

Journal of Range Management

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Managing Editor

CHARLES B. (BUD) RUMBURG
1839 York Street
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PATRICIA G. SMITH
Society for Range Management
1839 York Street
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KIRK MCDANIEL
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Catastrophe Theory: A unified paradigm for rangeland ecosystem dynamics

JEFFREY A. LOCKWOOD AND DALE R. LOCKWOOD

Authors are with the Department of Plant, Soil, and Insect Sciences, University of Wyoming, Laramie 82071; and Department of Mathematics, University of Arizona, Tucson 85718, respectively.

Abstract

Rangeland ecologists have elucidated 2 apparently distinct processes underlying rangeland dynamics. In some cases, disturbed or recovering rangelands move through a gradual, continuous series of changes which has been termed succession. In other instances, rangeland dynamics are typified by sudden, discontinuous changes in the vegetation, and this has been called state-and-transition. Catastrophe theory is a mathematical framework designed for the study of discontinuous phenomena, but it also generates models that permit continuous dynamics. Based on available literature, it appears that rangeland ecosystems conform to the mathematics of catastrophe theory. Rangelands exhibit the 5 essential symptoms of catastrophe systems: modality (distinct conditions or states of existence), inaccessibility (conditions which are very unstable), sudden changes (relatively rapid movement between states), hysteresis (processes associated with degradation or recovery are not readily reversible by simply inverting the sequence of events), and divergence (relatively small changes in initial conditions can result in dramatically different outcomes with time). Catastrophe theory has been successfully used to model rangeland grasshopper population dynamics, and it appears that many of the same control variables affecting insects (e.g., temperature and precipitation) may also underlie vegetative community dynamics. Application of catastrophe theory to empirical data sets will require relatively long-term but low-intensity research efforts.

Key Words: nonlinear models, succession, state-and-transition

Range management depends on accurate models of the dynamics which underlie the extractable resources of the world's rangelands. In this regard, there are 2 competing, conceptual models that have been used to explain rangeland ecosystem dynamics. The older model is that of range succession (Clements 1916, Sampson 1919, Dyksterhuis 1949). This concept calls for smooth, continuous, and reversible changes along a gradient of ecological states. The underlying theory depends on ecosystems having predictable, repeatable processes of development from a disturbed state through 1 or more seral stages and finally reaching a climax condition.

The alternative view recognizes the concept of discontinuous, irreversible changes, the nature of which may not be easily predictable over the long-term. Although this concept is not new, it has only recently been explored in terms of understanding rangeland dynamics with the development of the state-and-threshold model of Laycock (1991). In this paradigm, rangeland ecosystems do not necessarily return to an original or climax state following disturbance. Thus, eliminating the cause of a particular change in the system (e.g., reducing grazing or ending a drought) may not result

in a predictable sequence of events that return the system to its original condition.

Recent work (Dodd 1992, Friedel 1991, Laycock 1991, Westoby et al. 1988) has suggested a dichotomy between the 2 dominant conceptual models used to describe rangeland condition dynamics. The nature of these 2 paradigms (the continuous, reversible, predictable dynamics of the succession model versus the discontinuous, irreversible, unpredictable dynamics of the state-and-threshold model) results in 2 significant difficulties with the current state of ecological modeling in range management.

First, there appears to be a dilemma with respect to resolving the applicability of the succession and state-and-threshold models to any particular system. In classical scientific terms, it appears that the state-and-threshold paradigm excludes the possibility of an underlying continuous process inherent in the succession paradigm. It has not been suggested that the older model is without applicability (Dodd 1992, Westoby et al. 1989); rather, there are some demonstrable conditions under which it does not appear to function. As such, unless there is a single model that captures both continuous and discontinuous dynamics, range scientists are in the unenviable position of having to choose between these 2 paradigms (Dodd 1992). Such a choice is confounded by what appears to be little empirical evidence to determine which system is most likely to apply in any given ecosystem. Although Schlatterer (1989) developed a model that allows both successional (reversible) and irreversible changes, it did not clearly integrate the state-and-threshold model; the model did not include a means by which one might know (except retrospectively) which process would occur in a particular system; and it did not provide a coherent explanation of why both processes were possible.

Second, conceptual models (i.e., the current formulations of the succession and state-and-threshold systems) are extremely valuable initial tools for organizing, defining, describing, and categorizing; but they have serious limitations and must eventually mature into a mathematical framework to realize their full potential. Conceptual models are virtually always post factum descriptions of what has happened, and they provide relatively little information with respect to forecasting and prediction. As such, they are a starting point for, but do not in themselves constitute, an adequate theoretical base for a scientific discipline. Without an underlying mathematics to define the model, qualitative descriptions often given rise to a condition of multiple paradigms, which is considerably less valuable than a unified theory of system dynamics. Finally, a lack of mathematical rigor prevents the formulation of clear research questions with which to validate or dismiss a particular model. Without a mathematical system, the "testing" of a model becomes a process of accumulating retrospective case histories.

A solution to these 2 problems of conceptual models in range ecology must include both a unification of the succession model with the state-and-threshold model and accomplish this integra-

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tion through an established mathematical system. Although range scientists are aware of the ecological literature related to discontinuous systems, there is no widespread understanding of the associated mathematical theories which may be used to solve the dilemma of multiple, conceptual paradigms. It is the purpose of this paper to introduce the field of catastrophe theory and to explain how this theory may unify the existing range ecology paradigms with a single mathematical theory.

Catastrophe Theory

Catastrophe theory was developed by Thom (1972) to provide a theoretical framework for studying discontinuous phenomena in otherwise continuous systems. In some ways the original designation of the dynamics as "catastrophic" is unfortunate because this term is colloquially used to describe extreme and negative changes. In the mathematical usage (Thom 1972), the term refers to processes which are manifested as sudden, quantum changes in the state of the system (e.g., the shift of an animal's behavior from attack to submission, the perceptual shift which occurs with many optical illusions, or the changes in the state of an embryo during development [Saunders 1980]). Zeeman (1972, 1976, 1978) subsequently popularized the theory and suggested a wide spectrum of applications in the social and biological sciences. Despite the initial interest in catastrophe theory among ecologists, it has been the physical scientists and engineers who have made the greatest use of the mathematics. The irony in this situation was elucidated by Gilmore (1981), who observed that the physical sciences do not ultimately need catastrophe theory because the underlying equations for relevant dynamics already exist and their properties will eventually be discovered. Rather, it is in the life sciences, where the underlying equations are far from known, where catastrophe theory may have its greatest and most numerous applications. Although Gilmore (1981) went on to predict that catastrophe theory would remain largely in the realm of the physical and engineering sciences, the theory has garnered some attention in range management. Jameson (1988) noted the potential applicability of the theory to modelling ecosystem dynamics, but he overlooked one of the critical properties of catastrophic systems (inaccessibility, see **Catastrophic Symptoms**). More importantly, he viewed the theory as simply another tool, and failed to recognize the broader implications which allow for a unification of the successional and state-and-threshold concepts. Most recently, catastrophe theory has been used to gain insight to and generate accurate predictions of the dynamics of rangeland grasshopper populations (Lockwood and Lockwood 1991). It is largely from this work that we derive the following description of the theory.

Catastrophe theory deals directly with the properties of mathematical singularities (i.e., sudden changes or discontinuities) in systems which possess a smooth, underlying potential. The necessity of a smooth function arises from the fact that we are interested in the origin of discontinuities, and nothing is gained if we merely assume they are built into the dynamics. That is, if we are free to arrange the discontinuities as we please (as with some conceptual models) our models become simply descriptive accounts, without a clear rationale. As such, catastrophe theory is particularly appropriate for the study of systems whose inner workings are unknown and for situations in which reliable observations relate to the discontinuities. Thus, the theory appears to have significant potential in unifying the 2 paradigms of range ecology.

Catastrophe theory addresses the specific conditions in which discontinuous behavior (characteristic of the state-and-threshold paradigm) can emerge from an underlying smooth potential (characteristic of the succession paradigm). Perhaps the only drawback of the theory in this regard is that it is tailored to address the singularities rather than the continuous function. However, there

currently appears to be greater interest in the discontinuities in rangeland ecosystems, and this dynamic may be the more important feature of an effective management strategy (Ellis and Swift 1988).

Catastrophe theory describes the qualitatively different discontinuities in a given system that can be completely specified by 1 or more state variables (e.g., rangeland condition classes) and that is driven by 1 or more independent control variables (e.g., temperature, rainfall, and fire). The theory is constrained by a practical assumption. In Thom's (1975) definitions of elementary catastrophes, the control variables are restricted to 5. As Saunders (1980) points out, this assumption is less of a restriction than it might seem, because we can omit any independent control variables which do not have a significant effect on the discontinuity (remember that it is the sudden change, not the underlying continuous dynamic, that is the principal object of interest). Moreover, if more than 5 control variables are critically involved in the discontinuity of a system, then the analysis becomes intractable.

The simplifying elegance of catastrophe theory lies in the discovery that the number of qualitatively different discontinuities that can occur depends not on the number of state variables, which may be extremely large, but on the number of control variables, which is generally small (Saunders 1980). In range ecology there has been some rational reduction of the state variables into a limited set of functional groups (e.g., Friedel et al. 1988), and this process facilitates the application of catastrophe theory by defining the essential states of a system. However, even with this simplification of state variables, to model large and complex systems (such as rangelands composed of numerous soil types and dozens of plant species, each with its own set of herbivores and abiotic tolerances) by conventional, mechanistic means would require us to develop as many differential equations as there are state variables which specify the system, supply initial conditions, solve the equations, and then try to comprehend the solutions. Even if the rangeland ecosystem can be categorized into a relatively small number of states, mechanistic models of the dynamics are likely to be intractable. This may be particularly true if virtually every rangeland system has a unique set of regulatory mechanisms, which seems to be the case based on the models of Westoby et al. (1989). As noted by Lockwood and Lockwood (1991), a typical rangeland ecosystem is likely to be governed by more than 20,000 direct or primary relationships, and inclusion of indirect effects results in over 1 billion interactions between the living components of the system. If only 1% of the direct relationships are mechanistically important, we will need to develop and parameterize 200 mathematical expressions. With very few assumptions, catastrophe theory makes it possible to predict much of the qualitative behavior of a system without knowledge of these interactions, much less solutions to the associated differential equations (Saunders 1980). This is not to say that ordinary differential equations may not provide a powerful tool if the mechanisms of rangeland ecology are elucidated (catastrophic behavior can arise even in simple systems of ordinary differential equations [Murray 1980]), but at this time neither the precise mechanisms nor the quantitative relationships necessary to describe the mechanisms appear to be available.

Fold Catastrophe

The fold is the most simple expression of catastrophe theory. As described by Saunders (1980), the fold catastrophe occurs along a response curve of the state variable in relation to a single control variable, the result of which is a parabola defining the equilibrium surface (Fig. 1). As the state variable moves along the parabola, where $u < 0$, to the point of inflexion (at the origin: 0, 0), it "jumps" into the undefined region, where $u > 0$. The 2 limitations of the fold catastrophe in its most elementary form are that there is only a

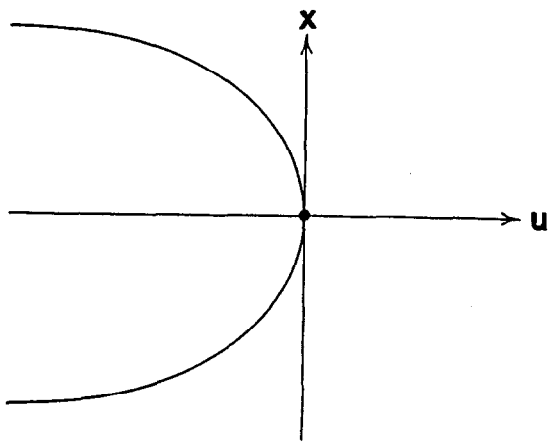


Fig. 1. The Fold Catastrophe, showing the response curve and the point of bifurcation.

single control variable, and unless we hypothesize a second fold or other modification (Saunders 1980), the dynamic is unidirectional because the state variable becomes undefined after a catastrophe. However, this model successfully demonstrates how a single expression can account for both smooth, continuous dynamics and sudden jumps.

