RESEARCH

Resilience, Stability, and Productivity of Alfalfa Cultivars in Rainfed Regions of North America

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ABSTRACT

Resilient, stable, and productive forage systems are needed to endure increasingly frequent climatic extremes. Resilience is the ability of a forage system to withstand a climatic crisis with high yields, stability is the minimal variability of yields across normal years, and productivity is the average yield across normal years. The goal of this research was to quantify resilience, stability, and productivity of alfalfa (*Medicago sativa* L.) cultivars to identify superior ones. Forage yield means from alfalfa cultivar trials from 11 US states and one Canadian province over 19 yr (1995–2013) were analyzed using linear mixed models. Locations with an extreme crisis year were identified, and quantitative measures for resilience and stability for each cultivar were calculated. Productivity, stability, and resilience were different among cultivars across locations, showing that some cultivars were consistently superior for each variable. Cultivar stability was not associated with productivity, and it was negatively associated with disease resistance. Cultivar resilience was negatively associated with productivity, and not associated with other traits. Cultivar productivity has increased with year of release of cultivar, stability has not changed, and resilience has decreased. Therefore, stability and resilience are different dimensions, explained by different traits. A coordinated evaluation effort across locations is needed to test and improve cultivar resilience in the future, and develop alfalfa cultivars more profitable for the long term.

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Climate change is a major challenge for agriculture and food security. Historical climate trends and future model projections have shown that climate variability is increasing at global and local scales (IPCC, 2013). For the midwestern United States, for instance, by 2070, rainfall is expected to increase on average by 20 to 100 mm, whereas consecutive dry days will increase by 1 to 3 d (Melillo et al., 2014). Therefore, more frequent water excesses and deficits are expected (Shiu et al., 2012), which would affect agriculture in general and forage production in particular.

Sustainability of agricultural systems involves economic, social, and environmental dimensions and can be evaluated by various attributes, such as productivity, efficiency, stability, resilience, reliability, adaptability, equitability, and autonomy, among others (Marten, 1988; López-Ridaura et al., 2005; Urruty et al., 2016). These attributes of sustainability can be evaluated at various hierarchical levels in the agroecosystems, including landscape, farm or cropping system, communities, or individual crop species (Marten, 1988; Oliver et al., 2015). In the face of increased climate variability, it is particularly relevant to focus on those attributes that reflect the performance of agricultural systems in the long term, such as resilience and stability. In fact, resilient and stable forage production is needed to endure increasingly frequent climatic crises such as drought or floods (Tracy et al., 2018).

Most research on forages has historically focused on maximizing productivity (i.e., the average forage dry matter biomass yield per unit of land per year; Barnes and Collins, 2003). It

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is indeed the most studied, measured, and understood attribute of sustainability: cultivars with larger average yields over time are the goal of breeders and farmers (Fig. 1a). Stability and resilience are concepts less understood, sometimes confused, and their evaluation is not straightforward (Urruty et al., 2016). Stability (Fig. 1b) is the minimal variability of yields over time under normal conditions (Marten, 1988; Dawson et al., 2010; Urruty et al., 2016), also referred to as constancy (Grimm and Wissel, 1997; Picasso et al., 2010), reliability (López-Ridaura et al., 2005), or the inverse of variability (Loreau et al., 2001). Resilience (Fig. 1c) is the ability to withstand a short-term crisis, perturbation, or shock, like a drought, by absorbing the perturbation and reorganizing to retain the same function, (Grimm and Wissel, 1997; Walker et al., 2004; López-Ridaura et al., 2005; Dawson et al., 2010; Tracy et al., 2018), also referred as resistance (Loreau et al., 2001), and robustness (Picasso et al., 2011, 2013, Sabatier et al., 2015; Urruty et al., 2016). Resilience (*latu sensu*) comprises two complementary dimensions (Hodgson et al., 2015): the ability to withstand a crisis and not deviate during the perturbation (i.e., resistance), and the ability to recover from a crisis and the speed of this recovery (i.e., recovery or resilience *strictu sensu*; Isbell et al., 2015; Oliver et al., 2015; Tracy et al., 2018). In this paper, we evaluated resilience (*latu sensu*) by measuring only the first dimension (resistance).

To understand how resilience and stability are determined, operational measures for these variables are needed (Urruty et al., 2016). Two major obstacles for studying stability and resilience are the need for clarification and consensus on how to measure these traits (Grimm and Wissel, 1997), and the lack of long-term datasets (10 to 20 yr), which are difficult to obtain within normal project timeframes. In the synthesis paper from the 2017 symposia "Resiliency in Forage and Grazinglands" from the Crop Science Society of America, it was concluded that long-term research projects are needed to measure and promote resilience integrating disciplines and regions (Tracy et al., 2018). Therefore, novel methods applied on large enough datasets are needed to assess stability and resilience. Although various studies have reported different measures of stability of crop cultivars (Finlay and Wilkinson, 1963; Eberhart and Russell, 1966; Piepho, 1998; Bernardo, 2002, Waldron et al., 2002), no study to our knowledge has reported resilience and stability as two different dimensions.

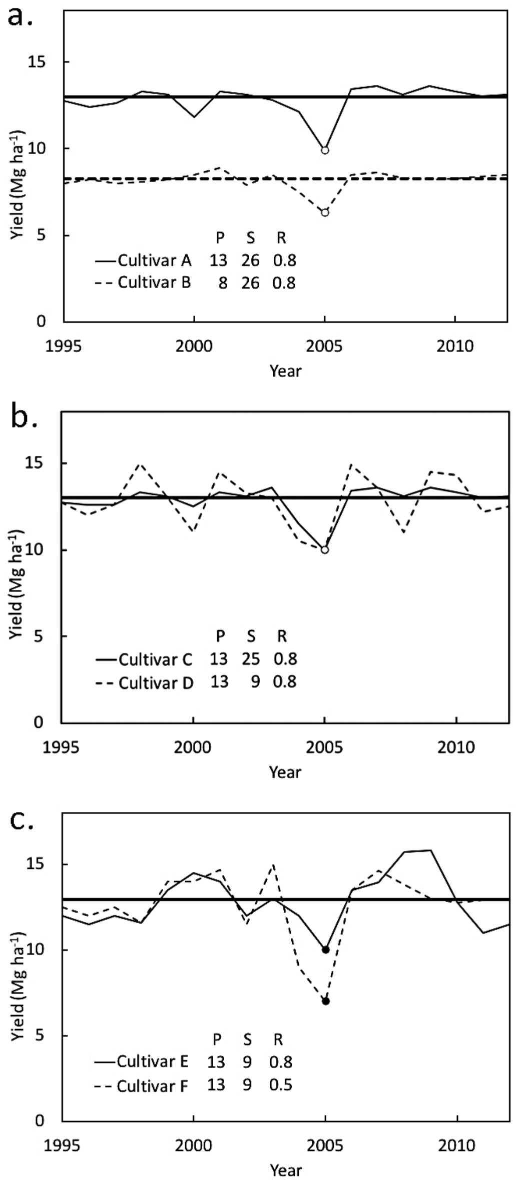

Fig. 1. Yields of theoretical alfalfa cultivars over time in one location where a drought occurred in year 2005, illustrating differences in (a) productivity, (b) stability, and (c) resilience. Panel a: productivity (P) is the mean yield over time, excluding the crisis year (horizontal wide lines). Cultivar A is more productive than Cultivar B. Panel b: stability (S) is the minimal variability of the yield over time, under normal climatic fluctuations (excluding the crisis year), calculated as the productivity divided by its SE. Cultivar C is more stable than Cultivar D. Panel C: resilience (*R*) is the ability to withstand a crisis (i.e., resistance), calculated as the yield in the crisis (black dots) divided by the productivity (horizontal line). Cultivar E is more resilient than Cultivar F.

