984b) reported that progenies from high root weight selections had greater root diameters, root branching, and shoot weights than progenies from low root weight selections in greenhouse trials. While conducting selection for increased alfalfa root yield in the greenhouse, Saindon et al. (1991) reported moderately high ($r = 0.71$ – 0.76) correlations between root branching and top yield. Contrary to all other reports, Busch and Davis (1969) transplanted alfalfa into competitive stands in the field and detected no correlation between herbage yield and the number of lateral roots.

Several studies have reported that the number of lateral roots or branched roots (Burton, 1937; Macintosh and Miller, 1981; Peterson, 1982; Pederson et al., 1984a; Johnson et al., 1996; Lamb et al., 1999) and fibrous root mass (Viands et al., 1981; Peterson, 1982; Johnson et al., 1996; Lamb et al., 1999) are heritable traits in alfalfa. We created unique experimental alfalfa populations that differ in fibrous root mass and/or lateral root number within four unrelated alfalfa germplasm sources (Lamb et al., 1999). The largest, healthiest plants displaying the root morphology trait of interest were selected in creating these divergent root morphology populations. Selecting plants in this manner may have influenced herbage yield by inadvertently selecting for changes in disease resistance response or root size and weight. Johnson et al. (1998) reported moderate negative correlations between fall dormancy and fibrous root mass ($r = -0.59$) and lateral root number ($r = -0.42$). Changes in dormancy response may have occurred while selecting for differences in root morphology and could have influenced herbage yield among these populations. We investigated the response of total herbage yield resulting from selection for root morphology traits in alfalfa. Our objectives were (i) to evaluate total herbage yield in these experimental populations, (ii) to identify any association between total herbage yield and root morphology traits, and (iii) to assess any changes in dormancy response or disease resistance that may have influenced total herbage yield.

MATERIALS AND METHODS

Development of Plant Materials

Four experimental germplasm sources were created for this study. MWNC (UMN 2892) was a composite of dormant ex-

Abbreviations: BRH, branch-rooted population; HF, population high in fibrous root mass; LF, population low in fibrous root mass; TAP, tap-rooted population.

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perimental populations selected for resistance to phytophthora root rot (*Phytophthora medicaginis* Hanson and Maxwell), aphanomyces root rot (*Aphanomyces euteiches* Drechs.), and the root-lesion nematode (*Pratylenchus penetrans* Cobb, Filipjev, and Schur-Stekhoven). NCPL (UMN 2893) was a composite of dormant experimental germplasms selected for differences in dinitrogen fixation and fibrous root mass (Viands et al., 1981). FLEM (UMN 2896) was a composite of moderately dormant experimental populations and cultivars with origins from the Flemish area of southern Europe (Barnes et al., 1977). NDRN (UMN 2894) was a composite of older (before 1970) nondormant cultivars and experimental germplasms selected for increased root N concentration.

Two selection schemes for root morphology traits were conducted under field conditions as described by Lamb et al. (1999). In the first scheme, MWNC and NCPL germplasm sources underwent two cycles of divergent selection for fibrous root mass, creating populations low in fibrous root mass (LF) and high in fibrous root mass (HF). The second cycle populations of HF or LF underwent one subsequent cycle of divergent selection for lateral roots resulting in HF and LF populations with either many lateral roots (branched roots, BRH) or few or no lateral roots (taprooted, TAP). This selection scheme created the following populations in both germplasm sources: HF_{C1}, HF_{C2}BRH, HF_{C2}TAP, LF_{C1}, LF_{C2}BRH, and LF_{C2}TAP. For the other selection scheme, FLEM and NDRN underwent two cycles of divergent selection for the number of lateral roots. This scheme created populations that were taprooted with few or no lateral roots (TAP) and branched types with many lateral roots (BRH). Populations created in both germplasm sources were BRH_{C1}, BRH_{C2}, TAP_{C1}, and TAP_{C2}. In both selection schemes, the largest and healthiest plants displaying the root traits of interest were selected.