Cusp Catastrophe

Of the 7 catastrophes that can occur with 4 or fewer control variables (Saunders 1980), the cusp catastrophe has had the greatest utility in the biological sciences (Zeeman 1976, Lockwood and Lockwood 1991). Although for some systems the overriding control may be expressed with a single variable (Lockwood and Lockwood 1988, Ellis and Swift 1988), this appears to be an exceptional condition. The utility of the cusp catastrophe may reflect the fact that it is the most parsimonious elementary catastrophe that includes more than a single control variable, and discontinuities in most living systems appear to be the consequence of more than a single factor. Thus, the sudden conversion of a dog's state from submission to attack has been modelled using the 2 behavioral parameters of rage and fear (Saunders 1980); cellular frontiers in embryology have been modelled using space and time as control variables (Zeeman 1974); prey biomass and time have been used to model predator outbreaks and crashes in chemostats (Bazin and Saunders 1979); and expressions of socio-political costs and threats have been used to understand the formation of government policy (Isnard and Zeeman 1976, Zeeman 1977). For the purpose of illustrating catastrophe theory in context of rangeland dynamics, the cusp catastrophe has the added advantage of having a solution that can be represented in 3 dimensions. While 3 and 4 variable systems can be used, if necessary (e.g., Jameson 1987), the essential features and properties are best illustrated with the cusp; rational extrapolations to the 4 and 5 dimensional solutions of more complex models should be apparent. Finally, there appears to be a number of cases in rangeland ecology where a 2-state system (e.g., arid and semiarid rangelands with distinct states represented by grassland and woodland or intact and degraded soil) having a pair of dominant control variables (Westoby et al. [1989] specifically argue that 2 control variables may very often capture the essential dynamics of rangeland systems) may be a reasonable reflection of reality (Foran et al. 1986, Friedel 1991).

The cusp catastrophe is the simplest of the bifurcation catastrophes, in which very small perturbations in initial conditions can lead to very different dynamics (see Appendix). The cusp catastrophe occurs in a response surface of a state variable in relation to 2 control variables. These latter variables are known as the normal

and splitting factors. That is, across a range of values for the normal factor, any change in the splitting factor results in only smooth or "successional" changes in the state of the system (Fig. 2).

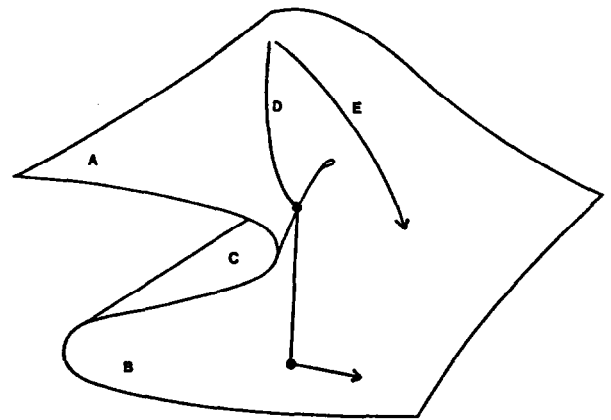


Fig. 2. The Cusp Catastrophe, showing the properties and symptoms of the model. Modality is indicated by the existence of an upper (A) and lower (B) sheet. The region of inaccessibility is shown as the infolded portion of the cusp (C). A trajectory resulting in a sudden jump from one state to another (from the upper sheet [A] to the lower sheet [B]) is indicated (D); this is the dynamic that has been previously identified in state-and-threshold models. A nearby trajectory (E) demonstrates the symptom of divergence, in which small deviations in initial conditions lead to very different behaviors. This trajectory (E) shows a process by which transition from one state to another is accomplished by a smooth, continuous dynamic, as in succession. If this trajectory (E) were to pass through the point at which the other trajectory (D) contacted the lower sheet or state (B), it would not then jump to the upper sheet (A) because this point does not represent contact with the region of inaccessibility (C). This phenomenon, in which dynamics are not strictly reversible, is termed hysteresis.

However, when the normal factor falls within another range of values, the equilibrium surface which defines the state of the system is split, and changes in the other variable may give rise to discontinuous or "state-and-threshold" dynamics (Fig. 2); that is, as the control variables change and the state variable crosses the cusp edge, it will suddenly jump to the other leaf of the surface. This bifurcation is of particular interest because it represents a catastrophic change in the system (e.g., a change of state from one condition class or habitat type to another). The nature of the control variables is not predetermined. Either intrinsic variables within a feedback system (e.g., herbivore grazing or decomposition rates) or extrinsic variables indirectly modifying or outside of a feedback loop (e.g., weather or herbicide application) may be appropriate (Zeeman 1974, 1977; Isnard and Zeeman 1976; Bazin and Saunders 1979).

Catastrophic Symptoms

Because application of catastrophe theory to an ecological problem is not a simple task nor are all ecological dynamics catastrophic in nature, it is useful to determine if a particular system is likely to be accurately described with the theory. In this regard, theoretical and empirical evidence (Zeeman 1978; Lockwood and Lockwood 1988, 1991) have established that catastrophic systems exhibit a unique set of symptoms. The 5 symptoms or flags of the cusp catastrophe have been clearly observed and documented in rangeland ecosystem dynamics.

The first symptom is modality, which refers to the existence of the system in distinct states. These states are represented by the 2 surfaces of the cusp (Fig. 2) or the multiple surfaces of more complex catastrophic models. It is clear that range ecologists have identified modality. Multiple ecological states appear to be com-

mon throughout the world (Ellis and Swift 1988, Westoby et al. 1989, Friedel 1991, Laycock 1991). While Westoby et al. (1989) recognized both states and transitions, they appear to have excessively complicated their models by defining even transitory conditions as states. The concept of discrete states of the system and the transitions between states has been clarified in recent studies. Most recently, Friedel (1991) refers to the existence of discontinuous environmental change between "alternative states" and graphically defines distinct states found in arid open woodland range. Laycock (1991) adopted and clearly applied the "state-and-threshold" concept to describe ecosystem dynamics and in so doing ascribed to the notion of modality.

The next symptom is inaccessibility, or the occurrence of unstable equilibria or thresholds (Berryman 1982), represented by the infolded region of the cusp (Fig. 2). Again, Westoby et al. (1980), and most recently both Friedel (1991) and Laycock (1991), have clearly and coherently argued for the existence of unstable equilibria. The "cup-and-ball" analogy has been used to capture the concept of thresholds which separate steady states (Hurd and Wolf 1974). Indeed, the cup-and-ball conceptualization can be found both in Laycock's (1991) model of rangeland dynamics and in Saunder's (1980) explanation of elementary catastrophes. What is expressed in the "cup-and-ball" is the perceived existence of singularities and attractors or local minima of the potential.

The third condition indicating a catastrophic system is the existence of sudden jumps, which are seen when a trajectory reaches an edge of the cusp (the area of inaccessibility) and jumps to the alternative sheet or condition (Fig. 2). The occurrence of quantum leaps or discontinuities is explicitly developed by Friedel (1991), who suggests that environmental change on rangeland can be "discontinuous" (Bradbury et al. 1983/4). This symptom is also implicitly supported by Laycock (1991) in the concept of thresholds through which a system passes rapidly between 2 steady states.

The next system is hysteresis, which refers to the property in which a trajectory associated with a jump in one direction (e.g., from the upper to the lower sheet of the cusp in Fig. 2) is different from the trajectory resulting in a jump in the opposite direction. That is, a trajectory passing through the point where the system falls to the lower sheet will not, at the same point, jump up to the upper sheet. Noy-Meir and Walker (1986) described hysteresis at the effect where decline and recovery follow different paths, and Friedel (1991) built on the work of Westoby et al. (1989) in adapting this property to a model of rangeland ecosystem dynamics. Friedel (1991) suggested that shifts between states of rangeland are not practically reversible without substantial human intervention, which is another formulation of the hysteresis property (see Coffin et al. 1991). Archer's (1989) study of the conversion of mesquite savannas to woodlands was used by Laycock (1991) to support the concept of hysteresis; he suggested that while heavy grazing may drive a rangeland plant community from one state to another, the simple elimination of grazing after the transition will not result in the return of the system to its original state. Indeed, Laycock (1991) deviates from the global model, which suggests that ecological systems always returns to a single climax state, by arguing that hysteresis must be considered as a component of the system.

Finally, divergence is the symptom which arises when relatively small changes in the control variables result in markedly different behaviors of the system (Fig. 2). This concept appears to be strongly supported by the work of Gleason (1926) and Egler (1954), which found that rangeland plant communities may be regulated by relatively small differences in the conditions at the time of disturbance. The work of Westoby et al. (1989) and West (1979, 1988) suggests that in at least some systems, seemingly small changes in control variables (e.g., rainfall events or light grazing)

may cause a transition between distinct states. Friedel (1991) also alludes to divergence in recognizing that different communities have different susceptibilities to change. Schlatterer's (1989) contention that the particular path of vegetative change is determined by the kind, duration, and intensity of disturbance also allows the property of divergence.

Advantages of Catastrophe Theory as a Framework

Appropriate policies and management strategies are only possible if the fundamental dynamics of the rangeland system are clearly understood (Ellis and Swift 1988). While Laycock (1991) is certainly justified in arguing that we should begin with conceptual models to organize available information, it is critical for ecologists to develop these models from systems of qualitative concepts, generalizations, and assumptions (Westoby et al. 1989) to rigorously testable systems with clearly defined relationships. Laycock (1991) observed that the conceptualized models of scientists (i.e., the system of discontinuous dynamics between multiple stable states of rangeland) must be communicated to managers; but it is equally essential that ecologists communicate their conceptual models to mathematicians in order to fully realize the potential of the models. The advantages of moving from conceptual models to mathematical formulations (when such a move is, in fact, possible) include the capacity to test and validate the model, the ability to modify a known mathematical expression to meet site specific conditions, and the capacity to manage the resources using objective, quantitative measures. In that there appears to be considerable consensus among range ecologists that some hybridization of the successional and state-and-threshold models is needed, catastrophe theory offers at least 3 advantages.

First, the mathematics of catastrophe theory allows for both continuous and discontinuous changes in a system, although the latter are the primary dynamics of interest. Because the control variables may include internal feedback factors and external stressors, the elements of successional and nonequilibrium (*sensu* Ellis and Swift 1988) dynamics can be addressed. As such, even a single rangeland site can be modeled with allowance for both types of dynamics, and such situations appear to be possible (Ellis and Swift 1988, Laycock 1991). Next, because the mathematical framework of catastrophe theory is established, the discontinuities in the system being modeled are truly emergent from the control variables. Thus, the transitions between states in the model are not conveniently imposed (as appears to be the general case in existing, conceptual models) but emerge from known qualitative and quantitative relationships. Lastly, because catastrophe theory does not require a strict formulation of the mechanistic processes underlying the dynamics, it is possible to apply the theory to extremely complex systems whose internal workings have yet to be quantitatively elucidated. It appears that available knowledge of rangeland ecology is much more consistent with qualitative nonmechanistic efforts than with mechanistic models and their associated need for parameterization (Friedel 1991).