Alfalfa (*Medicago sativa* L.) is a perennial legume forage crop, widely used for hay, pasture, and silage for livestock globally due to its high nutritional value, ability to symbiotically fix N, and the deep root system that improves soil health (Barnes and Collins, 2003; Undersander et al., 2011). Alfalfa grown in monoculture or in mixtures with cool-season grasses is highly productive and can effectively suppress weeds (Picasso et al., 2008). Alfalfa breeding efforts to increase yield have focused on disease and insect resistance, forage quality, and winter hardiness, but genetic yield gains have been low (Li and Brummer, 2012). In a study comparing alfalfa cultivars released over five decades, modern cultivars showed greater yields only in those environments with disease pressure (Lamb et al., 2006).

Plant traits (e.g., rooting depth, leaf architecture, or carbohydrate storage) affect yield and its variability over time. For instance, the ability of two different alfalfa cultivars to withstand a drought may be associated with their different rooting depths, which allow plants to explore different volumes of soil to tap water (Barnes and Collins, 2003). It is then reasonable to expect that some cultivars are consistently more resilient to drought and more stable in the long term than others, because of consistent differences in anatomical or physiological traits (Liu et al., 2018). Also, it could be expected that only environments with severe crisis can be used to discriminate among resilience of cultivars (Jaleel et al., 2009). Furthermore, the traits responsible for greater productivity in a normal year with limited biotic or abiotic stresses may be different from the ones responsible for greater productivity in a crisis year with severe stresses (Atlin and Frey, 1990). Therefore, the yield ranking of a cultivar under normal conditions may not be correlated with the yield ranking under stress (Ceccarelli and Grando, 1991; Ceccarelli et al., 1998; Annicchiarico et al., 2014). This means that tradeoffs may exist between maximizing productivity vs. resilience or stability. Finally, it is possible that traits related to resistance to stress (disease resistance or winter survival) are positively associated with resilience and/or stability.

The goal of this paper is to develop methods to study the stability and resilience of alfalfa cultivars (i) to identify superior cultivars for stability and resilience across environments, (ii) to explore the relationship between productivity, stability, and resilience, and (iii) to explore the association among these three variables and stress resistance traits in alfalfa cultivars. The following hypothesis were tested: (i) cultivars differ in stability and resilience across locations, (ii) cultivar productivity is not associated with cultivar stability or resilience, and (iii) cultivar stability and resilience is positively associated with winter survival and disease resistance.

MATERIALS AND METHODS

Database

A large database of forage yield for 679 alfalfa cultivars from 1060 public trials conducted between 1995 and 2013 was used, comprising 86 locations in 11 US states (Iowa, Illinois, Indiana, Kansas, Michigan, Minnesota, Nebraska, New York, Ohio, Pennsylvania, and Wisconsin) and one Canadian province (Ontario). A total of 28,070 observations were initially included, with an observation defined as a cultivar total annual yield mean across three to eight replicates per trial-year. Seeding year data were excluded from analyses, limiting the dataset to Years 2 through 6. Locations with less than six consecutive years of data collection were excluded, leaving 21,899 observations from 45 locations.

Each cultivar in the database was characterized based on published information from the Association of Official Seed Certifying Agencies (AOSCA) for various traits (NAAIC, 2017), including year of release, fall dormancy score, winter survival index, and a quantitative disease resistance index. Fall dormancy is the ability of alfalfa to grow tall in the fall, measured as plant height 25 d after a fall cutting; shorter plants mean more fall dormancy and less yield potential. Winter survival index rates the survival of alfalfa plants after a harsh winter, from 1 (little winter damage) to 6 (very susceptible to winterkill). The disease resistance index is the sum of disease ratings for six root and stem diseases (bacterial wilt [*Clavibacter michiganensis* subsp. *insidiosus*], Verticillium wilt [*Verticillium alfalfae*], Fusarium wilt [*Fusarium oxysporum* f. sp. *medicaginis*], anthracnose [*Colletotrichum trifolii*], Phytophthora root rot [*Phytophthora medicaginis*], and Aphanomices root rot [*Aphanomyces euteiches*] race 1), each one scored from 1 (susceptible) to 5 (highly resistant), so the total index ranged from 6 (susceptible to all diseases) to 30 (highly resistant to all diseases). Detailed protocols for all these measurements are available in NAAIC (2017).

Identification of Crisis Years

A crisis year for each location is a year when yields were significantly reduced for most cultivars across the entire trial, which can only occur with an extreme climatic event like drought or severe winter injury. To identify a crisis year in each location, trial means for all years in each location were analyzed. Least squares mean yields by location for all years were estimated from a model with cultivar and stand age as fixed effects. This analysis was conducted by location, so in each location, the mean yield of the trial for each year was identified. A crisis year was defined as the year with minimum mean trial yield for the times series for that location, and that mean was significantly different from all other year means in a Tukey's multiple comparisons test with $\alpha = 0.05$. Locations where the minimum mean yield was not different from others were not included in further analyses, to make sure that an extreme perturbation was occurring. This way, only years with significant overall yield reduction (across the trial) were identified as crisis years. This left 25 locations with identified crisis years, and 12,786 observations. This approach allowed us to conceptually separate the crisis year to evaluate resilience, and all other normal (although variable) years to evaluate stability. Normal years are therefore all years in the series for each location excluding the crisis year.

After identifying the crisis year, weather data were analyzed to identify the cause of the crisis. There are several abiotic environmental factors that can affect alfalfa yields; the two most important are drought (water stress) and cold (winter injury). A crisis year was classified as drought if the Palmer drought severity index (NOAA, 2017) for the state division for that location and year (for March through November, 9 mo) was below the average for the historical series, using data from the NOAA (2017) for locations in the United States. For the Canadian locations, a crisis year was classified as drought when total precipitation (for March through November) was below the historic average (no drought index was readily available), using information from the Government of Canada climate website (http://climate.weather.gc.ca). Cold or winter stress is difficult to quantify from weather variables. Winter injury can occur in extremely cold winters, as much as in warmer winters, depending on the snow cover and the succession of cold and warm temperatures. There are no available indices to quantify winter injury potential from a weather perspective across locations, so crisis years were not classified according to this criterion.