Experimental Design

All selected and original unselected source populations were established 10 to 17 May 1994 in two experiments at both the Rosemount, MN Agric. Exp. Stn. on a Tallula silt loam (coarse silty, mixed mesic, Typic Hapludoll) and the Becker, MN Sand Plains Agric. Exp. Stn. on a Hubbard loamy sand (sandy, mixed, frigid Entic Hapludoll). The Rosemount station was rainfed, while the Becker station was irrigated to meet plant moisture needs using the checkbook method (Wright and Bergsrud, 1991). One experiment at each location was evaluated for root morphology at the end of the establishment year (1994) and will be referred as the establishment-year experiment. The other experiment at each location was evaluated for root traits at the end of the first production year (1995) and will be referred to as the first-production-year experiment. Each experiment consisted of eight replications of a randomized complete block design with a split-plot arrangement of fertilizer rates (0 and 200 kg N ha⁻¹) as whole plots and alfalfa populations as subplots. Subplots were 30 by 30 cm and consisted of 16 plants seeded by hand in a four by four grid with 7.5 cm between all plants, creating a plant density of 170 plants m⁻². Each of the 16 positions within the four by four grid was planted with two to three seeds and thinned to one plant 10 to 15 d after planting. Each subplot was surrounded by a row of border plants also spaced on 7.5-cm centers. On 11 to 15 July 1994, herbage was removed and discarded from all plots because of plant differences in time of germination.

Herbage was harvested at early flower from all plots of the establishment-year experiment on 9 August and 4 October at Becker and 22 August and 28 September at Rosemount in 1994. Samples were oven dried (35°C) and weighed, and yield

was recorded as grams per square meter. All plants were dug to a depth of 22 cm on 28 to 30 Sept. 1994 at Rosemount and 4 to 5 Oct. 1994 at Becker. Roots were washed and scored for lateral root number, fibrous root mass, and taproot diameter as described by Lamb et al. (2000). Lateral root number was scored from one to five (1 = 1–2, 2 = 3–6, 3 = 7–10, 4 = 11–14, and 5 = 15 or more lateral roots per plant). Fibrous root mass was scored from one to five (1 = 0–10%, 2 = 10–30%, 3 = 30–70%, 4 = 70–90%, and 5 = 90–100% of the root area with fibrous roots). Taproot diameter was measured in mm 5 cm below the crown. Roots from each plot were then oven dried (35°C) and weighed for root dry weight (g m⁻²) to a depth of 22 cm. Final plant numbers per square meter were also recorded.

Herbage from all plots from the first-production-year experiment at Becker was harvested at early flower on 10 August and 5 Oct. 1994 and 6 June, 7 July, 3 August, and 13 Sept. 1995. The same experiment at Rosemount, MN, was harvested on 22 August and 29 Sept. 1994 and 19 June, 19 July, 21 August, and 26 Sept. 1995. Samples were again oven dried, weighed, and herbage yield was recorded (g m⁻²). On 13, 14, 26, and 27 Sept. 1995, all plants from both locations were dug to a depth of 22 cm, washed, scored for root morphology traits, dried, counted, and weighed for root yield in the same manner as described above.

Analysis of variance using a fixed-effects model was conducted to determine the effects of year (only in the first-production-year experiment), location, N fertility, and alfalfa populations on herbage yield within each of the four germplasm sources (SAS Institute, 1988). Means and standard errors were calculated for herbage yield for each alfalfa population. Herbage yield means for the first-production-year experiment were reported as total herbage yield means from all six harvests across the 2 yr (two from 1994 and four from 1995).

Correlations among root morphology traits and herbage yield were determined separately for the two experiments on the basis of the means of the selected populations for each of the four germplasm sources. All original germplasm parent sources were composites of cultivars and experimental populations where seed was produced in later synthetic populations (SYN₂–SYN₄ generations). Therefore, the parent populations were less vigorous and had much lower yields than populations from the two cycles of selection for root morphology traits where seed was from the first synthetic population (SYN₁ generation). Therefore, the unselected parent populations from the four germplasm sources were not included in the correlation analyses.

Selected and unselected populations for root morphology traits (with sufficient seed supply) were evaluated using standardized tests for dormancy response (Barnes et al., 1991) and resistance to phytophthora root rot (Thies and Barnes, 1991), fusarium wilt (Nygaard and Barnes, 1991), and bacterial wilt (Fox and Thies, 1991). Mean comparisons (LSD_{0.05}) were calculated for disease and dormancy traits within each of the four germplasm sources.