A final, possible advantage of catastrophe theory arises from the conceptual nature of the cusp (or more complex models). The cusp captures both the smooth, successional transitions and the discontinuous changes in a system. It may be that even if it takes some time to collect the necessary data to validate the catastrophic models, the conceptual model (Fig. 2) may prove valuable in capturing the processes that appear to occur on rangelands.

Limitations of Catastrophe Theory

In addition to limitations of catastrophe theory that arise from the nature of the mathematics (i.e., the model specifically focuses on the discontinuous events in a dynamic, there must be an underlying smooth potential or related function, and there can be no more than 4 control variables, for practical purposes), there are

some philosophical difficulties. Catastrophe theory has been legitimately criticized (Berryman and Stanseth 1984) for being a descriptive allegory that provides little mechanistic insight into the biological phenomena that give rise to catastrophic behavior (Sussman and Zahler 1976, 1978). Because catastrophe theory does not require precise knowledge of the manner in which the control variables impact the state variables (only that the latter have important effects on the former), it can be said that the theory fails to explain the underlying phenomenological causes (Berryman and Stanseth 1984). These objections to catastrophe theory require 2 responses in context of rangeland management.

First, from a management perspective we are not immediately concerned about the mechanistic explanation of rangeland dynamics. While this argument perhaps overstates the case, it is clear that the manager needs accurate qualitative information regarding the effects of control variables on future dynamics, not a definitive ecological theory or mechanism that explains why the forecast works (Dodd 1992). Knowledge of regulatory mechanisms is undeniably valuable in developing sound range management practices, but the manager benefits from qualitative solutions (e.g., will grazing result in a conversion of grassland to woodland?), not quantitative mechanisms. Although theoretical ecologists may be somewhat frustrated by the "black box" approach of catastrophe theory, it remains a useful tool for analysis of complex systems. This leads to the second response to the above criticisms.

As Saunders (1980) points out, the advantage of catastrophe theory lies in the modeling of systems with intractably complex inner workings. So, it hardly seems to be a weakness that catastrophe theory fails to explain mechanisms that are well beyond the scope of our current understanding. For example, while we do not know the precise mechanisms through which precipitation influences each rangeland plant species (e.g., direct water uptake, promotion of fungal diseases, mediation of herbivore populations, etc.), there appears to be no question that rainfall is a dominant catastrophic control variable on some rangelands. Because there is an imminent need for prediction of state shifts due to natural and management inputs and the determination of feedback and other mechanisms for each rangeland type is a long way from completion, catastrophe theory seems to be an appropriate technique for qualitative, nonmechanistic analysis and forecasting.

Application of the Theory: A Rangeland Example

Catastrophe theory was first applied to the rangeland ecosystem by Lockwood and Lockwood (1991) in understanding and predicting weather-driven grasshopper population dynamics. Although fluctuations in grasshopper populations and weather conditions are clearly interrelated, attempts at defining linear relationships had been largely unsuccessful (Watts et al. 1982). The accuracy of grasshopper population models had been unsatisfactory due to 2 factors. First, pest infestations exhibit extremely rapid increases and decreases in density and area, and these changes are difficult to capture with continuous or linear models (Lockwood and Lockwood 1988). Second, the precise role of weather in mediating grasshopper populations is unknown (Watts et al. 1982). Although weather acts directly on grasshopper physiology, its effects are also mediated through food plant quality and quantity, predators, parasites, and diseases (Joern and Gaines 1990). Thus, a nonmechanistic model that incorporated the possibility of sudden changes in the system was needed, and catastrophe theory provided such a tool.

It was not surprising to find that grasshoppers exhibited the 5 classical symptoms of a cusp catastrophe, given that these insects are intimately linked to rangeland plant dynamics which also appear to be catastrophic (see **Catastrophic Symptoms**). The element of modality or distinct states is apparent from the outbreak and nonoutbreak conditions of rangeland grasshoppers. In grass-

hopper populations, inaccessibility can be seen in the existence of unstable population densities, recognized as "threatening" conditions that are likely to precede an outbreak. Sudden jumps from low-to-high or high-to-low densities or areas of infestation are the classical population dynamics on western rangelands (Capinera 1987, Lockwood and Lockwood 1988). The symptom of hysteresis is evident from the realization that in grasshopper populations, simple reversal of the sequence of conditions that generate an outbreak is not likely to precipitate a crash. Finally, divergence or sensitivity to initial conditions is seen in rangeland grasshopper population dynamics. Small changes in weather may result in very different population dynamics. That is, outbreaks do not require years of serious drought, and population crashes may be induced by relatively discrete periods of rainfall (Pickford and Riegert 1964). Thus, all of the symptoms expected in a catastrophic system were found in rangeland grasshopper population dynamics.

Based on this qualitative assessment of grasshopper ecology, we used 28 years of bimonthly mean temperature and total precipitation data as the 2 control variables for a cusp catastrophe model, in which the state variable was the area infested at outbreak (≥ 9.6 grasshoppers m^{-2}) or threatening densities (> 3.6 grasshoppers m^{-2} but < 9.6 grasshoppers m^{-2}) (Lockwood and Lockwood 1991). The model was applied to 4 ecotopographic regions of Wyoming to determine the accuracy of both matching the observed, historical dynamics and predicting future conditions. With regard to matching observed dynamics, we used 3 scales of catastrophic change—a 15, 30, and 45% increase or decrease in the area of a region that was infested from 1 year to the next. With respect to predicting dynamics, data from 1988–1990 were not included in model development so that novel cases could be used for validation.

In all regions, the cusp catastrophe model generated a match to observed outbreaks and crashes at a frequency significantly ($P < 0.05$) better than chance (Lockwood and Lockwood 1991). In general, the model was most effective in regions that had the most serious history of outbreaks. The accuracy of the cusp catastrophe increased with the intensity and scale of the infestation (e.g., large-scale changes [$\geq 45\%$ of a region] were modeled without error). In general, outbreaks were more accurately modeled than were crashes, and weather in April–May provided the best control variables. The model was also useful in forecasting. In the Platte Valley (the region of most serious grasshopper outbreaks), the actual area of infestation fell within the forecasted range in each year of validation. In the Thunder Basin (a region of moderately severe grasshopper outbreaks), the predictions were accurate in 2 of 3 cases; in 1989 an outbreak of 27,000 ha was predicted but did not occur. Thus, a cusp catastrophe model matched historical grasshopper population dynamics and effectively predicted future changes in the area of infestation.

Future Directions

Presently, catastrophe theory is a tool with demonstrable potential but no proven applications to rangeland plant ecology. The finding that this mathematical theory accurately models rangeland grasshopper population dynamics in both *post facto* and predictive modes (Lockwood and Lockwood 1988, 1991) using weather variables, provides some encouraging evidence that other rangeland organisms with populations largely influenced by weather can be successfully modeled with this approach. Indeed, it seems likely that the types of data necessary to use and validate this theory on rangeland plant communities are forthcoming. Westoby et al. (1989) identified the need to determine the factors which result in particular transitions. Even without access to the mathematical theory, Laycock (1991) had the insight to express the fundamental elements of catastrophe theory; he recognized the imminent need for the identification (and measurement) of state and control vari-

ables. Fortunately, it appears that in many rangeland ecosystems 1 to 3 control variables are principally involved in the dynamics (i.e., fire, precipitation, and grazing [Ellis and Swift 1988, Westoby et al. 1989, Friedel 1991, Laycock 1991]). Indeed, Westoby et al. (1989) collapses all control variables into 2 types: natural events and management actions. The other essential components of catastrophe theory, state variables, appear to be quite highly refined and clearly defined for at least some ecosystems (e.g., Friedel et al. 1988).

The actual utility of catastrophe theory can be evaluated when data sets have been developed which include both state and relevant control variables over a reasonable period of time. This time period is critical. It must include examples of at least the principal dynamics that occur in the system and may, therefore, require several decades of data (although continuous records may not be essential). For the model to have sufficient information to construct a reasonable facsimile of the ecological events, at least 1 case (and preferably several) of each type of discontinuous event seen in the system must be available. In this regard, it is essential for the application of catastrophe theory, or even the further development of the existing conceptual models, that ecological data be collected with attention to the states and factors or control variables which likely produce these states (directly or indirectly). Thus, in developing data sets to validate catastrophe theory, the most reasonable state variables will likely be the condition classes or habitat types relevant to a particular rangeland ecosystem; and the most valuable control variables will probably include weather (temperature and precipitation), fire, and herbivore grazing intensity.

Conclusions

According to both Friedel (1991) and Laycock (1991), there is a largely insufficient existing theoretical base for the conversion of the conceptual models of rangeland ecosystem dynamics into sound management strategies. Catastrophe theory has allowed coherent synthesis and understanding of such complex systems as anorexia nervosa in humans (Zeeman 1976, Steward and Peregoy 1983), collapse of elastic structures (Zeeman 1976), and population dynamics of rangeland grasshoppers (Lockwood and Lockwood 1991). As such, it appears that this mathematical system represents the possibility of translating conceptual models into verifiable formats which may then be used in the development of management practices.

As a scientific field is studied, over time, there comes an increasing structure which is often mathematically based. Thus, physics, studied for millennia, is the most mathematical of the sciences (indeed in this century the boundaries between many mathematical subjects and physics have virtually disappeared). Chemistry was quantified next, but even today much of the biological sciences defies mathematical explanation. A portion of this apparent intractability is due to the inability of biologists to successfully assume complexity out of the systems that we study (as has been done in physics [Woodcock and Davis 1978]), and a part of the difficulty lies in the relative recency with which we have seriously studied living systems. However, a portion of the problem is the belief by some biologists that mathematics has little to contribute to problems as complex as ours. While we would hardly agree with Lord Rutherford that, "All science is either physics or stamp collecting," his observation that many subdisciplines are largely just collections of related facts rings true today. Fortunately, range science appears to be developing and adapting systematic theories of essential processes underlying the object of study. Ecological systems frequently do not allow the formation of paradigms or models based even roughly on mathematical structure when traditional tools are applied to the task. For example, the calculus is completely entrenched in continuity; discontinuity is marginalized

since most physical actions (e.g., rolling balls, falling objects, etc.) are continuous. Only in the last half of this century have mathematicians developed the tools for dealing with the enormous and unique difficulties of discontinuities which face the ecologist (and demographer, sociologist, and psychologist). It is incumbent upon us to begin the dialogue by exploring the uses and limits of paradigms such as catastrophe theory.

Appendix

The cusp catastrophe arises from a system with 1 state variable and 2 control parameters. Since a scalar differential equation has equilibria as the only interesting dynamical structure (there can not be limit cycles, homoclinic orbits, strange attractors, or other interesting dynamics in 1 dimension), the bifurcations will be of the number and type of equilibria as the control parameters vary.

The cusp is the universal unfolding of the topological singularity, x^4 . This means that the cusp is the simplest expansion around the singularity that exhibits all the possible dynamics present in any small perturbation of x^4 . The potential function for the cusp is given by,

$$V(x) = 0.25 x^4 + 0.50 ux^2 + vx \tag{1}$$

Where the dynamics system is given by,

$$x' = -\text{grad}V(x) = F(x) \tag{2}$$

So, if we consider the possible phase planes (the phase plane being a line in the case of one state variable) that can occur from (2) as u and v are allowed to vary, we see that there can be 1, 2, or 3 equilibria (Fig. 3). If there are 3 equilibria, it is always the case in the cusp that the middle one is unstable and the other 2 are stable.