Variable Operational Definitions

Cultivar productivity in each location is defined as

$$P_{jl} = \frac{\sum_{i}^{n-1} Y_{ijl}}{n-1} \qquad [1]$$

where Y_{ijl} is the yield of cultivar j in the year i for location l, and $n - 1$ is the number of normal years (i.e., all years except the crisis year). The larger the mean yield, the more productive the cultivar (Fig. 1a).

Cultivar stability in each location is defined as

$$S_{jl} = \frac{P_{jl}}{\mathrm{SE}\left(P_{jl}\right)} \qquad [2]$$

where $\mathrm{SE}(P_{jl})$ is the standard error of the productivity. The lower the variability relative to the mean, the more stable the cultivar (Fig. 1b). Note that stability is calculated considering all normal years in the series (i.e., excluding the crisis year). This definition of stability is unitless.

Cultivar resilience in each location is defined as

$$R_{jl} = \frac{\mathrm{Yc}_{jl}}{P_{jl}} \qquad [3]$$

where Yc_{jl} is the yield in the crisis year of cultivar j in location l. Therefore, the larger the yield of a cultivar in the crisis year, expressed as proportion of the productivity, the larger the resilience of that cultivar (Fig. 1c). This definition of resilience is unitless. Resilience is, essentially, a fraction that measures the proportion of productivity that is achieved in the crisis year.

The productivity of each location (P_l) is the least squares mean of the trial means across years. The crisis severity for each location is

$$\mathrm{CS}_l = 1 - \frac{\mathrm{Yc}_l}{P_l} \qquad [4]$$

so the larger the value of CS_l, the more severe is the crisis.

Because the set of cultivars evaluated in each location changed over time, the average yield for one particular year depended not only on the climatic conditions of the year, but also on the particular set of cultivars evaluated. Because cultivars were not evaluated in all locations in all years, not all cultivars were present in each location. For further analyses, only cultivars evaluated in at least six locations were used.

Statistical Analyses

To calculate cultivar productivity and stability, least squares means by location were estimated for yield of cultivars, considering cultivar, stand age, and year as fixed effects. To calculate the resilience, least squares means by location and year were estimated for yield of cultivars, considering cultivar and stand age as fixed. After identifying crisis years, resilience values were calculated for each cultivar in each location, as described above. Because many cultivars were evaluated in few locations, we excluded from further analyses cultivars present in less than three locations. Therefore, the final set of means consisted of 413 means, from 84 cultivars and 25 locations.

To test the hypothesis of differences among cultivars across locations, cultivar productivity, stability, and resilience in each location were analyzed with mixed models considering cultivar as fixed effect and location as random effect. Multiple comparisons test for least squares means of each cultivar were performed to identify the cultivars with superior performance in each variable, using Fisher's LSD test.

A simple linear regression between the estimated cultivar resilience and crisis severity of the locations was fit for each cultivar. This allowed further evaluation of the consistency of resilience of cultivars across locations. To test the hypothesis that cultivar productivity was not significantly associated with stability or resilience, simple linear regressions between the cultivar means across locations of resilience vs. productivity, stability vs. productivity, and resilience vs. stability were fit. Finally, simple linear regressions among these three attributes and other cultivar traits (fall dormancy, winter survival, disease resistance, and year of release) were fit. For regressions against year of cultivar release, we excluded the cultivars released before 1990, because they had a strong leverage on the regression, leaving the 45 most recent cultivars.

RESULTS

Characterization of Locations

A total of 25 locations were included in the final analyses, evaluated >11 consecutive years on average, ranging from 6 to 18 yr depending on location (Table 1). Mean productivity across locations was 13.8 Mg ha^{-1}, ranging from 6.2 to 22.5 Mg ha^{-1}. The range of crisis severity values was 0.18 to 0.61, with an average crisis severity of 0.38. The majority (80%) of the crises were related to drought events.

Characterization of Cultivars

Mean annual productivity of cultivars across locations ranged from 12.5 to 15.7 Mg ha^{-1}, and significant differences were detected among cultivars ($P < 0.01$). Mean stability of cultivars across locations ranged from 24 to 75, and cultivars were significantly different in stability ($P < 0.01$). Mean resilience of cultivars across locations was also significantly different among cultivars ($P < 0.01$), ranging from 0.53 to 0.67. The means for the subset of cultivars evaluated in more than three locations are presented in Table 2. The methodology used to evaluate resilience and stability was able to discriminate the cultivars with better performance over the long term.

Resilience vs. Crisis Severity

Estimated cultivar resilience values for each location were negatively and linearly associated with crisis severity for all cultivars evaluated in more than three locations (Fig. 2). Therefore, the estimated resilience value for each cultivar in each location was lower when the crisis severity of the location was larger. This was expected, since the more severe the crisis is, the lower the yields of the cultivars are overall. Adjusted R^2 of the

Table 1. Description of the locations included in the study of resilience of alfalfa cultivars: location name (in alphabetical order), state or province (S/P), number of observations (*N*), number of cultivars evaluated in the series, number of years in the series, location productivity (P_l), crisis year (CY), crisis severity value (CS), and whether a drought was identified in the crisis year (based on the Palmer drought severity index).

Location	S/P	N	Cultivars	Years	P_l	CY	CS	Drought
		no.			Mg ha^{-1}			
Ames	IA	641	6	12	12.3	1996	0.47	No
Arlington	WI	1758	53	18	14.2	2006	0.59	Yes
Belleville	IL	117	6	7	12.2	2006	0.60	Yes
Belleville	KS	104	9	6	11.7	2002	0.26	Yes
Chazy	NY	284	23	14	11.4	2005	0.47	No
Colby	KS	166	6	9	17.3	2002	0.19	Yes
Fond du Lac	WI	371	18	12	11.6	2006	0.45	Yes
Freeport	IL	533	28	13	14.5	2006	0.52	Yes
Garden City	KS	277	7	13	22.5	2013	0.34	Yes
Huron	ON	271	3	10	14.5	1998	0.42	Yes
Jackson	OH	104	6	7	10.5	2005	0.34	Yes
Kapuskasing	ON	209	10	6	6.2	1996	0.39	Yes
Lamberton	MN	581	5	18	12.5	2013	0.38	Yes
Lancaster	WI	373	24	14	14.5	2006	0.61	Yes
Landisville	PA	1395	29	16	14.7	2003	0.24	No
Lincoln	NE	244	14	7	18.6	2008	0.23	No
Marshfield	WI	1425	36	17	11.2	2006	0.55	Yes
Mead	NE	292	24	6	20.0	2005	0.22	Yes
Morris	MN	339	17	7	11.0	1997	0.32	No
Mound Valley	KS	107	8	8	10.5	2006	0.59	Yes
North Baltimore	OH	276	6	14	16.5	2001	0.27	Yes
Richmond	MN	128	5	7	16.0	2013	0.18	Yes
Rock Springs	PA	1454	40	16	14.4	2005	0.24	Yes
Rosemount	MN	1150	20	18	12.8	1996	0.19	Yes
Underwood	MN	187	10	9	13.9	2009	0.47	Yes

regressions were 0.87 on average for regressions of all cultivars evaluated in more than three locations. Intercepts of regressions were all similar, and not different from 1. The slopes of the regressions for all cultivars were similar, and not different from −1. This means that regression lines are parallel, and the ranking of resilience of cultivars would not change on average for different crisis severity levels. This suggests that it would be possible to evaluate resilience of cultivars in locations with minor crises, not necessarily requiring severe crises to obtain relevant and repeatable values.

