Crop traits for water stress tolerance

Edwin Donaldson

Abstract. Cultivars vary considerably in how they respond to moisture stress throughout crop development. In areas of the Pacific Northwest with less than 250 mm of annual rainfall, winter wheat is under moisture stress most of the time from planting to harvest. Cultivars must be able to absorb moisture, germinate, and emerge under high temperature, poor seed zone moisture, and deep seed cover. Moisture stress slows emergence and seedling development and reduces most yield components, including number of tillers, seeds per spike, seeds per unit area, seed size, and seed weight per unit volume. Additionally, leaf senescence and maturity are early under moisture stress conditions. A cultivar cannot obtain its potential yield with less than adequate moisture; therefore, under moisture stress fewer tillers and seeds are produced. Which plant structures are reduced is determined by the growth stage of the plant during stress, while the extent of this reduction is determined by the severity of moisture stress and the genotype of the cultivar.

Key words: wheat, moisture stress, cropping systems, emergence

Introduction

Crop traits that are advantageous for tolerance to water deficits vary greatly with the crop's environment. To describe desirable traits, we must specify the developmental stage of the crop when the water deficit occurs and the duration of the stress. Other stresses need to be understood, such as cold, heat, disease incidence and insect pressures. Certain traits may be advantageous in one environment and neutral or even harmful in another. If near-average production is essential every year, a different cultivar or even a different crop may be more desirable than one with a high yield in good years but a poor yield, or none at all, in unfavorable years. The possibility of replanting with the same crop or an alternative crop if the first crop fails must also be considered. For best moisture stress tolerance, growing alternative crops may be advantageous, such as barley (Hordeum vulgare L.) instead of wheat (Triticum aestivum L.) (Acevedo, 1987), or alfalfa (Medicago sativa L.) instead of other forage legumes (Peterson et al., 1992).

This paper emphasizes traits advantageous to production in the Pacific Northwest (PNW) of the United States, particularly in areas with less than 250 mm annual precipitation. The PNW is dominated by winter wheat grown in rotation with summer fallow, with some production of spring wheat, spring barley, Triticale, and canola (Brassica spp.). Except for two weeks to a month in the spring, crops are under continuous moisture stress from planting to harvest. Historically, winter kill occurs about once in ten years, but it occurred in 1989 and in 1991. The 1991 winter kill was the worst on record. However, winter injury is quite frequent, as are late spring frosts. Diseases include the foliar diseases stripe rust (caused by Puccinia striiformis) and leaf rust (P. recondita), and the root and crown diseases bare patch (Rhizoctonia spp.), strawbreaker foot rot (Pseudocercospora herpotrichoides), and dryland foot rot (Fusarium culmorum). Other pests include fall aphids, winter annual grasses, and broadleaf weeds. Other diseases and insects are less frequently of economic importance or are important in localized stress.

Cultural practices for winter wheat involve establishing an 8 to 16 cm dust mulch in the spring at the start of the summer fallow. This is usually accomplished with a primary tillage implement, such as a disc or cultivator, followed by a rod weeder. Summer fallow is maintained with the rod weeder, as necessary, for weed control. Under normal conditions, PNW soils have sufficient soil moisture (8-10%) immediately below the rod pan for wheat to germinate in the fall.

Cultivar Characteristics for Water Stress Tolerance

Germination and emergence

Stand establishment is the most consistent production problem in the low rainfall area of the PNW. A deep furrow drill is used to place seeds 3 to 5 cm into the moist soil below the dust mulch. Deep seeding often reduces emergence (Gan et al., 1992). Seed zone temperature ranges from 30°C or higher in late August to as low as 15°C around mid September. During that time seed zone moisture declines. Wheat emerges faster when seeded early because the soil is warmer and wetter. Other crops and some weeds respond similarly. In a model to predict emergence of the weed velvetleaf (Abutilon theophrasti), Forcella (1993) used moisture and temperature as the most important factors. Iribari et al. (1993) found that the emergence time for maize (Zea mays L.) increased by 2.8 degree days for each 1 cm increase in seed depth and 3.2 degree days for each 1% decrease in soil moisture. A rain that prevents emergence because of crust is more likely with later seeding because emergence is slower. The need to reseed because a surface crust prevents emergence is always a possibility. In general, better yields are obtained by early seeding the first time than by reseeding late, as may be necessary if the first seeding is delayed and fails to emerge. Seeding is usually completed before September 10.