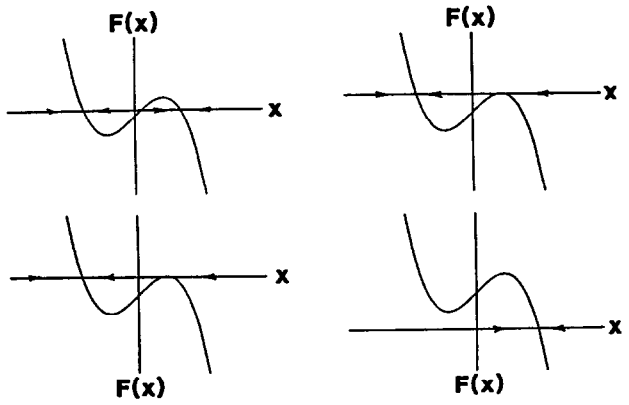


Fig. 3. Various phase portraits of the Cusp Catastrophe, showing 1, 2, and 3 equilibria.

In the case of 2 equilibria, 1 is nonhyperbolic (i.e., $F'(x) = 0$) and the other is hyperbolic and stable. Notice that the instability of the nonhyperbolic point is of a different form than the hyperbolic unstable point, thus giving rise to the hysteresis effect. Now, if the equilibrium manifold for (2) is generated, we get the object in Figure 2. The projection of this manifold into the $u-v$ plane yields the bifurcation diagram. The catastrophe set, which is the set of points that if crossed by the equilibrium trajectory results in a sudden jump, is given by,

$$27v^2 = 4u^3 \tag{3}$$

as seen in Figure 4.

It can be seen from the mathematics of the cusp that there is an implicit assumption about the system being modelled with this catastrophe. It is necessary to assume that the state variable equilibrates very quickly, so that the data can be interpreted as being

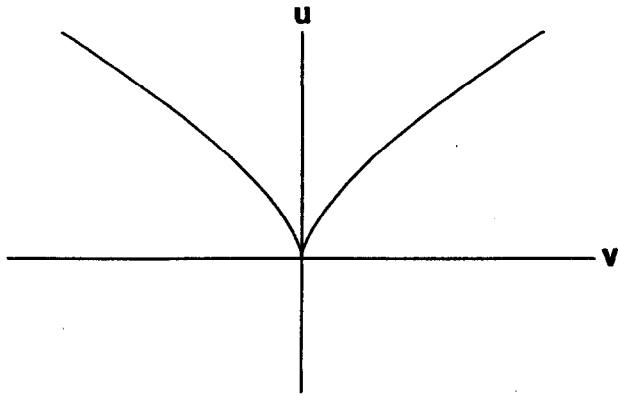


Fig. 4. Bifurcation diagram of the Cusp Catastrophe.

near the equilibrium surface. Motion near the equilibrium surface has no explicit time dependence, so without fully describing the dynamical system there can not be a deeper understanding of the asymptotic behavior of the state variable. There is also the ambiguity about the extent of the catastrophe in relation to the full dynamic. Since catastrophe theory is rooted in topology, the catastrophe can only be assumed to be a local effect of the singularity. This "localness" can only be experimentally determined, provided that the total dynamics are unknown.

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Habitat relationships of the pyrenean gray partridge

FRANÇOISE LESCOURET AND MICHEL GÉNARD

Authors at the time of the study were with Office National de la Chasse, BP34, F-31800 Saint-Gaudens; and GERA, Université de Bordeaux I, UER Biologie, Avenue des Facultés, F-33405 Talence Cédex. Authors are currently with INRA, Centre de Clermont-Ferrand-Theix, Laboratoire d'Ecopathologie, F-63122 Saint-Genès-Champagnelle; and INRA, Centre d'Avignon, Station d'Agronomie, Domaine Saint Paul, F-84143 Montfavet Cédex.

Abstract

Summer habitat relationships of the pyrenean gray partridge (*Perdix perdix hispaniensis*) were studied in the northern Pyrenees Mountains (France). Six available habitat types were defined, and those selected or avoided were identified. The only habitat type significantly ($p < 0.05$) selected was at intermediate altitudes, on fairly steep south-exposed slopes, with a moderate cover of woody plants. Two habitat types were significantly avoided. One occurred at low altitudes on mowed plateaus colonized by low woody plants, and the other was at high altitudes on slopes free of low woody plants. We suggest applications of the work in a model that should lead to valid habitat recommendations for restoring partridge populations.

Key Words: Pyrenean gray partridge (*Perdix perdix hispaniensis*), French Pyrenees, habitat, multivariate analysis

The gray partridge has disappeared from most European mountains. Nevertheless, populations of *Perdix perdix hispaniensis* still exist in the Pyrenees and Cantabrics (southern France and Spain) (De Juana 1980, Lescourret and Catusse 1987, Lescourret and Ellison 1987). These populations appear to be declining because of deterioration of their habitats (Lescourret 1988). Consequently, definition of habitat management policies for restoring the gray partridge is critical. This definition can only be based on sound knowledge of habitat relationships. Past studies of gray partridge habitat (Lescourret 1988, Novoa and Gonzalez 1988) have not treated vegetation structure and composition. Further, they used an univariate approach, which cannot give the synthetic picture of habitat relationships provided by multivariate analyses (Shugart 1981, Carnes and Slade 1982). Some multivariate studies have compared occupied and unoccupied sites using discriminant analysis (Johnson 1981). Unoccupied sites are frequently not known, and habitat studies are often limited to comparison between occupied sites and sites randomly chosen in the study area. Using discriminant analysis is then misleading (James et al. 1984). A better approach is to describe the environment using multivariate analysis of the random points. This provides habitat description over a reduced space, on which occupied sites can be positioned (Rotenberry and Wiens 1981).

We used such an approach to investigate habitat relationships of pyrenean gray partridge. The objectives were to (1) define summer habitat types available to gray partridge in the French Pyrenees, and (2) identify habitat types selected and those avoided.

Study Area

The study area included 1,745 ha, representing a large range of

habitat conditions (elevation, orientation, topography, vegetation) in the northern Pyrenees, in the valley of the Gave de Gavarnie (44° N. Lat., 0° Long.). The climate is oceanic montane and the landscape has been managed since 5000 B.C. to favor grazing (Cante-grel 1983, Jalut 1984).

The open montane zone (900–1,800 m) is *Brachypodium pinnatum* or *Festuca rubra* grasslands, and *Vaccinium myrtillus* or *Calluna vulgaris* heaths. The open subalpine zone (1,500–2,400 m) is *Festuca eskia* or *Nardus stricta* grasslands and *Rhododendron ferrugineum*, *Vaccinium myrtillus*, *Calluna vulgaris* or *Juniperus nana* heaths. The alpine zone (>2,200 m) is dominated by grasslands and boulders (Gruber 1978, Dupias 1985).

Methods

Sampling Design

The 1,745-ha study area was sampled by walking grid lines based on rectangles 250 × 500 m. The grid lines, totaling 48 km, were walked twice, in August and September 1987, by 2 observers traveling simultaneously along parallel strips. Observers looked for birds and signs of their presence (feathers, tracks, and droppings). Droppings constituted 74% of the signs observed. We verified that "field life" of droppings was short, by examining the gradual change of several samples of fresh droppings. All 155 droppings examined totally disintegrated within 40 days.

Habitat was described within a 50-m radius of each bird observation or sign of presence and at each grid intersection. Descriptors included elevation, topography, exposure, slope, dominant plant species, stone cover (<50 cm diameter), and boulder cover (>50 cm diameter). Cover of grasses, forbs, and woody plants was measured in 3 vegetation layers (0–10 cm, 11–25 cm, 26–50 cm). Percent cover was estimated by comparison with reference drawings representing imaginary covers of 1, 5, 10%, etc. (Prodon and Lebreton 1981). Habitat descriptions were made at 62 sites where birds or their signs were recorded and at 202 grid intersections.

Statistical Analysis

Prior to definition of available habitat types, we identified vegetation types by performing a correspondence analysis (C.A. (Benzécri 1973) on the dominant plant species recorded at the 202 grid sites. We used an eigenvector approach for the correspondence analysis, i.e., a special Principal Component Analysis for qualitative variables. These 202 sites were described by their scores on the highest ranking components clustered by an ascending hierarchical clustering using Ward's minimum-variance method (Ward 1963). Each cluster corresponded to a vegetation type.

Quantitative variables were transformed into categorical variables by creating classes (for example, <1,771, 1,771–1,915, 1,916–2,120, >2,120 m for elevation). Qualitative variables were also divided into categories (S, N, SW, etc. for exposure). Each site was assigned the number 1 for the class or category of a variable describing it and 0 for the other classes or categories (a site 1,900

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m-high was assigned a 1 in the 1,771–1,915 m class and a 0 in the other elevation classes). This procedure preserved nonlinear relationships between variables (Johnson 1981) and allowed qualitative and quantitative variables to be processed together. The 16 descriptors were represented by 62 categorical variables (Table 1).

Table 1. Categories of habitat variables (identified by numbers, adjectives, or letters).

Altitude, m	1:<1771	2:1771–1915	3:1916–2120	4:>2120
Topography				
slope	flat		hollow	
Exposure				
null	SW	SE	S	NW
NE	N	W	E	
Slope, °				
null:<10	slight:10–19	moderate:20–39	steep:>39	
Cover of stones, %				
1:0	2:1–5	3:6–10	4:11–80	
Cover of boulders, %				
1:0	2:1–5	3:6–10	4:11–60	
Cover of grasses 0–10 cm, %				
1:0–20	2:21–35	3:36–45	4:46–80	
Cover of grasses 11–25 cm, %				
1:0	2:1–5	3:6–25	4:26–80	
Cover of grasses 26–50 cm, %				
1:0	2:1–60			
Cover of forbs 0–10 cm, %				
1:0–15	2:16–20	3:21–35	4:36–100	
Cover of forbs 11–25 cm, %				
1:0	2:1	3:2–50		
Cover of forbs 26–50 cm, %				
1:0	2:1–40			
Cover of woody plants 0–10 cm, %				
1:0	2:1–10	3:11–20	4:21–70	
Cover of woody plants 11–25 cm, %				
1:0	2:1–5	3:6–20	4:21–70	
Cover of woody plants 26–50 cm, %				
1:0	2:1–45			

To identify the main habitat features in the study area, a multiple correspondence analysis was performed on the data from 202 grid sites by 62 categorical variables. The eigenvector approach was used. The search for contributive raw variables (i.e., not divided into classes) was helped by examining the correlation ratio between variable and factor (Pialot et al. 1984), which was

$$\mu^2(F_{\alpha}q) = v\lambda_{\alpha} \sum_{j \in J(q)} \text{CTR}_{\alpha}(j) \quad (1)$$

with F_{α} being factor α , λ_{α} its variance, q a variable, v the number of variables, $J(q)$ the set of categories of q , j one of them, $\text{CTR}_{\alpha}(j)$ the contribution of j to F_{α} , i.e., the part of F_{α} 's variance explained by j . It is easy to demonstrate from the formula that the mean of $\mu^2(F_{\alpha}q)$ among the variables is λ_{α} . Consequently, a variable was contributive when have $\mu^2(F_{\alpha}q) > \lambda_{\alpha}$. Grid sites described by their scores on the highest corresponding analysis ranking components were clustered by an ascending hierarchical clustering, allowing us to define available habitat types.