Furthermore, the analyses of these regressions provided further evidence of the consistency of the resilience of cultivars across locations. Cultivars with larger resilience across locations had larger resilience values for most locations evaluated (Fig. 2). For instance, 'Abundance' was a cultivar with one of the largest mean resilience across locations ($R = 0.62 \pm 0.03$), and 'WL357HQ' was a cultivar with one of the lowest mean resilience across locations ($R = 0.57 \pm 0.03$). Estimates of the resilience of the cultivar 'Abundance' in each location were consistently higher than estimates of cultivar 'WL357HQ' resilience in each location where both cultivars were evaluated together (i.e., Freeport, IL, Marshfield, WI, and Arlington, WI; Fig. 2).

Association between Cultivar Traits

Mean cultivar resilience across locations was negatively associated with mean cultivar productivity across locations ($r = -0.58$, $p < 0.01$, $N = 84$). Therefore, cultivars with greater productivity overall have lower resilience. Mean cultivar stability across locations was not associated with mean cultivar productivity ($p = 0.99$). Therefore, greater productivity does not mean greater or less stability. Mean cultivar stability and resilience were not associated either ($p = 0.13$). These findings suggest that resilience and stability are different traits, and greater stability does not mean greater resilience, or vice versa.

Cultivars with greater fall dormancy scores were positively associated with productivity ($r = 0.46$, $p < 0.01$, $N = 78$), negatively associated with resilience ($r = -0.28$, $p = 0.01$, $N = 78$), and not associated with stability ($p = 0.47$). Disease resistance index was positively associated with productivity ($r = 0.30$, $P < 0.01$, $N = 78$), negatively associated with stability ($r = -0.56$, $P < 0.01$, $N = 78$), and not associated with resilience ($p = 0.44$). Winter survival index was not associated with productivity ($p = 0.39$, $N = 48$), stability ($p = 0.38$, $N = 48$), or resilience ($p = 0.08$, $N = 48$).

Mean cultivar productivity was positively associated with year of release of the cultivar for cultivars released after

Table 2. Means and SEs for productivity, stability, and resilience for alfalfa cultivars across locations (cultivars in alphabetical order). Year of release of cultivar, fall dormancy score (FD), winter survival index (WS), and disease resistance index (DR) for cultivars are shown. The number of locations where each cultivar was evaluated for this analyses (*L*) is also shown.

		Productivity†		Stability		Resilience					
Cultivar	*L*	Mean	SE	Mean	SE	Mean	SE	Year‡	FD	WS	DR
		— Mg ha^{-1} —									
631	4	14.2	0.7	40	5	0.64	0.04	1992	4	3.6	25
5312	13	14.1	0.7	72	3	0.62	0.03	1993	3	2.9	29
5454	5	14.3	0.7	50	5	0.61	0.03	1991	4	2.7	24
6415	8	15.7	0.7	46	4	*0.57*	0.03	2002	4	2.1	30
6420	7	14.4	0.7	46	4	0.61	0.03	1999	4	–	27
6530	5	15.0	0.7	*27*	5	0.59	0.03	2002	5	–	30
4A421	5	15.5	0.7	45	5	*0.59*	0.03	2002	4	2.5	30
4R429	4	14.6	0.7	*30*	5	0.59	0.03	2005	4	3.9	30
53Q30	5	14.6	0.7	*27*	5	*0.57*	0.03	2004	3	2.7	30
54H91	10	*13.5*	0.7	*31*	4	0.62	0.03	2001	4	3	28
54Q25	6	14.5	0.7	*31*	4	0.61	0.03	2003	4	–	29
54V46	12	15.1	0.7	42	3	0.59	0.03	2003	4	2.9	29
6200HT	4	14.2	0.7	*35*	5	0.60	0.03	–	3	2.2	30
6400HT	9	14.5	0.7	35	4	*0.58*	0.03	2002	4	2.4	30
A3006	5	14.2	0.7	41	5	0.59	0.03	1999	4	1.8	30
Abundance	5	14.5	0.7	37	5	0.62	0.03	1996	4	3.3	27
Ameristand407TQ	6	15.4	0.7	43	4	0.61	0.03	2006	4	—	30
Baralfa53HR	4	14.6	0.7	*30*	5	*0.59*	0.03	2003	5	—	29
Dakota	6	15.0	0.7	*30*	4	0.60	0.03	2002	4	3.3	19
DK127	4	13.9	0.8	41	5	0.64	0.04	1994	3	2.9	28
DKA3316	7	15.4	0.7	*34*	4	*0.57*	0.03	2003	3	–	30
DKA4215	4	15.5	0.7	53	5	0.62	0.03	2000	4	2.5	30
DKA5018	5	15.6	0.7	38	5	0.60	0.03	2003	5	–	30
Enhancer	5	14.6	0.7	40	5	0.61	0.03	1994	4	2.5	26
Everlast	5	14.1	0.7	*25*	5	*0.59*	0.03	2005	4	–	29
Feast+EV	5	13.9	0.7	46	5	0.59	0.03	2000	3	2.2	29
FSG351	4	15.3	0.7	*36*	5	*0.58*	0.03	2003	3	—	28
FSG400LH	5	*13.6*	0.7	*33*	5	0.61	0.03	2004	4	—	30
FSG406	5	14.4	0.7	36	5	0.60	0.03	2002	4	2.1	30
FSG408DP	4	15.1	0.7	42	5	*0.57*	0.04	2003	4	–	28
FSG505	6	15.6	0.7	41	4	0.60	0.03	2004	5	2.9	30
Genoa	5	15.3	0.7	39	5	*0.55*	0.03	2003	4	2.1	30
Goldleaf	4	14.9	0.7	39	5	0.61	0.03	1999	3	2.9	27
Hybriforce400	5	14.3	0.7	40	5	0.63	0.03	2003	4	2.8	26
Hybriforce420/Wet	10	15.1	0.7	36	4	0.59	0.03	2003	4	3.1	27
Integrity	4	14.7	0.7	25	5	*0.57*	0.04	2004	4	2.4	30
JourneyBrand204HA	5	14.6	0.7	*36*	5	0.59	0.03	2003	4	—	28
Kanza	4	14.4	0.7	70	5	*0.55*	0.04	1968	5	—	9
L311	4	14.5	0.7	*25*	5	0.59	0.03	2005	3	—	30
L447HD	4	15.1	0.7	*37*	5	0.62	0.03	2005	4	—	29
Legendairy 50	5	15.7	0.7	*36*	5	*0.57*	0.03	—	—	—	—
Magnum V	4	14.7	0.7	50	5	0.59	0.03	—	—	—	—
OneidaVR	12	*13.5*	0.7	75	3	0.62	0.03	1986	3	—	21
Perry	5	14.3	0.7	61	5	*0.53*	0.03	1979	3	—	15
Phirst	6	14.6	0.7	*33*	4	0.60	0.03	—	4	—	28
Power42	6	15.0	0.7	*35*	4	0.60	0.03	—	—	—	–
Prolific	4	14.7	0.7	37	5	0.59	0.03	2000	3	3.1	27
Rebound50	5	15.7	0.7	41	5	*0.56*	0.03	—	—	—	—
Reward II	5	14.4	0.7	*35*	5	*0.58*	0.03	2003	4	—	27
Starbuck	4	14.9	0.7	49	5	0.63	0.03	2001	4	—	29
Vernal	20	*13.1*	0.7	69	3	0.62	0.03	1953	2	2	11
WL319HQ	5	14.6	0.7	*34*	5	0.59	0.03	2001	3	1.8	30
WL348AP	6	14.7	0.7	*33*	4	0.60	0.03	2003	4	2.3	30
WL357HQ	9	15.7	0.7	*32*	4	*0.57*	0.03	2002	5	2.2	30