Because of differences in seed size and hardness, cultivars of wheat (Lafond and
Baker, 1986), beans (*Phaseolus vulgaris*) (Huel, 1993), and other legumes (Hadas, 1976) differ in speed of germination under stress. High temperature dormancy of freshly harvested seeds can restrict emergence of winter wheat, particularly under moisture limiting conditions (M.W. Simmon, Research Leader, USDA-ARS, Pullman, Washington, private communication, August 1995). Some cultivars have lower dormancy than others.

In an experiment conducted for several years at the Dry Land Research Unit, Lind, Washington (unpublished), the highest yields were obtained when seeding was between September 10 and September 20. However, there was no statistical difference in grain yield among seeding dates in September. Reduced yields were obtained with seeding in late August or early October. This result was consistent for the five cultivars tested. However, some cultivars had a wider range of acceptable planting date than others. In the 1991-92 crop, seeding on September 20 was too late to obtain maximum yield. Seed zone moisture had decreased to where a good stand could not be obtained; where a stand was obtained, plant development was insufficient before winter because of moisture stress. In years favoring fall plant development, early seeding can create more fall growth than is desirable, extracting soil moisture in the fall that could be better used to increase grain yield in the spring (Winter and Musick, 1993).

For seedling in this area, cultivars must be able to germinate under low soil moisture and emerge rapidly through several centimeters of dry soil. Table 1 shows the results of a yield trial conducted in Horse Heaven Hills, Washington, where seeding was deep into marginal seed zone moisture. Coleoptile length is correlated with ability to emerge, particularly in semi-dwarf wheats such as 'Batum' and 'Andrews.' 'Buchanan' has the weakest straw. 'Weston' is the tallest. Tall plants with long coleoptiles and weak straw appear to emerge best. Semi-dwarfs with weak straw appear to emerge better than stiff strawed semi-dwarfs. With adequate moisture, all winter wheat cultivars in advanced testing in Washington, Idaho, and Oregon will produce adequate stands when covered with 13 cm of soil, as they did in the Connell yield trial in 1992 (data not shown).

### Winter survival

Moisture stress is usually not considered a component of winter kill. However, winter kill in this area is usually associated with snow mold caused by *Typhula incarnata*, *Fusarium nivale*, or both, or with spring desiccation. Winters usually have several cycles of freezing and thawing, with plant growth resuming during the warm periods, as happened in 1979. Following winter injury, roots usually are not functional in the spring. The soil surface has been dried by wind and freezing. Plant crowns that have been weakened by winter conditions must reroot to initiate spring growth. In dry soil the crowns cannot reroot. Deep crowns may be beneficial for rerooting since the crown is more likely to be in contact with adequate soil moisture. In the two years where a single freezing event damaged the wheat, 1989 and 1991, a strong wind was accompanied by temperatures of −15°C to −20°C. In yield trials involving different rates and dates of seeding in 1989 and 1991, plants were more likely to survive where the seeding rate was high and the plants were large, possibly because the crown was protected from wind under these conditions. Plants protected from the wind by either crop or weed residue also survived. Also, plants in a wet, firm seed bed survived better (preirrigated vs. dryland planting). Cultivars with deep crowns again appeared to have some advantages. Some wheat cultivars establish crowns several centimeters below the soil surface when seeded deep. The crown is always established above the seed, however. 'Hatton' has a deep crown, while Buchanan has a shallow crown. Hatton is more winter hardy than Buchanan.

### Early plant development

Moisture stress early in the plant's life delays development. When soil moisture is marginal, wheat seedlings can emerge from deep seeding and survive for at least four weeks with only two to four leaves above ground. However, crowns will not develop. Cultivars are needed that can extract moisture better. With adequate seed zone moisture, crowns will form in the dust mulch, but crown roots will not develop. Short crown roots developed in about ten days following a 20 mm rain at the Dry Land Research Unit in October 1993. The wheat had been planted about fifty days earlier. Similarly, NeSmith and Ritchie (1992) found delayed development in maize grown under moisture stress.