RESULTS

Herbage Yield

Total herbage yield response to selection for root morphology differed among the four germplasm sources and between the establishment-year and first-production-year experiments (Tables 1–4). Herbage yield was greater at Rosemount than Becker in three of the four germplasm sources in the establishment-year experi-

Table 1. Alfalfa herbage yield mean squares from the establishment-year experiment at two Minnesota locations in four germplasm sources selected for root morphology.

| Source | df | FLEM | NDRN | df | MWNC | NCPL |
|------------------|----|--------|--------|-----|--------|--------|
| Location (Loc) | 1 | 221** | 208 | 1 | 1286** | 3306** |
| N Rate | 1 | 6120** | 4790** | 1 | 4195** | 3972** |
| Loc × N Rate | 1 | 6 | 3 | 1 | 98 | 548 |
| Error a | 28 | 210 | 344 | 28 | 231 | 187 |
| Population (P) | 3 | 2591** | 3230** | 6 | 5707** | 421** |
| Loc × P | 3 | 129 | 4 | 6 | 93 | 72 |
| N Rate × P | 3 | 133 | 9 | 6 | 44 | 66 |
| Loc × N Rate × P | 3 | 87 | 92 | 6 | 166 | 46 |
| Error b | 84 | 161 | 201 | 164 | 130 | 110 |
| CV, % | | 21 | 19 | | 18 | 20 |

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

ment (Table 1). In the first-production-year experiment herbage yield was the same at both locations in 1994, but was greater at Becker than Rosemount for three of four of the germplasm sources in 1995, which precipitated a year × location interaction (Table 2). Winter injury occurred at Rosemount and wet soil conditions delayed first harvest by nearly 2 wk in 1995. First harvest in 1995 for all plots at Rosemount were taken at ≈50 to 70% bloom and had suffered yield loss from lodging and wet conditions.

Annual addition of 200 kg N ha⁻¹ increased total herbage yield in all populations from all four germplasm sources at both locations in both years of these experiments (Tables 1 and 2). Low application rates of N fertilization have been recommended for increased herbage yield in alfalfa during the seeding year (Tesar and Marble, 1988). Giddens (1959) reported increased herbage yields with N fertilizer rates of at least 100 kg N ha⁻¹. The additions of N fertilizer is generally not recommended to increase herbage yield in established stands of alfalfa (Undersander et al., 1994). However, seasonal herbage yield increases from N fertilizer applications to established stands of alfalfa have been reported (Giddens, 1959; Moline and Robison, 1971; Lee and Smith, 1972).

In both the FLEM and NDRN germplasm sources, BRH_{C2} had greater total herbage yield than either TAP_{C1} or TAP_{C2} in both the establishment-year and first-pro-

duction-year experiments (Tables 1–4). A year × population interaction was found for herbage yield in the NDRN germplasm source in the first-production-year experiment (Table 2). NDRNBRH_{C2} had greater herbage yield than NDRNTAP_{C2} in both years of the experiment, but was only significantly greater in 1994 (data not shown).

In the establishment-year experiment, MWNC HF_{C2}BRH had greater herbage yield than any of the other MWNC populations selected for root morphology (Table 3). In the first-production-year experiment, year × population, location × population, and year × location × population interactions were found for herbage yield in the MWNC germplasm source (Table 2). The populations generally ranked the same at both locations in both years, but herbage yield means were different only in 1995 at Becker, MN. However, the overall total herbage yield was greater for MWNC HF_{C2}BRH than MWNC LF_{C2}TAP (Table 4). Delay of the first harvest at Rosemount in 1995 may have contributed to the lower herbage yields at Rosemount than at Becker.