Sites used by partridges were assigned to vegetation type and then to habitat type, using a proximity rule. First, scores of the use sites on the corresponding analysis components used for clustering were calculated using the eigenvectors matrix. Second, the Mahalanobis distance from each site to each center of the clusters corresponding to the types was calculated. Each site was then assigned to the cluster of the closest center.

Distribution of 202 grid and 62 use sites among the habitat types was compared using a chi-square goodness-of-fit test. In the case of rejecting the null hypothesis (similar distribution), simultaneous confidence intervals were calculated (Neu et al. 1974, Marcum and Loftsgaarden 1980, Byers and Steinhorst 1984).

Vegetation Types

Five vegetation types were defined (Table 2). Type A (montane zone vegetation) was characterized by plants common on mowed grasslands and on productive pastures. Its species richness was high (25) and it included numerous forbs. Type B (also montane zone vegetation) was generally found on southern or western slopes. Types C and D were dominated by subalpine vegetation, with C on northern slopes and D on southern slopes. Type E included rocky biotopes and represented the high subalpine and low alpine zones.

Table 2. Frequency of occurrence (%) of plant species in 5 vegetation types.

Categories/species	Montane -----> Alpine				
	A	B	C	D	E
≅ sites	33	61	64	23	21
Richness ^a	25	20	21	15	16
<i>Achilleum millefolium</i>	24	0	0	0	0
<i>Agrostis</i> sp.	20	0	0	0	0
<i>Potentilla</i> sp.	29	3	0	0	0
<i>Trifolium pratense</i>	20	3	1	0	9
<i>Juniperus nana</i>	39	15	14	9	5
<i>Galium verum</i>	59	24	3	4	14
<i>Festuca rubra</i>	67	30	0	0	0
<i>Nardus stricta</i>	59	21	17	4	38
<i>Brachypodium pinnatum</i>	5	50	0	0	0
<i>Pteridium aquilinum</i>	0	15	0	0	0
<i>Festuca scoparia</i>	0	3	0	0	0
<i>Helianthemum nummularium</i>	29	72	1	9	5
<i>Calluna vulgaris</i>	23	48	8	17	0
<i>Carex</i> sp.	8	21	3	0	14
<i>Potentilla tormentilla</i>	21	24	22	0	0
<i>Hieracium pilosella</i>	8	9	6	4	5
<i>Plantago alpina</i>	2	0	5	0	0
<i>Vaccinium myrtillus</i>	18	24	58	26	5
<i>Rhododendron ferrugineum</i>	13	0	48	9	5
<i>Vaccinium uliginosum</i>	6	0	28	0	0
<i>Trifolium alpinum</i>	23	0	48	13	24
<i>Festuca eskia</i>	21	3	87	83	43
<i>Cerastium fontanum</i>	0	0	1	0	0
<i>Thymus serpyllum</i>	15	48	20	74	43
<i>Veronica fruticans</i>	0	6	1	52	0
<i>Senecio adonidifolius</i>	0	0	0	48	0
<i>Alchemilla</i> sp.	6	6	11	9	19
Mosses	2	3	5	0	28
<i>Lotus corniculatus</i>	6	0	0	4	43
<i>Plantago atrata</i>	2	0	1	0	62

^aRichness = number of species or categories per type.

Available Habitat Types

The main habitat features in the study area were represented by the first 4 factors F1–F4 of the multiple correspondence analysis (Figs. 1, 2), whose eigenvalues were 0.28, 0.21, 0.17, and 0.15.

The most important feature was elevation, which had the greatest correlation ratio with factor F1. Cover of stones increased and that of grasses >25 cm decreased with altitude. Another important feature was a gradient of colonization by low woody plants, noticeable especially on F2, but also on F1, through strong correlation ratios of covers of woody plants <10 cm and 11–25 cm. Plateau stations (flat topography, null slope, and exposure) were separated from the others on the F1 × F2 plane. The pattern of vegetation types in the F1 × F2 plane was parabolic, indicating a relation of plant species composition with elevation and colonization by woody plants (Fig. 1).

An exposure gradient from cold (N) to warm (S) exposures was expressed on F3. Cover of woody plants was related to this gradient, being highest in cold situations where rhododendron domi-

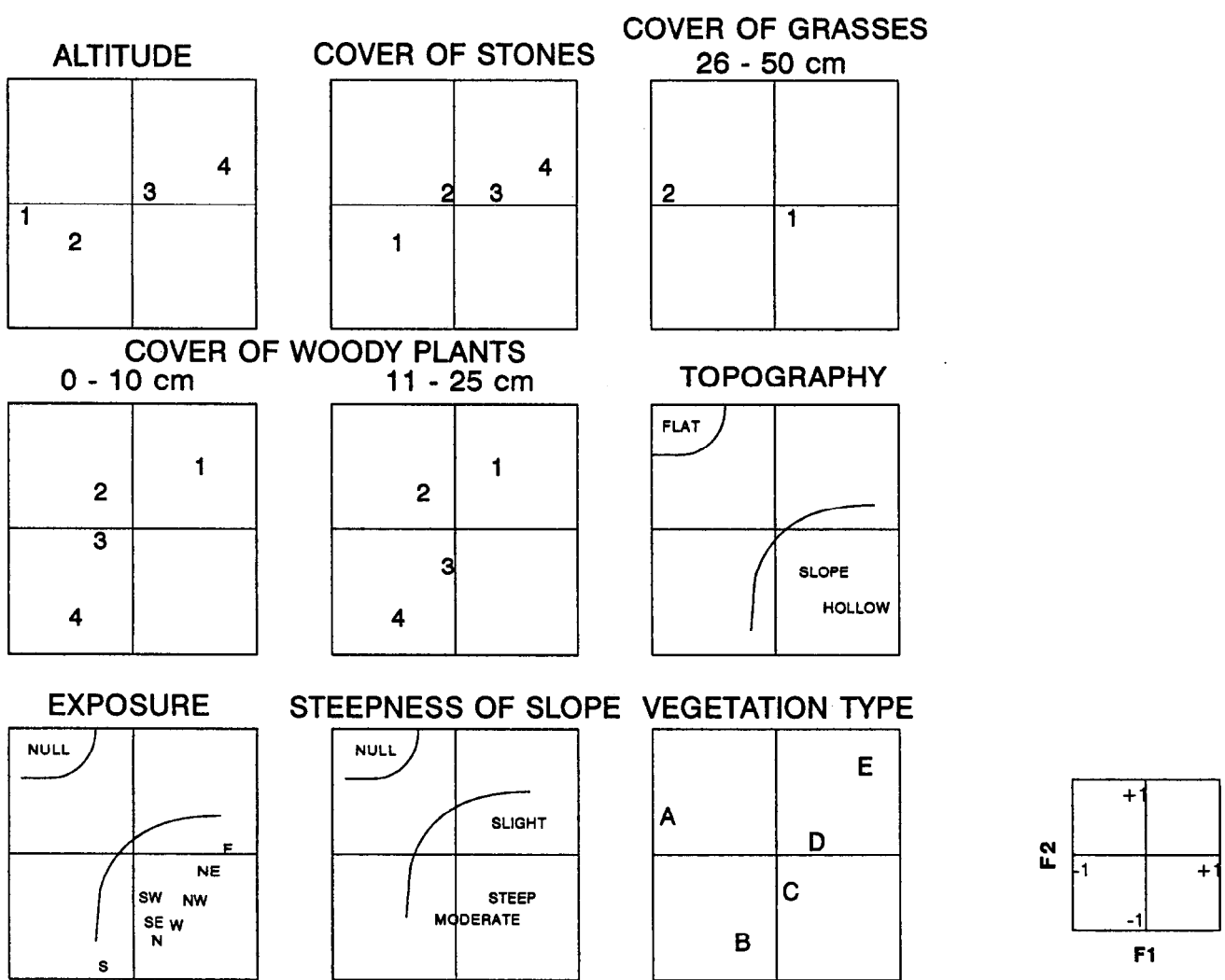


Fig. 1. Distribution of categories of contributive habitat variables in the $F1 \times F2$ plane of the multiple correspondence analysis. Categories are represented by numbers, letters or adjectives (Table 1).

nated. Factor F4 represented both an increase in cover of low grasses (<25 cm) and a decrease in cover of boulders and 11–25 cm forbs. Cover of woody plants 11–25 cm was also related to F4. Vegetation types B, C, D seemed to be especially linked to factors 3 and 4 (Fig. 2).

Clustering allowed us to define 6 available habitat types whose main features can be synthesized by projecting the types on the factor planes. Habitat types 1, 2, 3, and 6 were separated from each other and from the group of habitat types 4+5 on the $F1 \times F2$ plane (Fig. 3). Habitat types, 1, 2+3, 4+5, and 6 were ordered on the elevation gradient, and 2+6, 1+4+5, and 3 on the gradient of colonization by low woody plants. Habitat types 4 and 5 were separated from each other on the exposure gradient, with 4 on south slopes and 5 on north slopes (Fig. 4, Table 3).

Selected and Avoided Habitat Types

Use sites were associated with habitat types 3, 4, and 5, i.e., with intermediate altitudes, medium to high cover of woody plants, vegetation types B, C, and D, and fairly steep slopes (Figs. 3, 1). None of the variables correlated with F3 (exposure) or F4 (boulders and forbs) seemed to be critical for partridges, as use sites were almost randomly distributed on the $F3 \times F4$ plane (Fig. 4).

Only habitat type 4 was significantly ($p < 0.05$) selected (Fig. 5). It was at intermediate altitudes, on south slopes, with vegetation types B and D, and a moderate cover of woody plants. Habitat

types 1 and 6 were significantly ($p < 0.05$) avoided (Fig. 5). Habitat type 1 was at low altitudes, on plateaus well colonized by low woody plants, and was characterized by vegetation type A. Habitat type 6 was at high altitudes on slopes free of low woody plants, and was characterized by vegetation types C and E.

Discussion

Elevation, exposure, and slope features of the habitat types selected by gray partridge in this study resembled those reported in earlier investigations (Lescouret 1988, Novoa and Gonzalez 1988). Gray partridges preferred slopes to flat ground, apparently to facilitate escape flights from predators or humans. They also selected southern exposures (habitat type 4), where early snow melt and warm temperatures may favor nesting and fledging success. Habitat type 6 may have been avoided because of more inclement weather conditions that normally prevail at higher altitudes.