Cultivars differ in how they respond to row spacing and plant density. Plant density determines the number of individuals sharing limited resources; plant arrangement or row spacing controls the interception or retrieval of that resource (Wade et al., 1993). In the PNW, a higher seeding rate is needed for maximum yield when seeding is delayed, because the delay decreases plant development before winter. Spring seeding rates usually are higher and recommended row spacing narrower, partly because a deep furrow drill is not required for establishing a stand of spring crops. Producers in this area also use a higher seeding rate in the higher rainfall areas and under irrigation. Generalizations about how seeding rates must be adjusted for seeding date and row spacing cannot be extended to all locations and all crops (Silim et al., 1993). Cultivars also differ in their ability to germinate uniformly. Greater uniformity of seedling emergence could result in higher grain yields (Gan et al., 1992).

Rapid growth may be a disadvantage in winter wheat sown early where too much water can be extracted from the soil in the fall (Winter and Musick, 1993). However, early vigor and an accumulation of biomass before anthesis is usually an advantage in wheat (Turner and Nicolas, 1987), lentils (*Lens culinaris* Medik.) (Silim et al., 1993) and maize (Sinclair et al., 1990). Poorly adapted genotypes brought into this area produce less pre-anthesis biomass and mature earlier than adapted genotypes.

### Table 1. Stand and grain yield at Horse Heaven, 1987, and growth chamber coleoptile length at 15°C.

<table>
<thead>
<tr>
<th>Cultivar</th>
<th>Yield (kg/ha)</th>
<th>Stand (%)</th>
<th>Coleoptile Length at 15°C (mm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Buchanan</td>
<td>2380</td>
<td>94</td>
<td>146</td>
</tr>
<tr>
<td>Blizzard</td>
<td>1840</td>
<td>78</td>
<td>117</td>
</tr>
<tr>
<td>Weston</td>
<td>1700</td>
<td>60</td>
<td>120</td>
</tr>
<tr>
<td>Hatton</td>
<td>1430</td>
<td>44</td>
<td>104</td>
</tr>
<tr>
<td>Batum</td>
<td>680</td>
<td>29</td>
<td>84</td>
</tr>
<tr>
<td>Andrews</td>
<td>820</td>
<td>23</td>
<td>107</td>
</tr>
</tbody>
</table>

American Journal of Alternative Agriculture
Roots

Roots from short season crops or crops whose seeding is delayed may not penetrate deeply enough into the soil to capture the available water (Winter and Musick, 1993). Root growth is greater in moist than in wet soil (Xu and Bland, 1993). When plants are stressed early and the stress is then removed, root growth recovers and continues later into the season (Meisner and Karnok, 1992). Roots of some cultivars penetrate compacted soil layers better than other cultivars (Kasperbauer and Busscher, 1991). Plants tend to root deeper in dry soil or when irrigated less frequently (Dwangan et al., 1992). Deep rooting ability is an advantage in many moisture deficient areas, but may also be a disadvantage (Ludlow and Muchow, 1990) or of no value where the rooting ability exceeds the wetting front.

For water stress tolerance, plants need to extract as much moisture as possible from the soil. Early establishment of a deep and profuse root system is desirable both for extraction of soil water and competition with weeds. However, there probably is no advantage in having a rooting ability beyond the limitations of soil depth or wetting front. Rooting capabilities may be as specific for an area as other selection characteristics. The wheat cultivar ‘Wanser’ draws moisture from only about 1.4 m of soil while other cultivars draw moisture from much deeper (unpublished). Wanser has been competitive in the lower rainfall areas of Washington because its roots penetrate as deep as the wetting front in these areas.

Pests

Any pest that limits the amount of water available to the plant will increase moisture stress. Crop plants need to be competitive with troublesome weeds. Rapid early growth with quick ground cover is desirable. Good rooting cultivars that can extract soil moisture better than weeds have a competitive advantage. Resistance to prevalent sucking and chewing insects reduces the moisture required for high yield. Wheat cultivars susceptible to the toxin of the greenbug (Schizaphis graminum) may show a detrimental interaction when attacked by aphids while under moisture stress (Ryan et al., 1987). Asghar and Ingram (1993) simulated the chewing insect damage by mechanical defoliation of wheat after anthesis and found a loss in grain yield caused primarily by a reduction in kernel size, with results similar to post-anthesis chemical desiccation.