† Means underlined are not different from the highest value and means *in italics* are not different from the lowest value for each variable, respectively (Fisher protected LSD, $\alpha = 0.05$).

‡ Cultivars with no data are shown as –.

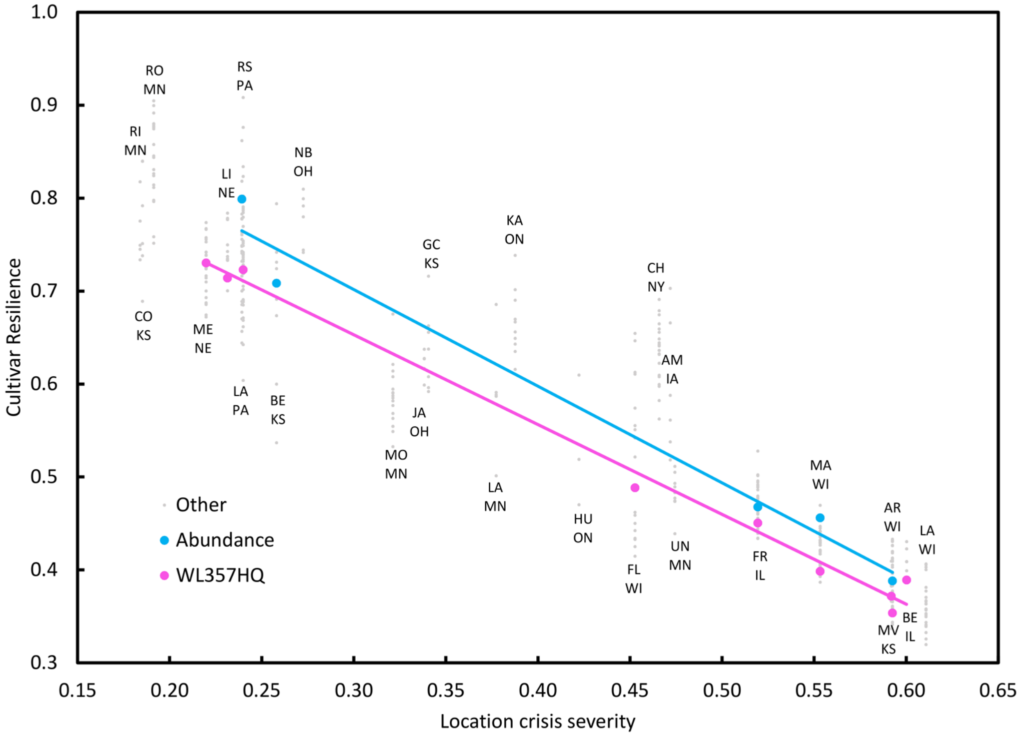

Fig. 2. Estimated cultivar resilience for each location vs. crisis severity of the location for ‘Abundance’ (blue dots), ‘WL357HQ’ (magenta dots), and all other alfalfa cultivars (gray points). Linear regression lines are shown for the two example cultivars. Linear regression equations are: ‘Abundance’ $R = -1.04\text{CS} + 1.01$ ($R^2 = 0.97$), and ‘WL357HQ’ $R = -0.97\text{CS} + 0.94$ ($R^2 = 0.99$), where CS is the crisis severity value. Codes for locations are the first two letters of the location names listed in Table 1, followed by the state or province abbreviation.

1985 ($r = 0.63$, $p < 0.01$, $N = 69$; Fig. 3). Mean cultivar stability was not associated with year of release ($p = 0.20$, $N = 69$). Mean cultivar resilience was negatively associated with year of release ($r = -0.56$, $p < 0.01$, $N = 69$). Fall dormancy scores of cultivars increased with year of release of cultivars ($r = 0.38$, $p < 0.01$, $N = 69$). Disease resistance index increased with year of release of cultivars ($r = 0.46$, $p < 0.01$, $N = 69$). Winter survival index was not associated with year of release ($p = 0.18$, $N = 45$).

DISCUSSION

Resilience vs. Stability

The goal of this study was to develop methods to quantify stability and resilience of alfalfa cultivars. We identified superior cultivars for stability and resilience across locations, so our first hypothesis that cultivars differ in stability and resilience across locations was not rejected. For instance, cultivars ‘Abundance’, ‘5454’, and ‘631’ were highly resilient cultivars, and ‘OneidaVR’, ‘5312’, and ‘Vernal’ were highly stable, and this was consistent across locations (Table 2). Our second hypothesis that cultivar productivity was not associated with cultivar stability or resilience was rejected. Productivity was negatively associated with resilience. Therefore, it may be difficult to identify cultivars with relatively large values for both productivity and resilience. This is consistent with studies on other crops showing no correlation between cultivar yields in low-yielding locations and average yields (Ceccarelli et al., 1998). Our resilience concept relates to the concept of low-yielding locations from plant breeding literature, but instead of focusing on different geographic locations, we focused on the years with lowest yields (crises years) within the same location. A key finding of our study is that we provided evidence that stability and resilience are two different traits and should not be confused. For instance, ‘L447HD’ was a cultivar not different from the most resilient and least stable cultivars, at the same time (Table 2). As we propose below, resilience and stability can be explained by different mechanisms.