Invasion of the study area by low woody plants was indicative of a decrease in grazing pressure in recent years. Although declines of populations following abandonment of grazing have been documented in the literature for different galliforms (ONC 1986, Magnani 1988, Novoa and Gonzalez 1988, Génard and Lescouret 1990), we found no evidence that partridge numbers decreased following invasion of low woody plants in our study area. On the contrary, signs of partridge were more frequent when cover of

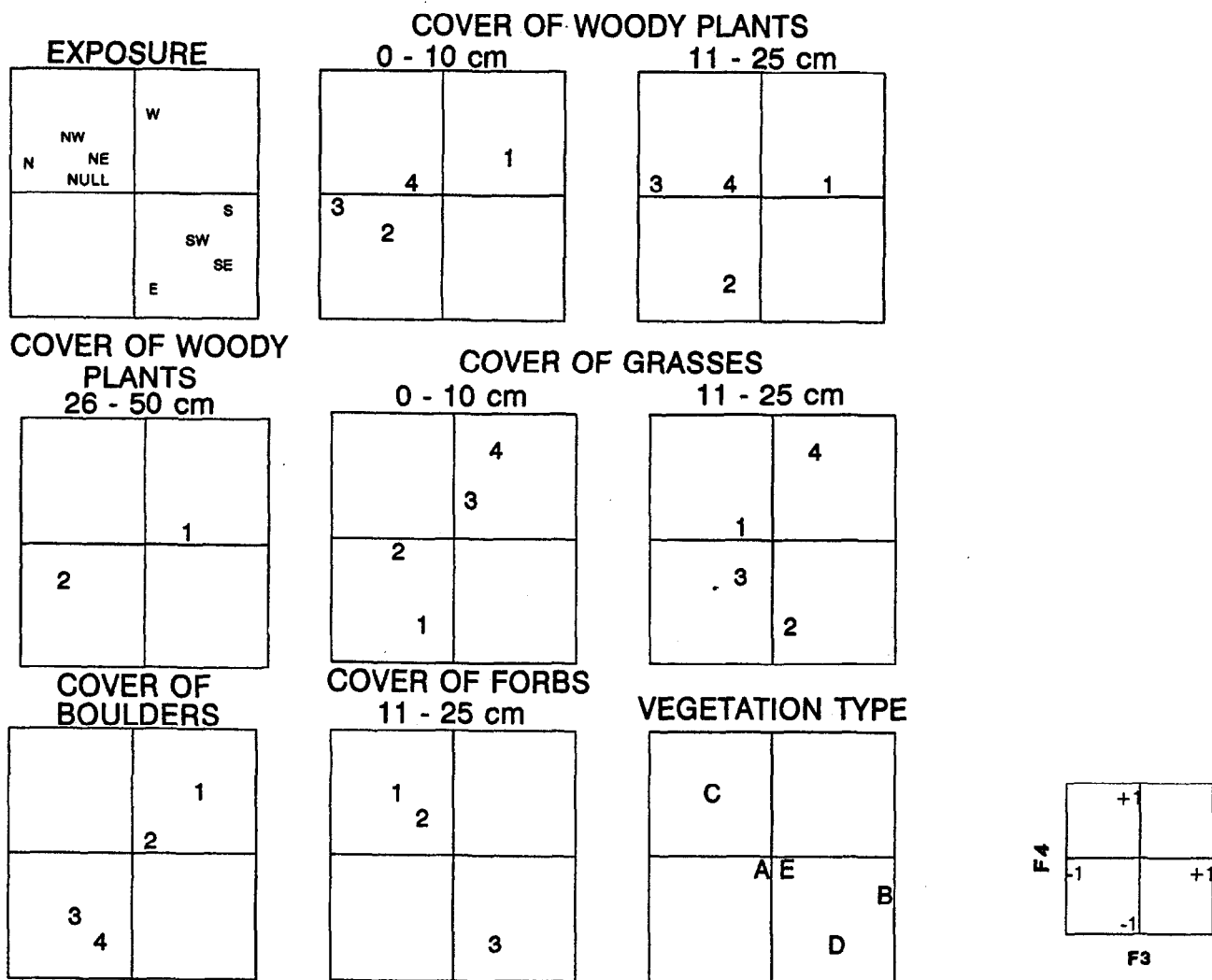


Fig. 2. Distribution of categories of contributive habitat variables in the F3×F4 plane of the multiple correspondence analysis. Categories are represented by numbers, letters, or adjectives (Table 1).

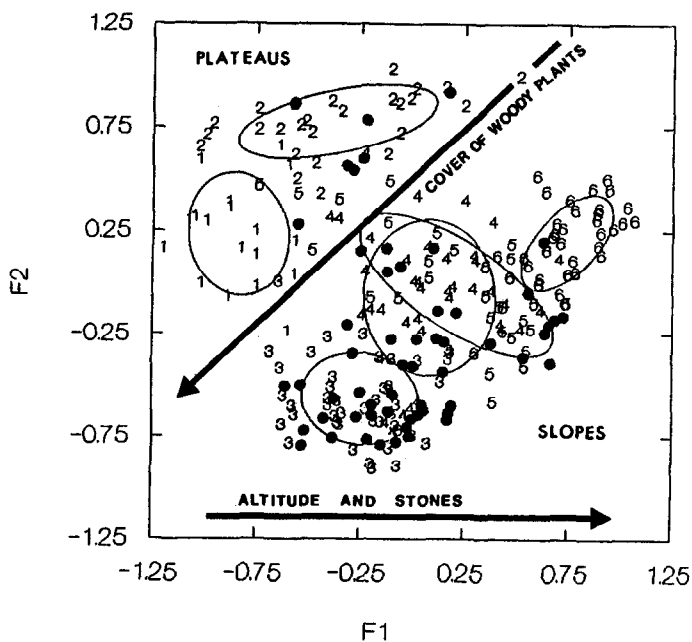


Fig. 3. Projection on the F1×F2 plane of the multiple correspondence analysis of (i) 6 habitat types represented by contents (grid sites) and dispersion ellipses ($\sqrt{x \pm SD}$), (ii) partridge use sites (black spots).

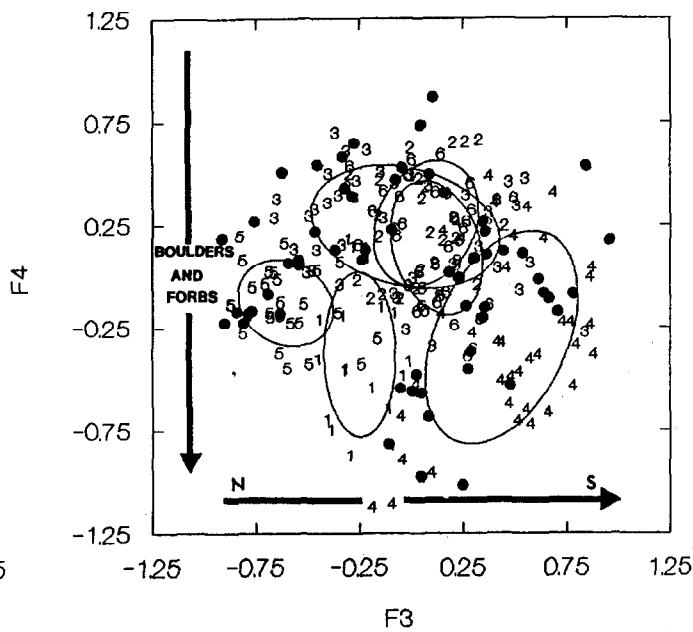


Fig. 4. Projection on the F3×F4 plane of the multiple correspondence analysis of (i) 6 habitat types represented by contents (grid sites) and dispersion ellipses ($\sqrt{x \pm SD}$), (ii) partridge use sites (black spots).

Table 3. Frequency of occurrence (%) of habitat categorical variables by habitat type.

Variables	Montane					Alpine
	1	2	3	4	5	6
≅ sites	18	26	49	42	30	37
Altitude, m						
1:<1771	94	23	35	21	10	0
2:1771-1915	0	39	51	21	13	0
3:1916-2120	6	27	14	48	44	8
4:>2120	0	11	0	10	33	92
Topography						
slope	22	0	94	96	67	89
flat	78	1	2	2	23	0
hollow	0	0	4	2	10	11
Exposure						
null	69	100	2	2	23	0
SW	0	0	10	26	0	15
SE	0	0	6	24	0	4
S	0	0	25	19	0	9
NW	8	0	21	0	14	9
NE	8	0	12	7	30	37
N	15	0	18	7	30	0
W	0	0	6	3	0	13
E	0	0	0	12	3	13
Slope, °						
null:<10	77	96	2	2	27	0
slight: 10-19	11	4	14	12	23	30
moderate: 20-39	6	0	49	57	37	35
steep: >39	6	0	35	29	13	35
Cover of stones, %						
1:0	67	61	84	24	7	13
2:1-5	11	23	16	22	36	11
3:6-10	17	12	0	27	27	14
4:11-80	5	4	0	27	30	62
Cover of boulders, %						
1:0	17	35	72	29	3	32
2:1-5	33	35	18	29	10	5
3:6-10	28	7	8	16	40	20
4:11-60	22	23	2	26	47	43
Cover of grasses 0-10 cm, %						
1:0-20	33	4	8	50	46	38
2:21-35	28	15	33	9	37	22
3:36-45	22	19	29	17	10	24
4:46-80	17	62	30	24	7	16
Cover of grasses 11-25 cm, %						
1:0	11	38	4	10	60	51
2:1-5	61	31	10	45	13	8
3:6-25	22	8	29	24	27	22
4:26-80	6	23	57	21	0	19
Cover of grasses 26-50 cm, %						
1:0	28	65	65	62	90	97
2:1-60	72	35	35	38	10	3
Cover of forbs 0-10 cm, %						
1:0-15	17	12	28	26	40	41
2:16-20	17	19	33	21	17	32
3:21-35	22	27	37	10	33	19
4:36-100	44	42	2	43	10	8
Cover of forbs 11-25 cm, %						
1:0	6	85	82	31	90	97
2:1	33	11	14	7	7	0
3:2-50	61	4	4	62	3	3
Cover of forbs 26-50 cm, %						
1:0	39	89	67	69	100	100
2:1-40	61	11	33	31	0	0
Cover of woody plants 0-10 cm, %						
1:0	0	77	0	57	0	92
2:1-10	44	19	12	22	33	5
3:11-20	28	4	21	7	44	3
4:21-70	28	0	67	14	23	0

(Continued on page 294).

Table 3. Continued.

Variables	Montane						Alpine
	1	2	3	4	5	6	
Cover of woody plants 11-25 cm, %							
1:0	0	85	0	63	0	95	
2:1-5	39	11	4	14	23	0	
3:6-20	33	4	41	9	54	5	
4:21-70	28	0	55	14	23	0	
Cover of woody plants 26-50 cm, %							
1:0	6	96	33	60	17	97	
2:1-45	94	4	67	40	83	3	
Vegetation type							
A	100	62	26	19	18	0	
B	0	0	31	41	0	3	
C	0	15	43	7	64	46	
D	0	8	0	31	4	19	
E	0	15	0	2	14	32	

woody plants increased (low values of factor F2). We conclude that extent of colonization of low woody plants was not yet important enough to cause a decline in partridge numbers.

The diet of the pyrenean gray partridge is composed of green plant material, bulbs, insects (30% of which are Orthoptera), seeds, and dry fruits (Novoa in Bernard-Laurent 1986). These foods are abundant at low and intermediate altitudes, but they are scarce at high altitudes, which may be another reason partridges avoided habitat type 6. The rock ptarmigan (*Lagopus mutus*) is the only galliform occupying high altitude areas likely to compete with the gray partridge. Rock ptarmigan prefer high subalpine and alpine zones that tend to be relatively cold and rocky and less steep than areas usually occupied by partridges (Novoa and Gonzalez 1988). These features are similar to those of habitat type 6, which suggests that a competitive exclusion may also influence partridge distribution. Finally, open grassy areas offer little cover to protection against predators, which may also contribute to low use of habitat types 2 and 6.

Our results can be used to predict the presence or absence of the Pyrenean gray partridge. The methodological design of our work can be transcribed in a stepwise model allowing assignment of any new site to a vegetation type and to a habitat type, on the basis of a few habitat measurements, by means of the eigenvector matrices and proximity rules we calculated. Presence or absence of partridges in the site can be predicted from the suitability of the habitat (preferred or avoided). Such a model can also be used to assess changes in the occurrence of the species induced by changes in the landscape (Génard and Lescourret 1990). The model must be tested in other areas to determine if it is robust enough to be applied generally in the Pyrenees. The tests will require a thorough examination of both its internal validity (stability of the detected structure), and its external validity (statistical inference).