Diseases that restrict root growth, damage the crowns or restrict water movement can cause symptoms similar to drought stress (Talboys, 1968). Moisture stress appears to predispose plants to certain vascular diseases, such as dryland foot rot (caused by Fusarium culmorum) (R.J. Cook, Research Leader, USDA-ARS, Pullman, Washington, private communication, 1985).

We have tested the possibility of using a lack of disease symptoms to identify cultivars with drought resistance. Table 2 shows the potential loss of grain yield caused by dryland foot rot in ‘Kharkof’ winter wheat. One plot of the five replicates in a yield trial was severely infected (over 70% white heads). This procedure was tested by visually estimating the response of four hard red winter wheats to dryland foot rot during two years (Table 3). These winter wheats are all adapted to the area. ‘Lewjain’, a soft white winter wheat with good tolerance to dryland foot rot was used as a check. Buchanan tends to overtill and place itself under moisture stress. Hatton has the highest grain weight per unit volume, with Weston higher than Batum or Buchanan. Reaction to dryland foot rot gave only a rough estimate of tolerance to moisture stress. For moisture stress tolerance, as determined by grain yield and weight per unit volume when grown for several years under moisture stress, the order of the varieties is Hatton > Weston > Batum > Buchanan.

Osmotic adjustment

Osmotic adjustment varies with genotype (Morgan, 1977) and is positively related to grain yield (Morgan, 1983) when stress occurs either pre-anthesis (Ludlow et al., 1990a) or post-anthesis (Ludlow et al., 1990b). Osmotic adjustment has the advantage of being measurable in the greenhouse, where environmental variation can be controlled (Morgan et al., 1986). However, selection for high levels of osmotic adjustment may lower the tolerance to desiccation (Basnayake et al., 1993).

Maturity and foliar characteristics

Many researchers agree that early maturity is associated with high grain yield under stress (Austin, 1987; Bidinger et al., 1987; Sillm et al., 1993). However, in the PNW, the highest grain yields are usually obtained with later maturing cultivars, although these sometimes suffer from lower kernel weight due to moisture stress during grain fill. Under terminal moisture stress, early maturity to avoid the stress is advantageous. However, it is much less important where moisture is sufficient (irrigation) or where yields are limited by stresses occurring early in the development of the plant so that sufficient water is available to fill the kernels that do form. Early maturity limits the time for biomass production and grain fill. Better grain fill should be possible by selecting for

<table>
<thead>
<tr>
<th>Cultivar</th>
<th>Harrington 1988</th>
<th>Lind 1989</th>
<th>Rating 0–5(^7)</th>
<th>Yield (kg/ha)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Hatton</td>
<td>9</td>
<td>3000</td>
<td>1.7</td>
<td>3270</td>
</tr>
<tr>
<td>Weston</td>
<td>31</td>
<td>2650</td>
<td>1.5</td>
<td>3060</td>
</tr>
<tr>
<td>Batum</td>
<td>17</td>
<td>2930</td>
<td>4.7</td>
<td>2790</td>
</tr>
<tr>
<td>Buchanan</td>
<td>30</td>
<td>2590</td>
<td>4.5</td>
<td>3610</td>
</tr>
<tr>
<td>Lewjain</td>
<td>5</td>
<td>3330</td>
<td>0.5</td>
<td>2520</td>
</tr>
</tbody>
</table>

\(^7\) Rating: 0 = no white heads; 5 = severe damage.
Techniques for Selecting Cultivars

Early vigor (Turner and Nicolas, 1987) and percentage ground cover (Silim et al., 1993) are associated with total biomass production and yield (Sinclair et al., 1990). Biomass production in cereal cultivars can be ranked using field spectroscopy at early growth stages (Smith et al., 1993), thereby eliminating much of the labor.

Haley et al. (1983) found that the rate of water loss from excised wheat leaves from plants grown under favorable moisture conditions was correlated with grain yield and weight per unit volume under moisture stress conditions. They concluded that selection for low rate of water loss in irrigated environments could benefit grain yield and weight per unit volume in dryland environments, despite observed genotype by environment interactions and the lack of any difference in rate of water loss in dryland environments.

Selection for lower transpiration rates from full canopy coverage improves water use efficiency. Hattendorf et al. (1990) identified an alfalfa cultivar with lower transpiration, indicating that selection for this characteristic might be possible in other crops.