Populations differed in total herbage yield in the NCPL germplasm source in both the experiments, with NCPL HF_{C2}BRH, having significantly greater total herbage yield than the other NCPL populations only in the first-production-year experiment (Tables 1–4). NCPL LF_{C2}BRH had greater herbage yield than the other low fibrousness selections at Becker, MN, but

Table 2. Alfalfa herbage yield mean squares from the first-production-year experiment across 2 yr and two Minnesota locations in four germplasm sources selected for root morphology.

| Source | df | FLEM | NDRN | df | MWNC | NCPL |
|-----------------------|-----|-----------|----------|-----|-----------|----------|
| Year (Yr) | 1 | 110 868** | 78 818** | 1 | 236 967** | 68 421** |
| Location (Loc) | 1 | 5 878** | 25 180** | 1 | 32 159* | 311 |
| Yr × Loc | 1 | 8 330** | 16 699** | 1 | 23 216** | 1 231 |
| Rep (Loc) | 14 | 686 | 972 | 14 | 1 362 | 473 |
| N Rate | 1 | 8 373** | 8 398** | 1 | 24 365** | 16 493** |
| Yr × N Rate | 1 | 81 | 138 | 1 | 572 | 31 |
| Loc × N Rate | 1 | 580 | 32 | 1 | 2 340 | 326 |
| Yr × Loc × N Rate | 1 | 8 | 68 | 1 | 0 | 768 |
| Error a | 41 | 1 002 | 904 | 41 | 829 | 373 |
| Population (P) | 3 | 6 504** | 9 512** | 6 | 18 201** | 2 837** |
| Yr × P | 3 | 496 | 1 019* | 6 | 2 222** | 177 |
| Loc × P | 3 | 325 | 223 | 6 | 1 116** | 604** |
| N Rate × P | 3 | 105 | 305 | 6 | 210 | 116 |
| Yr × Loc × P | 3 | 83 | 195 | 6 | 814* | 67 |
| Yr × N Rate × P | 3 | 59 | 45 | 6 | 61 | 71 |
| Loc × N Rate × P | 3 | 82 | 113 | 6 | 282 | 294 |
| Yr × Loc × N Rate × P | 3 | 81 | 50 | 6 | 128 | 28 |
| Error b | 162 | 226 | 308 | 322 | 302 | 160 |
| CV, % | | 19 | 22 | | 20 | 19 |

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

Table 3. Herbage yield and root trait means from unselected and selected alfalfa populations for root morphology across two Minnesota locations for four germplasm sources from the establishment-year experiment.

| Population | Dry matter herbage yield | Fibrous root mass | Lateral root number | Taproot diameter | Dry matter root weight | Plant count |
|----------------------------|--------------------------|--------------------|---------------------|------------------|------------------------|---------------------|
| | g m ⁻² | score [†] | score [‡] | mm | g m ⁻² | no. m ⁻² |
| FLEM BRH _{C2} § | 755 | 1.20 | 2.17 | 6.3 | 301 | 151 |
| FLEM BRH _{C1} ¶ | — | — | — | — | — | — |
| FLEM—Parent | 519 | 1.12 | 1.73 | 5.4 | 199 | 128 |
| FLEM TAP _{C1} | 660 | 1.13 | 1.71 | 5.9 | 251 | 145 |
| FLEM TAP _{C2} | 655 | 1.13 | 1.58 | 6.1 | 273 | 150 |
| LSD _{0.05} | 68 | NS | 0.25 | 0.3 | 33 | 16 |
| NDRN BRH _{C2} § | 945 | 1.25 | 2.11 | 7.0 | 425 | 157 |
| NDRN BRH _{C1} | 827 | 1.15 | 1.95 | 6.8 | 366 | 143 |
| NDRN—Parent | 680 | 1.10 | 1.80 | 6.4 | 300 | 128 |
| NDRN TAP _{C1} ¶ | — | — | — | — | — | — |
| NDRN TAP _{C2} | 843 | 1.13 | 1.60 | 6.9 | 414 | 157 |
| LSD _{0.05} | 76 | 0.06 | 0.13 | 0.3 | 42 | 9 |
| MWNC HF _{C2} BRH# | 819 | 1.66 | 2.29 | 6.2 | 314 | 151 |
| MWNC HF _{C2} TAP | 740 | 1.63 | 2.08 | 6.2 | 285 | 146 |
| MWNC HF _{C1} | 687 | 1.48 | 2.21 | 6.0 | 264 | 138 |
| MWNC—Parent | 377 | 1.11 | 1.67 | 5.3 | 154 | 114 |
| MWNC LF _{C1} | 742 | 1.19 | 2.01 | 6.1 | 289 | 142 |
| MWNC LF _{C2} BRH | 742 | 1.18 | 2.03 | 6.2 | 314 | 149 |
| MWNC LF _{C2} TAP | 733 | 1.15 | 1.75 | 6.0 | 303 | 158 |
| LSD _{0.05} | 60 | 0.10 | 0.12 | 0.3 | 26 | 10 |
| NCPL HF _{C2} BRH# | 648 | 1.36 | 2.17 | 5.9 | 233 | 141 |
| NCPL HF _{C2} TAP | 593 | 1.39 | 1.94 | 5.6 | 224 | 150 |
| NCPL HF _{C1} | 590 | 1.28 | 3.02 | 5.6 | 211 | 140 |
| NCPL—Parent | 514 | 1.14 | 1.90 | 5.7 | 195 | 127 |
| NCPL LF _{C1} | 519 | 1.08 | 1.76 | 5.5 | 179 | 130 |
| NCPL LF _{C2} BRH | 591 | 1.07 | 1.82 | 5.7 | 239 | 149 |
| NCPL LF _{C2} TAP | 574 | 1.09 | 1.67 | 5.7 | 226 | 148 |
| LSD _{0.05} | 55 | 0.08 | 0.13 | 0.3 | 23 | 10 |