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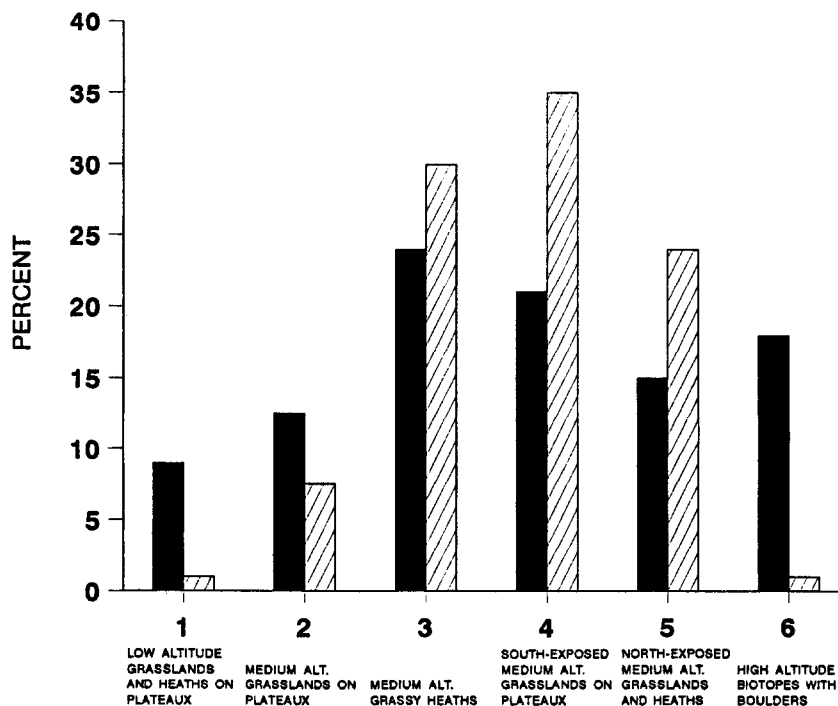


Fig. 5. Frequency of occurrence of grid sites (black) and of partridge use sites (cross-hatched) in 6 habitat types.

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Range condition influences on Chihuahuan Desert cattle and jackrabbit diets

ALIPAYOU DANIEL, JERRY L. HOLECHEK, RAUL VALDEZ, ACKIM TEMBO, LEWIS SAIWANA, MICHAEL RUSCO, AND MANUAL CARDENAS

Authors are graduate research assistant (deceased) and professor, Dept. of Animal and Range Sciences; professor, Dept. of Fishery and Wildlife Sciences; graduate research assistant, graduate research assistant, and graduate research assistant, Dept. of Animal and Range Sciences; and professor, Dept. of Exp. Sta. New Mexico State Univ., Las Cruces, 88003.

Abstract

Knowledge of comparative diet selection by cattle and black-tailed jackrabbits (*Lepus californicus*) would permit better estimation of grazing capacity on Chihuahuan desert ranges. Cattle and black-tailed jackrabbit diets were evaluated seasonally on good and fair condition ranges over a 2-year period. Fecal samples analyzed by the microhistological technique were used to determine diets of both animals. Key forage species in cattle diets were dropseeds (*Sporobolus* sp.), black grama (*Bouteloua eriopoda* Torr.), leatherweed croton (*Croton pottsii* Lam.), and bush muhly (*Muhlenbergia porteri* Scribn.). Key forage species in jackrabbit diets were honey mesquite (*Prosopis glandulosa* Torr.), cactus (*Opuntia* sp.), dropseed, broom snakeweed (*Gutierrezia sarothrae* Pursh.), and black grama. Overall diet botanical composition data showed cattle consumed 58% grass compared to 22% for jackrabbits ($P < 0.05$). Forb consumption was similar between the 2 animals and averaged about 31%. Shrub consumption averaged 47% and 12% for jackrabbits and cattle, respectively ($P < 0.05$). Range condition did not influence total grass consumption by either animal. Both animals, however, had lower forb and higher shrub consumption on fair compared to good condition range. Overall dietary overlaps between jackrabbits and cattle were 40 and 42% on good and fair condition ranges, respectively. Poisonous plants contributed up to 14 and 36% of cattle and jackrabbit diets, respectively. Data from this study show little forage competition occurs between cattle and jackrabbits when stocking rates and jackrabbit numbers are moderate. Several plants poisonous and unpalatable to cattle were important jackrabbit foods. These plants were more prevalent on the fair compared to the good condition range.

Key Words: rangeland, wildlife, livestock, arid lands, poisonous plants, grazing management

Information on influence of range condition on diets of black-tailed jackrabbits (*Californicus lepus*) and cattle on Chihuahuan desert rangeland is lacking. Knowledge of the role condition plays on degree of dietary overlap between jackrabbits and cattle would permit better estimation of grazing capacity. At population peaks jackrabbits may become primary consumers of rangeland vegetation competing with livestock and wildlife (Currie and Goodwin 1966, Johnson 1979) and possibly altering plant succession (Uresk 1978, Roundy et al. 1985).

Information on the levels of poisonous plants consumed by the 2 species under different range conditions could be useful in development of grazing strategies to minimize livestock losses. Consumption or rejection of plants poisonous to livestock by jackrabbits could influence the rate of recovery of degraded Chihuahuan

desert rangeland. The objective of this study was to determine the influence of range condition on jackrabbit and cattle diets on Chihuahuan desert rangelands. Diet composition of both species was quantified with microhistological analysis of fecal material.

Material and Methods

The 2 study ranges are located 37 km north of Las Cruces, N.M. Their western boundaries are adjacent to Interstate 25. The study area is on the southern end of the Jornada Del Muerto Plain, a desert basin which varies from 1,188 to 1,371 m elevation with level or gently rolling hills. Pasture soils are primarily shallow, fine sandy loams of the Simona-Cruces association (fine loamy, mixed, thermic, typic Haplargids). The topography is relatively flat with all slopes less than 5%.

Seasonal patterns of precipitation are characterized by small amounts (8 to 10%) in spring and a peak (20 to 25%) in late summer (August) with gradually reduced amounts during fall. A smaller peak (13 to 15%) occurs in early winter (Pieper and Herbel 1982). Temperatures reach a peak (35° C) in June and decline until December (13° C) (Pieper and Herbel 1982).

Vegetation on the Jornada Plain is classified as Chihuahuan desert grassland and shrubland (Paulsen and Ares 1962). Most of the grassland areas have been invaded by brushy species during the last 100 years (Brown 1950, Dick-Peddie 1965).

The principal grassland types are black grama (*Bouteloua eriopoda* Torr.) and tobosa (*Hilaria mutica* [Buckley] Benth.) with mesa dropseed (*Sporobolus flexuosus* [Thurb.] Rydb.) intermixed (Paulsen and Ares 1962, Pieper and Herbel 1982). The shrub types are mesquite sandhills (*Prosopis glandulosa* Torr.), creosotebush (*Larrea tridentata* Lar.) and tarbush (*Flourensia cernua* D.C.) with snakeweed (*Gutierrezia* spp.) invading certain sites. Annual forbs include leathercroton (*Croton pottsii* Lam.), nightshades (*Solanum* sp.), globemallow (*Sphaeralcea* sp.), and Russian thistle (*Salsola iberica* L.). The presence of these forbs is dependent on seasonal precipitation. The reader is referred to Daniel (1991) for a more detailed discussion of the study area.

Grazing History

The grazing history of the 2 study areas appears fairly similar until 1922, when the College Experimental Ranch was established. Prior to that time, most of both study areas was apparently black grama grassland with a minor brush component (mostly mesquite). In the mid-1920's the College Ranch was fenced and a large herd of wild horses were driven from the College Ranch onto the adjacent federal land. During the 1930's and the 1940's, the College Ranch range was stocked conservatively at about 40 ha per animal unit (Neale 1937, Valentine 1947, Knox et al. 1951) and

the forage utilization averaged 35%. In contrast forage utilization averaged somewhere between 50 and 60% on the Bureau of Land Management (BLM) study range.

In 1967, the College Ranch study area was placed under intensive grazing management and the stocking rate was reduced from 41 to 67 ha per animal unit (Beck 1978, Beck et al. 1987). Since then, utilization of the key forage species has averaged about 30%. The stocking rate has been increased from 67 ha per animal unit (1967) to 45 ha per animal (1986–1991) with no increase in degree of forage use or sacrifice in cattle performance (Beck et al. 1987, Beck and Kiesling 1991). Overall condition using the Soil Conservation Service approach developed by Dyksterhuis (1949) has improved from mid-fair to high-good (66% of climax) during the 24-year period (Beck 1978, McNeely 1983, Tembo 1990). Forage production at the end of the 1990 growing season was 356 kg/ha.

The grazing history of the BLM range is rather vague for the 1950 to 1980 period, but detailed records have been kept since 1981. Prior to 1981, the general grazing plan was to remove about 50% of the perennial grass production using continuous grazing. The stocking rate from the late 1960's to 1981 was 42 ha per animal unit. Stocking rate averaged 72 ha per animal unit for the 1981 to 1990 period. BLM records indicate conservative utilization of key forage species for the 1981 to 1991 period (20 to 40% use). In 1990 range condition was high-fair (40% of climax).

Eight permanent transects (6.4 km in length) were located in each study range (College Range and Bureau of Land Management ranges) for a total of 16 transects. Percent canopy cover was measured seasonally in the fall of 1988 using a modification (Holechek and Stephenson 1983) of the line intercept procedure outlined by Canfield (1941). A rod 1 meter in length, incremented in millimeters was laid down every 100 paces perpendicular to the transect that was walked. On each of the 16 transects 64 points were sampled. Plants that were located on the plane vertically above the meter stick were measured and recorded. Plant heights were also measured and reported in Daniel (1991). Portions of the canopy of honey mesquite and soaptree yucca (*Yucca elata* Engelm.) were out of reach of jackrabbits.

Feces of jackrabbits and cattle were collected simultaneous with vegetation sampling. Sixty jackrabbit fecal pellets were collected from each of the 16 transects. On the average 10 pellets per km were taken to insure collection from the entire length of the transect. Only 1 to 2 pellets from each excretion were picked. Each range condition study area was divided into 2 blocks of transects. Fecal collections from each block made up 1 composite sample, for a total of 4 composite samples for each season. Seasons sampled included summer 1988 and 1989, fall 1988 and 1989, winter 1989 and 1990, and spring 1989 and 1990. Summer collections were made in August, fall collections in late October and early November, winter collections in January, and spring collections in late April and early May.

Cattle feces were collected from 4 watering points, 2 in each range condition class. From each watering point, 5 patties were selected at random to make 1 composite sample. About 20 gm of fresh feces were collected from each patty. All fecal collections were put in plastic bags and stored in a refrigerator 1 to 3 weeks until they were ground and placed on microscope slides.

Fecal Analysis

All fecal collections were dried in a forced air oven at 60° C for 72 hours then ground through a micro-Wiley mill with 1-mm mesh screen. Each ground sample was mixed thoroughly to insure particle uniformity. Slide preparation followed the method of Sparks and Malechek (1968) as modified by Holechek (1982).

An observer, trained by the procedure of Holechek and Gross (1982a), analyzed the fecal samples using a Nikon binocular microscope. Samples were analyzed at 100X and 200X used for some

particle identification. Twenty systematically selected fields were observed on each slide. Species were recorded as being present or absent until a total of 100 fields were recorded per sample. The frequency addition procedure described by Holechek and Gross (1982b) was used to calculate the percentage botanical composition by weight.