In environments with terminal drought stress, a chemical desiccant to defoliate the plants after anthesis can be used to identify post-anthesis stress resistance. For this procedure to work, plants must have high carbohydrate reserves in the biomass combined with efficient translocation of assimilates to the grain (Hossain et al., 1990). Regan et al. (1993) found that for best results, selection should be confined to wetter sites or seasons.

Final testing must be carried out in the field in the environment where the cultivar will be grown. Field testing, unfortunately, is affected by many environmental variations within a year and among years. Small variations in the field that are undetectable to the eye and that seem small when tested (for example, seed zone moisture) can have significant effects on plant growth. Under poor seeding conditions, wheat will emerge and grow in a chaff row created by the harvest of the previous crop, although moisture between the chaff rows is insufficient for germination and growth. This problem was not observed with a 3.5-m harvester header, but was noticeable when a 5-m harvester header had been used to harvest the previous crop. Tractor tracks from the summer fallow tillage operations sometimes can be detected by reductions in final stand and early plant growth because of increased evaporation in the track. A crawler tractor, which creates less compaction than a wheel tractor, helps reduce the problem. In evaluating field performance, multiple locations, years, seeding dates, and replications are even more important in dry environments than in high moisture environments.

In the advanced lines shown in Table 4, yield selection was for competitive yields in low-yield locations and a favorable yield increase in high-yield locations. If the average across locations is the variable used for selection, the small differences in yield on poor locations can be lost by the larger yield differences in high-yield locations. This becomes equivalent to testing only in more favorable environments, which may not be reliable (van Oosterom et al., 1993). Grain yield was the primary reason for selecting either WA007678 or WA007679. With additional data across years, regression analysis of yield as yield potential of the environments will aid in final evaluation.

Comparison of cultivars for grain yield and weight per unit volume among locations differing in stress is easily accomplished using line source irrigation. Mahalakshmi et al. (1990), using pearl millet (Pennisetum glaucum [L.] R. Br.), concluded that when genotype response to the stress gradient is linear, the difference in response between the high (irrigated) treatment and the low (unirrigated) treatment can be used for genotype evaluation with little loss of information.

In the lower rainfall areas of the PNW, moisture stress that limits grain yield often occurs before or during anthesis. As rainfall increases, terminal moisture stress is more likely. Thus, within the desired area of adaptation of cultivars, the yield-limiting moisture stress could be either pre- or post-anthesis. Desirable genotypes should have competitive yields under both kinds of stress and should maintain good seed weight per unit volume. In Table 5, the yield-limiting stress was pre-anthesis at Lind and terminal at Harrington. Weston and 'Hoff' showed small differences in yield between the sites because of the poor performance at Harrington. Weston and Andrews showed the least change in weight per unit volume. Evaluated within this data set, Andrews has the desirable attributes of good yield at the American Journal of Alternative Agriculture
Table 4. Yields (kg/ha) of commercially grown hard winter wheat cultivars and two advanced lines grown at four locations in eastern Washington varying in available moisture, 1993.

<table>
<thead>
<tr>
<th>Cultivar</th>
<th>Horse</th>
<th>Finley</th>
<th>Waterville</th>
<th>Lind</th>
<th>Preirr.</th>
<th>Average</th>
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<tbody>
<tr>
<td>Hatton</td>
<td>1946</td>
<td>2796</td>
<td>3061</td>
<td>4449</td>
<td>3063</td>
<td></td>
</tr>
<tr>
<td>Weston</td>
<td>2061</td>
<td>3054</td>
<td>3184</td>
<td>4122</td>
<td>3105</td>
<td></td>
</tr>
<tr>
<td>Blizzard</td>
<td>2095</td>
<td>2707</td>
<td>2850</td>
<td>3571</td>
<td>2806</td>
<td></td>
</tr>
<tr>
<td>Buchanan</td>
<td>1980</td>
<td>2714</td>
<td>3646</td>
<td>3939</td>
<td>3070</td>
<td></td>
</tr>
<tr>
<td>WA7678</td>
<td>1939</td>
<td>3503</td>
<td>4061</td>
<td>4136</td>
<td>3410</td>
<td></td>
</tr>
<tr>
<td>WA7679</td>
<td>1898</td>
<td>2925</td>
<td>3993</td>
<td>3551</td>
<td>3092</td>
<td></td>
</tr>
</tbody>
</table>

Table 5. Effect of time of maximum moisture stress on yield and weight per unit volume for hard red winter wheat grown on dryland at Lind and Harrington, Washington, 1990. Harrington shows terminal stress, low grain weight per unit volume. Stress at Lind was at an earlier plant growth stage, limiting yield but with sufficient moisture to fill the kernels.