[†] Fibrous roots scored from 1 to 5; 1 = 0–10%, 2 = 10–30%, 3 = 30%–70%, 4 = 70–90%, 5 = 90–100% of the root area with fibrous roots.

[‡] Lateral root number scored from 1 to 5; 1 = 1–2, 2 = 3–6, 3 = 7–10, 4 = 11–14, 5 = 15 or more lateral roots per plant.

[§] FLEM and NDRN germplasm sources underwent two cycles of divergent selection for lateral root number; BRH is branch-rooted population and TAP is taprooted population.

[¶] Populations not included due to insufficient seed supply.

[#] MWNC and NCPL germplasm sources underwent two cycles of divergent selection for fibrous root mass and one subsequent cycle of divergent selection for lateral root number.

all LF selections yielded the same at Rosemount, MN, causing the population × location interaction (data not shown).

Correlations between Total Herbage Yield and Root Morphology Traits

In all four germplasm sources, no association was evident between total herbage yield and lateral root number in the establishment-year experiment (Table 5). However, in the first-production-year experiment, correlations ($r = 0.41$ – 0.67) between these two traits in all germplasm sources showed that alfalfa populations with more lateral roots had greater total herbage yield.

Positive correlations between fibrous root mass and total herbage yield were found only for FLEM and NCPL in the establishment-year experiment and for NDRN and MWNC in the first-production-year experiment. Neither FLEM nor NDRN were selected for differences in fibrous root mass, and the overall fibrous root mass of these two germplasm sources was low compared with other germplasm sources (Tables 3 and 4). Lamb et al. (1999) reported a strong association between lateral root number and fibrous root mass ($r = 0.75$ – 0.77) and suggested that selection for either one of these root traits would modify the other.

Taproot diameter was positively correlated with herbage yield in the first-production-year experiment for NCPL and in both experiments for NDRN. No relation-

ship between herbage yield and taproot diameter was found in either the FLEM or MWNC germplasm sources. Positive correlations between herbage yield and dry matter root weight were found only in the first-production-year experiment in just the NDRN and MWNC germplasm sources. Associations between plant count and herbage yield were found only in the first-production-year experiment. These two traits were positively correlated in NDRN and negatively correlated in the FLEM and NCPL germplasm sources. Winter injury at Rosemount in 1995 probably influenced the positive correlations between herbage yield and dry matter root weight and plant count in the nondormant NDRN germplasm source. The negative correlations between herbage yield and plant count in FLEM and NCPL imply that plots with fewer plants produced more herbage yield. Fewer plants would imply less plant to plant competition and greater area in which to grow per plant. These results agree with previous reports of increased herbage yield per plant with greater space between plants (Johnson et al., 1996; Burton, 1937)