Mechanisms and Traits

Resilience is expressed under severe climatic crisis, like droughts or winters with severe injury or winterkill. Stability is expressed under normal variability, which includes minor or short-term droughts, winter injury, and biotic stresses like pest or disease pressure. Therefore, different cultivar traits were found to be associated with resilience or stability. Our third hypothesis that cultivar traits related to resistance to stress (disease resistance and winter survival) were associated with resilience or stability was partially supported. Disease resistance was negatively associated with stability, but not with resilience. This intriguing finding could be explained by the fact that in extreme climatic years of severe winters or drought, plants, insects, and diseases are all negatively affected by the abiotic factors, and therefore, disease resistance is not

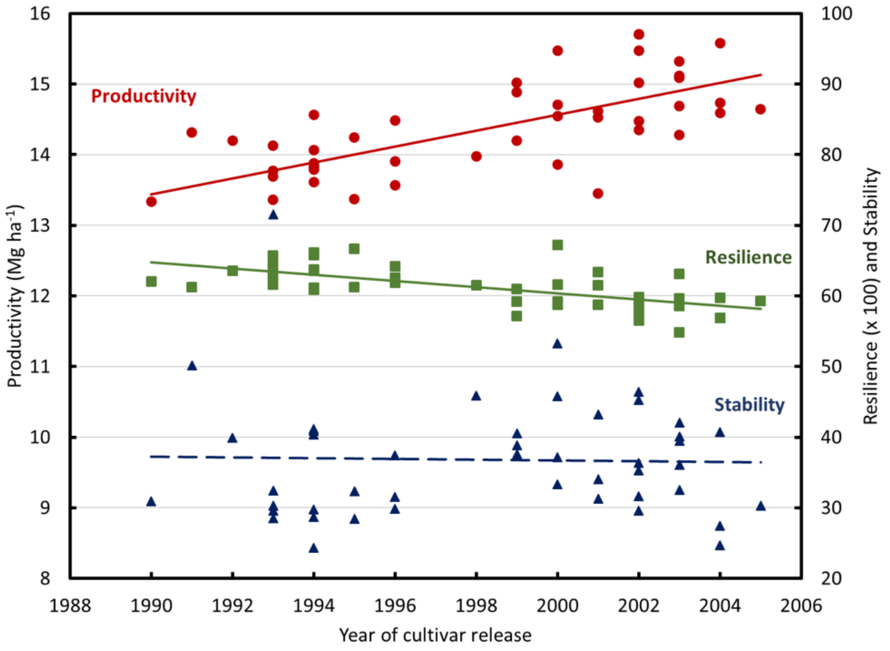

Fig. 3. Mean cultivar productivity (P, Mg ha^{-1}), stability (S), and resilience (R×100) vs. year of release (X) for alfalfa cultivars released between 1990 and 2005 across 25 locations in North America. Equations for shown regression lines, adjusted R^2, and p values are: $P = 0.11X - 211.47$ (adjusted $R^2 = 0.46$, $p < 0.01$); S, $p = 0.86$; $R = -0.004X + 9.472$ (adjusted $R^2 = 0.41$, $p < 0.01$).

relevant to explain the performance of alfalfa in a crisis year (Wegulo et al., 2013). On the other hand, for normal years, the prevalence of diseases is more variable, so cultivars with greater disease resistance would yield above the average only in years of high disease pressure, but not necessarily in years of low disease pressure. Therefore, cultivars with greater disease resistance could have more variable yields in normal years, thus having lower stability. Our findings are consistent with the observations of Lamb et al. (2006) that disease pressure may explain why some locations have shown yield increases over the last 50 yr, whereas others have not.

We did not find association between winter survival index and productivity, stability, or resilience. It is possible that yields of cultivars with severe winterkill in one specific year are not reported in cultivar trials, which may have reduced the number of cultivars reported in crisis years, affecting our ability to detect associations. Extreme winters that cause winterkill are hard to detect from the climatic records, because they are the results of cold temperatures, lower snow cover, and sometimes short periods of warmer temperatures that melt snow and then refreeze it, creating ice cover and a lack of O_2 belowground. It should be noted that only 20% of the crisis were not drought related (Table 1), so those are likely to be related to winter injury. Considering the recent trend to use alfalfa cultivars with higher fall dormancy scores (i.e., less dormancy), quantification of winter survival scores is more critical than in the past. Therefore, winter survival is a very relevant trait for the northern latitudes that requires more research and better quantification in the future. On the other hand, given that 80% of the crisis years were related to drought events, resilience of alfalfa cultivars in rainfed environments may be dependent on resistance or tolerance to drought. The lack of standard procedures for evaluation of drought tolerance (NAAIC, 2004) is a challenge that should be addressed in the near future by the alfalfa research community.

Oliver et al. (2015) reviewed several mechanisms underpinning resilience at the individual species level. Among those, they list (i) sensitivity to locational change (e.g., sensitivity to drought in trees is explained by different nonstructural carbohydrate levels), (ii) adaptive phenotypic plasticity (e.g., reduction in stomatal conductance in response to drought), and (iii) genetic variability (e.g., more diverse populations have a greater chance to include genotypes tolerant to a perturbation). Alfalfa plants, which allocate fewer carbohydrates to root growth than to aboveground leaf growth, may be more productive in a normal year but less productive in a drought year (Crutsinger et al., 2006). Further studies are needed to identify the mechanisms underpinning resilience in alfalfa cultivars, with special attention to drought resistance.

Trends over Time

Cultivars released in recent years show higher average productivity (Fig. 3), which can be explained by several confounded and complementary factors. This could suggest that plant breeding has increased alfalfa yields over time, but not all research agrees with this conclusion (Volenec et al., 2002; Lamb et al., 2006; Li and Brummer, 2012). Modern cultivars have higher fall dormancy scores (lower dormancy) and higher disease resistance, which suggests they should be more productive. This can also mean that agronomic practices in the experimental trials have improved, and cutting schedules may have intensified; therefore, cultivars entering trials in later years show higher yields. An additional explanation could be that locational factors, such as increasing temperatures, rainfall, and CO_2 concentrations, have increased yields in recent years, as has been shown for corn (*Zea mays* L.) and soybeans [*Glycine max* (L.) Merr.] (Kucharik and Serbin, 2008; Kucharik 2006). All three factors may complement each other to explain this trend, but more research is needed to disentangle these factors.

Average cultivar stability did not change over time with year of release of the cultivar. This could also be attributed to plant breeding (e.g., reduced stability associated with increased yield potential), improved agronomic practices, or locational factors, but it can also be an artifact of the data analyses: older cultivars have been evaluated more years than modern cultivars, and stability is related to the variability over time. The fact that resilience of cultivars decreased with year of release is a problematic finding, again due to many possible reasons. As resilience is a trait that is expressed only in extreme years, trends over time are difficult to interpret. It could be related to changes in climatic variability and extremes, or plant breeding (i.e., focus on breeding for productivity may have negatively affected performance in crisis years), or other factors.

Testing for Resilience

It was not the objective of this paper to propose how to breed cultivars for improved resilience. Resilience as described here can be evaluated only after the cultivar has being tested at multiple sites. Plant breeders have demonstrated that direct breeding in the target location achieves greater yield gains than indirectly breeding in a different (usually higher yielding) location for cool-season forages (Brummer and Casler, 2014), barley (*Hordeum vulgare* L.; Ceccarelli et al., 1998, Ceccarelli and Grando, 1991), oats (*Avena sativa* L.; Atlin and Frey, 1990), wheat (*Triticum aestivum* L.; Brancourt-Hulmel et al., 2005), and corn (Bänziger and Cooper, 2001). Because resilience is expressed in extreme years, which occur once every 4 to 6 yr, on average (Table 1), breeders can make gains for this trait only by serendipity or through the use of controlled locations.