<table>
<thead>
<tr>
<th>Cultivar</th>
<th>Lind</th>
<th>Harr.</th>
<th>Diff.</th>
<th>Weight per unit volume (kg/ha)</th>
<th>Lind</th>
<th>Harr.</th>
<th>Diff.</th>
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<tbody>
<tr>
<td>Hatton</td>
<td>2476</td>
<td>3531</td>
<td>1055</td>
<td>82.1</td>
<td>76.1</td>
<td>6.0</td>
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<tr>
<td>Weston</td>
<td>2469</td>
<td>3156</td>
<td>687</td>
<td>81.4</td>
<td>76.8</td>
<td>4.6</td>
<td></td>
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<tr>
<td>Andrews</td>
<td>2490</td>
<td>3939</td>
<td>1449</td>
<td>78.8</td>
<td>75.6</td>
<td>3.2</td>
<td></td>
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<tr>
<td>Hoff</td>
<td>2290</td>
<td>3197</td>
<td>898</td>
<td>81.4</td>
<td>75.0</td>
<td>6.4</td>
<td></td>
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<tr>
<td>Buchanan</td>
<td>2054</td>
<td>3293</td>
<td>1239</td>
<td>79.9</td>
<td>73.3</td>
<td>6.6</td>
<td></td>
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<tr>
<td>Batum</td>
<td>2354</td>
<td>3816</td>
<td>1462</td>
<td>78.7</td>
<td>72.0</td>
<td>6.7</td>
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</table>

low-production site, high yield at the higher-production site, and a small difference in weight per unit volume. Andrews is the earliest maturing cultivar in the set.

At Lind, spring wheat was seeded in adjacent areas on summer fallow ground and on ground that had spring wheat the previous year (Table 6). Unseasonably hot weather occurred between Julian days 130 and 140, placing the wheat under stress. The earlier heading (anthesis) cultivars had the highest weights per unit volume in the area cropped annually, but had poor grain yields under both summer fallow and annual cropping. An exception was ‘Express’, which yielded well under annual cropping and showed little difference in weight per unit volume between treatments. ‘Wampum’ showed favorable yields in both treatments, but had considerable difference in weight per unit volume. Selection for high yield under Washington conditions has resulted in later maturing genotypes that lose weight per unit volume under severe terminal moisture stress. Low weight per unit volume under stress conditions is a major constraint in developing higher yielding cultivars of both spring and winter wheat in Washington State.

References


<table>
<thead>
<tr>
<th>Cultivar</th>
<th>Head Date</th>
<th>Fallow</th>
<th>Annual</th>
<th>Diff.</th>
<th>Fallow</th>
<th>Annual</th>
<th>Diff.</th>
</tr>
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<td>Spillman</td>
<td>156</td>
<td>2660</td>
<td>1565</td>
<td>1095</td>
<td>78.7</td>
<td>68.9</td>
<td>9.8</td>
</tr>
<tr>
<td>Wampum</td>
<td>156</td>
<td>2619</td>
<td>1687</td>
<td>932</td>
<td>79.6</td>
<td>69.9</td>
<td>9.7</td>
</tr>
<tr>
<td>Express</td>
<td>154</td>
<td>2422</td>
<td>1633</td>
<td>789</td>
<td>79.9</td>
<td>75.3</td>
<td>4.5</td>
</tr>
<tr>
<td>Butte 86</td>
<td>152</td>
<td>2306</td>
<td>1286</td>
<td>1020</td>
<td>79.5</td>
<td>73.4</td>
<td>6.1</td>
</tr>
<tr>
<td>906R</td>
<td>150</td>
<td>2306</td>
<td>1429</td>
<td>877</td>
<td>79.5</td>
<td>76.2</td>
<td>3.2</td>
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