Dormancy and Disease Resistance Response

Selection for fibrous root mass or lateral root number had no effect on fall growth score in any of the four germplasm sources (Table 6). Dormancy class, estimated from fall growth scores, did not differ between the unselected parent vs. any of the selected populations

Table 4. Herbage yield and root trait means from unselected and selected alfalfa populations for root morphology across 2 yr and Minnesota locations four germplasm sources from the first-production-year experiment.

| Population | Dry matter herbage yield | Fibrous root mass | Lateral root number | Taproot diameter | Dry matter root weight | Plant count |
|----------------------------|--------------------------|--------------------|---------------------|------------------|------------------------|---------------------|
| | g m ⁻² | score [†] | score [‡] | mm | g m ⁻² | no. m ⁻² |
| FLEM BRH _{C2} § | 1901 | 1.39 | 2.74 | 7.6 | 348 | 121 |
| FLEM BRH _{C1} ¶ | — | — | — | — | — | — |
| FLEM—Parent | 1377 | 1.26 | 2.31 | 7.1 | 248 | 93 |
| FLEM TAP _{C1} | 1729 | 1.28 | 2.20 | 7.5 | 311 | 108 |
| FLEM TAP _{C2} | 1719 | 1.27 | 2.15 | 7.4 | 335 | 126 |
| LSD _{0.05} | 151 | 0.10 | 0.18 | 0.4 | 36 | 11 |
| NDRN BRH _{C2} § | 2205 | 1.47 | 2.41 | 8.2 | 426 | 125 |
| NDRN BRH _{C1} | 2003 | 1.29 | 2.16 | 7.9 | 345 | 140 |
| NDRN—Parent | 1580 | 1.16 | 2.24 | 7.9 | 259 | 120 |
| NDRN TAP _{C1} ¶ | — | — | — | — | — | — |
| NDRN TAP _{C2} | 1993 | 1.16 | 1.90 | 7.8 | 402 | 146 |
| LSD _{0.05} | 185 | 0.17 | 0.38 | NS | 58 | 23 |
| MWNC HF _{C2} BRH# | 2158 | 1.74 | 2.90 | 7.5 | 393 | 128 |
| MWNC HF _{C2} TAP | 2115 | 1.79 | 2.75 | 7.6 | 402 | 127 |
| MWNC HF _{C1} | 1755 | 1.53 | 2.78 | 7.7 | 333 | 101 |
| MWNC—Parent | 1090 | 1.15 | 1.92 | 6.5 | 187 | 89 |
| MWNC LF _{C1} | 1887 | 1.26 | 2.44 | 7.4 | 348 | 122 |
| MWNC LF _{C2} BRH | 2062 | 1.22 | 2.48 | 7.7 | 393 | 125 |
| MWNC LF _{C2} TAP | 1983 | 1.22 | 2.19 | 7.3 | 374 | 128 |
| LSD _{0.05} | 172 | 0.10 | 0.18 | 0.3 | 44 | 12 |
| NCPL HF _{C2} BRH# | 1660 | 1.38 | 2.38 | 7.0 | 270 | 111 |
| NCPL HF _{C2} TAP | 1490 | 1.33 | 2.10 | 6.5 | 221 | 113 |
| NCPL HF _{C1} | 1405 | 1.31 | 2.25 | 6.7 | 214 | 95 |
| NCPL—Parent | 1148 | 1.17 | 2.18 | 6.7 | 169 | 81 |
| NCPL LF _{C1} | 1418 | 1.10 | 2.02 | 6.4 | 202 | 102 |
| NCPL LF _{C2} BRH | 1462 | 1.10 | 2.02 | 6.6 | 233 | 109 |
| NCPL LF _{C2} TAP | 1389 | 1.11 | 1.77 | 6.7 | 236 | 114 |
| LSD _{0.05} | 118 | 0.07 | 0.15 | 0.4 | 58 | 10 |

[†] Fibrous roots scored from 1 to 5; 1 = 0–10%, 2 = 10–30%, 3 = 30–70%, 4 = 70–90%, 5 = 90–100% of the root area with fibrous roots.

[‡] Lateral root number scored from 1 to 5; 1 = 1–2, 2 = 3–6, 3 = 7–10, 4 = 11–14, 5 = 15 or more lateral roots per plant.