This study therefore raises some questions regarding the potential to test cultivars for resilience in practice. The quantitative measures proposed here require long-term databases that span many years, so a relevant question is how resilience could be measured in alfalfa cultivar trials spanning only 4 yr. Furthermore, it is reasonable to expect that a larger number of locations would be needed to evaluate resilience. One possible approach would be to identify locations where crises are more frequent, or more severe. Another approach could be to test cultivars in locations where stresses (e.g., water deficit) could be experimentally imposed and compare the performance of cultivars under stress vs. normal conditions. A more efficient and less expensive approach may involve higher coordination among alfalfa breeders and testing sites, so that the same cultivars are evaluated across many locations during the same years, as already occurs for other crops.

One limitation of this study was the imbalance of the alfalfa cultivars database in terms of locations and years. The rapid turnover of cultivars generally dictates that evaluation in public trials of each cultivar usually does not last more than 4 yr. This limited the number of cultivars that were found in a specific crisis year, and therefore the final number of resilience values, affecting the power to draw conclusions. Therefore, a more coordinated approach to testing alfalfa cultivars would significantly expand the alfalfa forage yield databases, where modern cultivars could be evaluated in several locations over the same years, making it possible to identify more crisis locations and reliably evaluate resilience. Overlapping of cultivars across locations, rather than identifying better testing locations, is a critical factor to evaluate resilience. Nevertheless, this only solves the issue of evaluating synthesized cultivars for resilience. Evaluation of parents and early generations of breeding materials will necessitate identification of proper test locations that allow the breeder to reliably select stress-tolerant genotypes.

The resilience, stability, and productivity of forage systems depends on many factors, including genetic (e.g., cultivars), ecological (e.g., forage mixture composition), and management practices (e.g., tillage system, grazing, and harvest schedule) and their multiple interactions. In this paper, the focus was on the genetic factor (i.e., differences among cultivars), but to design more sustainable forage systems, it is highly relevant to evaluate the relationship between resilience and the other factors (Lin, 2011; Oliver et al., 2015; Tracy et al., 2018). The methods and operational definitions proposed here can contribute to measure and disentangle the complex interactions between these relevant variables.

Concluding Remarks

The challenges that agriculture faces are growing, and so is the interest from scientists and decision makers for developing sustainable, productive, stable, and resilient systems. As a first step, the public discourse has embraced these concepts, but there is still much confusion regarding their meaning and practical evaluation. A second step is to clarify the difference between the performance of agricultural systems in the face of normal variability (i.e., stability) and their performance in the face of major perturbations or crises (i.e., resilience). A third step is to develop metrics and operational measures for these two concepts. Finally, these variables can be used to identify the causal mechanisms for stability and resilience at various agroecosystem levels, and to evaluate alternatives (e.g., cultivars, practices, or management systems) to design improved systems.

This paper provided a conceptual framework, operational definitions, and empirical evidence for assessing the stability and resilience of alfalfa cultivars. We found that alfalfa cultivars differ in stability and resilience and that these variables represent two very different dimensions of the long-term performance of cultivars. A coordinated testing approach across many locations is proposed to improve alfalfa resilience in the future. The methodology proposed in this paper can be applied in the future to other crops and cropping systems, to advance the understanding of the long-term performance of agricultural systems in the face of an increasingly changing climate.

Conflict of Interest

The authors declare that there is no conflict of interest.

Acknowledgments

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References

Annicchiarico, P., B. Barrett, E.C. Brummer, B. Julier, and A.H. Marshall. 2014. Achievements and challenges in improving temperate perennial forage legumes. Crit. Rev. Plant Sci. 34:327–380. doi:10.1080/07352689.2014.898462

Atlin, G.N., and K.J. Frey. 1990. Selecting oat lines for yield in low-productivity environments. Crop Sci. 30:556–561. doi:10.2135/cropsci1990.0011183X003000030017x

Bänziger, M., and M. Cooper. 2001. Breeding for low input conditions and consequences for participatory plant breeding: Examples from tropical maize and wheat. Euphytica 122:503–519. doi:10.1023/A:1017510928038

Barnes, R., and M. Collins. 2003. Forages: An introduction to grassland agriculture. Iowa State Press, Ames, IA.

Bernardo, R. 2002. Breeding for quantitative traits in plants. Stemma Press, Woodbury, MN.

Brancourt-Hulmel, M., E. Heumez, P. Pluchard, D. Beghin, C. Depatureaux, A. Giraud, and J. Le Gouis. 2005. Indirect versus direct selection of winter wheat for low-input or high-input levels. Crop Sci. 45:1427–1431. doi:10.2135/cropsci2003.0343

Brummer, E.C., and M.D. Casler. 2014. Cool-season forages. In: S. Smith, et al., editors, Yield gains in major U.S. field crops. CSSA Spec. Publ. 33. ASA, CSSA, and SSSA, Madison, WI. p. 33–52. doi:10.2135/cssaspecpub33.c3

Ceccarelli, S., and S. Grando. 1991. Environment of selection and type of germplasm in barley breeding for low-yielding conditions. Euphytica 57:207–219. doi:10.1007/BF00039667

Ceccarelli, S., S. Grando, and A. Impiglia. 1998. Choice of selection strategy in breeding barley for stress environments. Euphytica 103:307–318. doi:10.1023/A:1018647001429

Crutsinger, G.M., M.D. Collins, J.A. Fordyce, Z. Gompert, C.C. Nice, and N.J. Sanders. 2006. Plant genotypic diversity predicts community structure and governs an ecosystem process. Science 313:966–968. doi:10.1126/science.1128326

Dawson, T.P., M.D. Rounsevell, T. Kluvánková-Oravská, V. Chobotova, and A. Stirling. 2010. Dynamic properties of complex adaptive ecosystems: Implications for the sustainability of service provision. Biodivers. Conserv. 19:2843–2853. doi:10.1007/s10531-010-9892-z

Eberhart, S.A., and W.A. Russell. 1966. Stability parameters for comparing varieties. Crop Sci. 6:36–40. doi:10.2135/cropsci1966.0011183X000600010011x

Finlay, K., and G. Wilkinson. 1963. The analysis of adaptation in a plant-breeding programme. Aust. J. Agric. Res. 14:742–754. doi:10.1071/AR9630742

Grimm, V., and C. Wissel. 1997. Babel, or the ecological stability discussions: An inventory and analysis of terminology and a guide for avoiding confusion. Oecologia 109:323–334. doi:10.1007/s004420050090

Hodgson, D., J.L. McDonald, and D.J. Hosken. 2015. What do you mean 'resilient'? Trends Ecol. Evol. 30:503–506. doi:10.1016/j.tree.2015.06.010

IPCC. 2013. Climate change 2013: The physical science basis. Cambridge Univ. Press, Cambridge, UK. doi:10.1017/CBO9781107415324

Isbell, F., D. Craven, J. Connolly, M. Loreau, B. Schmid, C. Beierkuhnlein, et al. 2015. Biodiversity increases the resistance of ecosystem productivity to climate extremes. Nature 526:574–577. doi:10.1038/nature15374

Jaleel, C.A., P. Manivannan, A. Wahid, M. Farooq, H.J. Al-Juburei, R. Somasundaram, and R. Panneerselvam. 2009. Drought stress in plants: A review on morphological characteristics and pigments composition. Int. J. Agric. Biol. 11:100–105.