[§] FLEM and NDRN germplasm sources underwent two cycles of divergent selection for lateral root number; BRH is branch-rooted population and TAP is taprooted population.

[¶] Populations not included due to insufficient seed supply.

[#] MWNC and NCPL germplasm sources underwent two cycles of divergent selection for fibrous root mass and one subsequent cycle of divergent selection for lateral root number.

for root morphology. Resistance to bacterial wilt, fusarium wilt, and phytophthora root rot was not different between TAP and BRH selections in any of the four germplasm sources (Table 6). Only the FLEM germplasm source showed a significant gain in resistance to fusarium wilt and phytophthora root rot in both the BRH_{C2} and TAP_{C2} populations compared with the original unselected parent population. Flemish germplasms are known to be susceptible to systemic diseases (Barnes et al., 1977). Therefore, indirect selection for resistance probably occurred in both the TAP and BRH populations when we selected the largest and healthiest plants displaying the root morphology traits of interest.

DISCUSSION

In all four germplasm sources, the populations selected for more fibrous or lateral roots (HF_{C2}BRH or BRH_{C2}) had greater herbage yield than those selected for no or few fibrous or lateral roots (LF_{C2}TAP or TAP_{C2}). The magnitude of herbage yield difference between these divergent root types varied among the germplasm sources and was affected by environmental conditions. Other researchers have also reported that the relationship between herbage yield and root morphology traits varied in different field environments. McIntosh and Miller (1980) reported that correlations between lateral root number and herbage yield differed

Table 5. Pearson correlations between herbage yield and root morphology traits for selected populations in each of the four germplasm sources, excluding the unselected parent populations, across two Minnesota locations and 2 yr.

| Root trait | Herbage yield | | | | | | | |
|------------------------|--------------------|-----------------|--------------------|-----------------|--------------------|-----------------|--------------------|-----------------|
| | FLEM | | NDRN | | MWNC | | NCPL | |
| | Establishment year | Production year |
| Fibrous root mass | 0.75** | 0.55 | 0.56 | 0.61* | 0.39 | 0.41* | 0.44* | 0.31 |
| Lateral root number | 0.50 | 0.66* | 0.46 | 0.65* | 0.36 | 0.44* | 0.36 | 0.67** |
| Taproot diameter | 0.40 | 0.52 | 0.57* | 0.60* | 0.27 | 0.28 | 0.34 | 0.71** |
| Dry matter root weight | 0.43 | 0.20 | 0.41 | 0.84** | 0.21 | 0.47* | 0.29 | 0.37 |
| Plant count | -0.14 | -0.62* | 0.02 | 0.64* | -0.12 | -0.08 | -0.06 | -0.42* |

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

Table 6. Fall growth scores, dormancy, and disease ratings of unselected and selected alfalfa populations for root morphology traits.

| Entry† | Fall growth score | Dormancy class | Resistance | | |
|---------------------------|-------------------|----------------|----------------|---------------|-----------------------|
| | | | Bacterial wilt | Fusarium wilt | Phytophthora root rot |
| | | | % | | |
| NCPL HF _{C2} BRH | 4.3 | 3 | 54 | 41 | 38 |
| NCPL HF _{C2} TAP | 4.3 | 3 | 52 | 49 | 52 |
| NCPL HF _{C1} | 4.7 | 3 | 60 | 50 | 36 |
| NCPL—Parent | 4.5 | 3 | 58 | 39 | 31 |
| NCPL LF _{C1} ‡ | 4.6 | 3 | — | — | — |
| NCPL LF _{C2} BRH | 4.5 | 3 | 64 | 39 | 56 |
| NCPL LF _{C2} TAP | 4.0 | 3 | 67 | 39 | 38 |
| MWNC HF _{C2} BRH | 4.0 | 3 | 49 | 46 | 37 |
| MWNC HF _{C2} TAP | 4.1 | 3 | 44 | 45 | 53 |
| MWNC HF _{C1} ‡ | 4.4 | 3 | — | — | — |
| MWNC—Parent | 4.2 | 3 | 31 | 31 | 60 |
| MWNC LF _{C1} ‡ | 3.8 | 3 | — | — | — |
| MWNC LF _{C2} BRH | 4.0 | 3 | 43 | 31 | 48 |
| MWNC LF _{C2} TAP | 3.9 | 3 | 40 | 31 | 41 |
| FLEM BRH _{C2} | 3.2 | 4 | 18 | 39 | 25 |
| FLEM BRH _{C1} | 3.4 | 4 | — | — | — |
| FLEM—Parent | 3.9 | 4 | 21 | 19 | 18 |
| FLEM TAP _{C1} | 3.5 | 4 | 29 | 41 | 19 |
| FLEM TAP _{C2} | 3.4 | 4 | 28 | 45 | 36 |
| NDRN BRH _{C2} | 2.3 | 8 | 4 | 50 | 37 |
| NDRN BRH _{C1} | 2.6 | 8 | 7 | 55 | 43 |
| NDRN—Parent | 2.8 | 8 | 10 | 50 | 36 |
| NDRN TAP _{C1} § | — | — | — | — | — |
| NDRN TAP _{C2} | 2.3 | 8 | 3 | 53 | 30 |
| LSD _{0.05} | 0.7 | — | 16 | 16 | 30 |
| Resistant check | — | — | 41 | 54 | 43 |
| Susceptible check | — | — | 8 | 9 | 5 |

† BRH is branch-rooted population; TAP is taprooted population.

‡ Insufficient seed supply to test for disease response.

§ Insufficient seed supply to test for dormancy response.

between spring, summer, and fall harvests during the first production year. Peterson (1982) reported that soil types (confounded with location) also affected associations of herbage yield with both lateral root number and fibrous root mass.

Correlations between these root morphology traits and herbage yield ranged from moderately high to no association at all. Few associations between root morphology traits and herbage yield were found in the establishment-year experiment. Lamb et al. (2000) and Carlson (1925) reported that the distinctive characteristics of alfalfa roots do not fully develop until after ≈3 to 4 mo of normal growth. It is possible that root morphology traits in the establishment-year study did not develop rapidly enough to influence herbage yield sufficiently to exhibit a correlation in some of the germplasm sources. Positive correlations between lateral root number and herbage yield were also reported by McIntosh and Miller (1980), Peterson (1982), and Saindon et al. (1991).

Busch and Davis (1969) found no association between the number of lateral roots and herbage yield. They transplanted alfalfa seedlings into the field rather than direct seeding. Lamb et al. (2000) found no correlation between transplanted and seeded field plants for lateral root number. The majority of lateral roots in the transplanted alfalfa plants arose from the position of taproot tip at the time of transplanting, while seeded plants had lateral roots arising in a random pattern from all areas of the taproot. Using transplants may have contributed to the lack of association between herbage yield and

lateral root number in the study conducted by Busch and Davis (1969).

Selecting the largest and healthiest plants displaying the root morphology trait of interest may have inadvertently led to changes in root size and weight, disease resistance, dormancy response, and survivability in the selected populations. In all four germplasm sources, dry matter root weight, number of plants, and taproot diameter were all significantly greater in the second cycle of selection populations compared with the original parent sources (Tables 3 and 4). However, these three traits were not different between the BRH_{C2} and TAP_{C2} populations in either the FLEM or NDRN germplasm sources or between the HF_{C2}BRH and LF_{C2}TAP populations in either of the MWNC and NCPL germplasm sources. Also, no differences between BRH_{C2} and TAP_{C2} or HF_{C2}BRH and LF_{C2}TAP populations were found for disease resistance or fall dormancy response. Therefore, differences in plant number, root mass, taproot diameter, disease resistance, and dormancy response cannot explain the differences in total herbage yield between BRH_{C2} and the TAP populations in FLEM and NDRN or between HF_{C2}BRH and the LF populations in MWNC and NCPL. Herbage yield of the BRH_{C2} or HF_{C2}BRH populations was 7 to 14% greater than the TAP_{C2} or LF_{C2}TAP populations in the establishment-year experiment and 9 to 16% greater in the first-production-year experiment. These results indicated that in the tested environments herbage yield was positively associated with increased amounts of fibrous or lateral roots within these alfalfa germplasm sources.

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