Kucharik, C.J. 2006. A multidecadal trend of earlier corn planting in the central USA. Agron. J. 98:1544–1550. doi:10.2134/agronj2006.0156

Kucharik, C.J., and S.P. Serbin. 2008. Impacts of recent climate change on Wisconsin corn and soybean yield trends. Environ. Res. Lett. 3:034003.

Lamb, J., C.C. Sheaffer, L.H. Rhodes, R.M. Sulc, D.J. Undersander, and E.C. Brummer. 2006. Five decades of alfalfa cultivar improvement. Crop Sci. 46:902–909. doi:10.2135/cropsci2005.08-0236

Li, X., and E.C. Brummer. 2012. Applied genetics and genomics in alfalfa breeding. Agronomy 2:40–61. doi:10.3390/agronomy2010040

Lin, B.B. 2011. Resilience in agriculture through crop diversification: Adaptive management for environmental change. Bioscience 61:183–193. doi:10.1525/bio.2011.61.3.4

Liu, Y., Q. Wu, G. Ge, G. Han, and Y. Jia. 2018. Influence of drought stress on alfalfa yields and nutritional composition. BMC Plant Biol. 18:13. doi:10.1186/s12870-017-1226-9

López-Ridaura, S., H.V. Keulen, M.V. Ittersum, and P.A. Leffelaar. 2005. Multiscale methodological framework to derive criteria and indicators for sustainability evaluation of peasant natural resource management systems. Environ. Dev. Sustain. 7:51–69. doi:10.1007/s10668-003-6976-x

Loreau, M., A. Downing, M. Emmerson, A. Gonzalez, J. Hughes, P. Inchausti, et al. 2001. A new look at the relationship between diversity and stability. In: M. Loreau, et al., editors, Biodiversity and ecosystem Function: Synthesis and perspectives. Oxford Univ. Press, New York. p. 79–91.

Marten, G.G. 1988. Productivity, sustainability, equitability and autonomy as properties for agroecosystem assessment. Agric. Syst. 26:291–319. doi:10.1016/0308-521X(88)90046-7

Melillo, J.M., T.C. Richmond, and G.W. Yohe, editors. 2014. Climate change impacts in the United States: The third national climate assessment. US Global Change Res. Progr., Washington, DC. doi:10.7930/J0Z31WJ2

NAAIC. (North American Alfalfa Improvement Conference). 2004. Standard tests to characterize alfalfa cultivars. 3rd ed. (Amended 2004). NAAIC. https://www.naaic.org/resource/stdtests.php (accessed 15 Oct. 2017).

NAAIC. (North America Alfalfa Improvement Conference). 2017. Description of alfalfa cultivars and germplasm. NAAIC. https://www.naaic.org/resource/cultivar.php (accessed 15 Oct. 2017).

NOAA. 2017. National Centers for Environmental Information. Climate at a glance: U.S. time series, Palmer drought severity index (PDSI). NOAA. http://www.ncdc.noaa.gov/cag/ (accessed 12 Apr. 2017).

Oliver, T.H., M.S. Heard, N.J.B. Isaac, D.B. Roy, D. Procter, F. Eigenbrod, et al. 2015. Biodiversity and resilience of ecosystem functions. Trends Ecol. Evol. 30:673–684. doi:10.1016/j.tree.2015.08.009

Picasso, V., L. Astigarraga, I. Buffa, D. Sotelo, G. Américo, R. Terra, et al. 2011. Robustness of livestock farmers to climate variability: A case study in Uruguay. Paper presented at the 5th World Congress of Conservation Agriculture incorporating the 3rd Farming Systems Design Conference, Brisbane, Australia. 26–29 Sept. 2011.

Picasso, V.D., E.C. Brummer, and M. Liebman. 2010. Diversity and stability in experimental grassland communities. Grassl. Sci. Eur. 15:827–829.

Picasso, V.D., E.C. Brummer, M. Liebman, P.M. Dixon, and B. Wilsey. 2008. Crop species diversity affects productivity and weed suppression in perennial polycultures under two management strategies. Crop Sci. 48:331–342. doi:10.2135/cropsci2007.04.0225

Picasso, V., C. Lizarralde, C. Molina, D. Bartaburu, H. Morales, and L. Astigarraga. 2013. A quantitative assessment of robustness to drought in livestock grazing systems in Uruguay. Paper presented at the First International Global Food Security Conference, Noordwijkerhout, the Netherlands. 29 Sept.–2 Oct. 2013.

Piepho, H.-P. 1998. Methods for comparing the yield stability of cropping systems. J. Agron. Crop Sci. 180:193–213. doi:10.1111/j.1439-037X.1998.tb00526.x

Sabatier, R., L.G. Oates, G.E. Brink, J. Bleier, and R.D. Jackson. 2015. Grazing in an uncertain environment: Modeling the trade-off between production and robustness. Agron. J. 107:257–264. doi:10.2134/agronj14.0357

Shiu, C.J., S.C. Liu, C. Fu, A. Dai, and Y. Sun. 2012. How much do precipitation extremes change in a warming climate? Geophys. Res. Lett. 39:L17707. doi:10.1029/2012GL052762

Tracy, B.F., J.L. Foster, T.J. Butler, M.A. Islam, D. Toledo, and J.M.B. Vendramini. 2018. Resilience in forages and grazinglands. Crop Sci. 58:31–42. doi:10.2135/cropsci2017.05.0317

Undersander, D., D. Cosgrove, E. Cullen, C. Grau, M.E. Rice, M. Renz, et al. 2011. Alfalfa management guide. ASA, CSSA, SSSA, Madison, WI. doi:10.2134/2011.alfalfamanagementguide

Urruty, N., D. Tailliez-Lefebvre, and C. Huyghe. 2016. Stability, robustness, vulnerability and resilience of agricultural systems. A review. Agron. Sustain. Dev. 36:15. doi:10.1007/s13593-015-0347-5

Volenec, J.J., S.M. Cunningham, D.M. Haagenson, W.K. Berg, B.C. Joern, and D.W. Wiersma. 2002. Physiological genetics of alfalfa improvement: Past failures, future prospects. Field Crops Res. 75:97–110. doi:10.1016/S0378-4290(02)00020-5

Waldron, B.L., K.H. Asay, and K.B. Jensen. 2002. Stability and yield of cool-season pasture grass species grown at five irrigation levels. Crop Sci. 42:890–896. doi:10.2135/cropsci2002.8900

Walker, B.H., C.S. Holling, S. Carpenter, and A. Kinzig. 2004. Resilience, adaptability, and transformability in social-ecological systems. Ecol. Soc. 9:5. doi:10.5751/ES-00650-090205

Wegulo, S., L. Giesler, R. Harveson, T.A. Jackson-Ziems, B. Liu, and K. Korus. 2013. Impacts of drought on disease development and management. Plant Pathology Paper 537. Univ. Nebraska–Lincoln. http://digitalcommons.unl.edu/plantpathpapers/537 (accessed 30 Mar. 2018).