Statistical Analysis

Percent botanical composition (% dry weight) values were analyzed using a time series split plot ANOVA. Animals (2), pastures (2), seasons (4), and years (2) were used as factors. Animals and pastures were main plots and seasons and years were sub-plots. The composite samples from each of the 2 blocks within pastures were used as replicates (2). Least significant difference (LSD) tests were utilized for mean separation when a significant ($P < 0.05$) F-test occurred. Step-wise discriminant analysis was used to discern differences among range condition classes/animal species (Johnson and Wichern 1982). Diet data were further pooled by years and segregated into grasses, forbs, and shrubs for animal species comparison. Hotelling T² (Johnson and Wichern 1982) analysis was done to determine the difference between the 2 animal species within range condition class and year. Similarity indices were calculated using Kulczynski's formula (Oosting 1956). These indices illustrate: (1) how similar the diets of each animal species were between the 2 range condition classes and (2) dietary overlap between the 2 animal species within each range condition class.

Vegetation cover was evaluated with a time series split plot ANOVA with pastures (2) and periods (7) as factors and transects (8 per pasture) as replications. Pastures were main plots and periods sub-plots. Least significant difference tests were used for mean separation when a significant ($P < 0.05$) F-tested occurred.

Results and Discussion

Main and minor effects for most diet components were significant ($P < 0.05$). We will concentrate on those aspects of our results we consider most important and refer the reader to Daniel (1991) for a detailed discussion of the various interactions.

Jackrabbit Diets

Black-tailed jackrabbit diets on both fair (FC) and good condition (GC) ranges were dominated by shrubs (Table 1). Grasses comprised only 22% of the diet when data were pooled across years, seasons, and range condition classes.

From most to least important, the 3 primary grasses consumed were: dropseeds, black grama, and fluffgrass (*Erioneuron pulchellum* [H.B.K.] Tateoeka). Highest consumption of grasses on both range condition classes occurred during summer and lowest consumption occurred in the winter.

Total cover of grasses between the good and fair condition range classes (Table 2) showed a significant difference ($P < 0.05$, 22% vs 14%). Apparently this difference did not affect the amount of grasses consumed by jackrabbits between the 2 range condition classes. Jackrabbits primarily utilized green grasses (Currie and Goodwin 1966, Fatehi 1986) which were readily available on both condition classes during active growth.

Highest forb consumption ($P < 0.05$) occurred on the good condition range. Major forbs in jackrabbit diets included: dwarf dalea (*Dalea nana* Torr.), silverleaf nightshade (*Solanum elaeagnifolium* Nutt.), leatherweed croton, desert marigold (*Baileya multiradiata* Harv. & Gray), wooly paperflower (*Psilostrophe tagetina* [Nutt.] Greene), and globemallow (*Sphaeralcea* sp.). All except leatherweed croton were consistently higher in the diets of jackrabbits on the good condition range. Forb cover was greater on the good than on fair condition range. The relatively high use of forbs in fall of 1988 is explained by precipitation 28% above average

Table 1. Forage foliar cover, relative percent cover and average diet botanical composition by weight of cattle and jackrabbits on good and fair condition ranges pooled across years and seasons.

Forage species	Good condition	Fair condition	Good condition	Fair condition	Good condition		Fair condition		Overall diet			
					Cattle	Rabbit	Cattle	Rabbit	Cattle	Rabbit		
	--- % Cover ---				--- % Relative cover ---				--- % Diet ---			
Grasses												
Threecawn	4.1 ^a	1.8 ^b	10.1	3.75	5 ^a	1 ^b	5 ^a	2 ^b	5 ^a	2 ^b		
Black grama	3.9 ^a	0.7 ^b	9.6	1.5	16 ^a	6 ^b	10 ^a	5 ^b	13 ^a	6 ^b		
Fluffgrass	1.1	1.3	2.7	2.7	1a	4 ^b	1 ^a	4 ^b	1 ^a	4 ^b		
Tobosa	t	t	t	t	1	0	1	t	1	t		
Bush muhly	t	t	t	t	5	1	7	1	6 ^a	1 ^b		
Dropseeds	8.6 ^a	5.3 ^b	21.1	11.0	29 ^a	2 ^b	30 ^a	2 ^b	30 ^a	2 ^b		
Other grasses	3.9	4.4	9.6	9.1	3	8	3	8	3	7		
Total grasses	21.6 ^a	13.5 ^b	53.1	28.0	60 ^a	22 ^b	57 ^a	22 ^b	59 ^a	22 ^b		
Forbs												
Loco	t	t	t	t	0	3	0	1	0	2		
Desert marigold	t	t	t	t	1	4	1	2	1	2		
Desert senna	t	t	t	t	1	2	t	1	1	2		
Leatherweed croton	1.4	0.1	3.4	0.2	12 ^a	4 ^b	4	4	8 ^a	4 ^b		
Dwarf dalea	t	t	t	t	1 ^a	6 ^b	t	2	1 ^a	4 ^b		
Wooly paperflower	t	t	t	t	t	4	0	1	0	2		
Silverleaf nightshade	t	t	t	t	6	5	4	4	5	4		
Globemallow	t	t	t	t	2	3	3	2	2	2		
Other forbs	3.0	2.0	7.4	4.1	12	9	12	7	12	10		
Total forbs	4.5 ^a	3.1 ^b	11.1	6.4	35 ^a	40 ^b	24 ^a	24 ^a	30 ^a	32 ^a		
Shrubs												
Honey mesquite	3.6 ^a	15.1 ^b	8.9	31.3	2 ^a	8 ^b	1 ^a	13 ^b	2 ^a	10 ^b		
Fourwing saltbush	t	t	t	t	t	2	6 ^a	2 ^b	3	2		
Common winterfat	t	t	t	t	t	t	1	0	1	t		
Broom snakeweed	10.1 ^a	14.5 ^b	24.8	30.0	t ^a	5 ^b	t ^a	8 ^b	t ^a	6 ^b		
Creosotebush	t	t	t	t	0	2	0 ^a	5 ^b	0 ^a	3 ^b		
Cactus	t	t	t	t	0 ^a	9 ^b	0 ^a	11 ^b	0 ^a	10 ^b		
Soaptree yucca	0.7	1.9	1.7	3.9	2	6	7	7	4	6		
Total shrubs	14.6 ^a	31.7 ^b	35.9	65.6	6 ^a	38 ^b	16 ^a	55 ^b	11 ^a	47 ^b		

^a^bDifferent superscripts within rows and category reflect differences ($P < 0.05$) using least significant difference test.

Table 2. Grass, forb, and shrub composition % of cattle and jackrabbit feces for different seasons and years on good (GC) and fair (FC) condition Chihuahuan desert range.

	Jackrabbit							
	Summer 1988		Fall 1988		Winter 1989		Spring 1989	
	GC	FC	GC	FC	GC	FC	GC	FC
Grasses (%)	37 ^a	37 ^a	12 ^a	16 ^a	9 ^a	8 ^a	14 ^a	19 ^a
Forbs (%)	42 ^a	30 ^b	52 ^a	37 ^b	35 ^a	6 ^b	48 ^a	21 ^b
Shrubs (%)	22 ^a	32 ^b	34 ^a	46 ^b	55 ^a	86 ^b	38 ^a	60 ^b
	Cattle							
	Summer 1988		Fall 1988		Winter 1989		Spring 1989	
	GC	FC	GC	FC	GC	FC	GC	FC
Grasses (%)	45 ^a	57 ^b	49 ^a	49 ^a	82 ^a	57 ^b	71 ^a	58 ^b
Forbs (%)	55 ^a	43 ^b	44 ^a	24 ^b	9 ^a	4 ^a	21 ^a	22 ^a
Shrubs	1 ^a	1 ^a	8 ^a	26 ^b	8 ^a	38 ^b	81 ^a	20 ^b
	Jackrabbit							
	Summer 1989		Fall 1989		Winter 1990		Spring 1990	
	GC	FC	GC	FC	GC	FC	GC	FC
Grasses (%)	38 ^a	34 ^a	26 ^a	27 ^a	15 ^a	11 ^a	27 ^a	27 ^a
Forbs (%)	30 ^a	28 ^a	36 ^a	24 ^b	30 ^a	13 ^b	34 ^a	28 ^a
Shrubs (%)	32 ^a	38 ^a	39 ^a	51 ^b	55 ^a	77 ^b	38 ^a	44 ^a
	Cattle							
	Summer 1989		Fall 1989		Winter 1990		Spring 1990	
	GC	FC	GC	FC	GC	FC	GC	FC
Grasses (%)	53 ^a	54 ^a	53 ^a	70 ^b	66 ^a	58 ^b	61 ^a	54 ^a
Forbs (%)	45 ^a	36 ^b	44 ^a	23 ^b	14 ^a	29 ^b	6 ^a	20 ^b
Shrubs (%)	2 ^a	8 ^a	3 ^a	7 ^a	14 ^a	29 ^b	6 ^a	20 ^b

Row means within period and year with different superscripts ($P < 0.05$) using least significant difference (LSD) test.
T = trace amount less than 1%.

during the growing season that year.

Major shrubs consumed by jackrabbits on both range condition classes were honey mesquite, prickly pear (*Opuntia* spp.), soaptree yucca, snakeweed, and mormon tea (*Ephedra trifurca* Torr.) (Table 2). Those shrubs were consistently higher in diets of jackrabbits and in cover on fair than good condition range. Maximum consumption of shrubs by jackrabbits occurred in winter and minimum use in summer.

Shrubs play an important role in allowing jackrabbits to maintain their water balance during dry periods (Hayden 1966). The shrubs consumed in our study have a high moisture content in most instances. Availability of succulent forbs and green grasses probably influenced the seasonal variations in amounts of shrubs eaten by the jackrabbits.

Trends in grass, forb, and shrub consumption by jackrabbits in our study are similar to those reported by Dabo (1980), Fatehi

Table 3. Similarity indices for comparative diets within and between animal species for range condition and season.

Comparison	Between good and fair condition ranges							
	Spring	Summer	Fall	Winter				
Jackrabbit	79	83	84	73 [*]				
Cattle	72 [*]	80	72 [*]	69 [*]				
Cattle and Jackrabbit	Within good and fair condition ranges							
	GC	FC	GC	FC	GC	FC	GC	FC
	39 ^{**}	42 ^{**}	53 ^{**}	53 ^{**}	41 ^{**}	39 ^{**}	27 ^{**}	28 ^{**}

*Diets different ($P < 0.05$) using MANOVA.

**Diets different ($P < 0.01$) using MANOVA.

GC = Good condition range, FC = fair condition range.

Table 4. Poisonous plants (% dry weight) in the diets of cattle and jackrabbits on good (GC) and fair (FC) condition range classes.

Species	Cattle																		
	Summer 1988		Fall 1988		Winter 1989		Spring 1989		Summer 1989		Fall 1989		Winter 1990		Spring 1990		Mean		
	GC	FC	GC	FC	GC	FC	GC	FC	GC	FC	GC	FC	GC	FC	GC	FC	GC	FC	
	----- (% dry weight) -----																		
<i>Baileya multiradiata</i>	6	10	—	—	—	—	—	—	—	—	T	—	—	T	—	—	1	1	
<i>Cassia bouhinioides</i>	T	—	3	T	—	—	1	T	T	T	T	—	—	1	2	1	1	T	
<i>Hymenoxys odorata</i>	3	1	2	3	T	—	T	2	1	T	—	—	—	—	1	1	1	1	
<i>Psilostrophe tagetina</i>	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	T	—
<i>Salsola australis</i>	4	3	3	7	—	—	11 ^a	2 ^b	3	2	1	3	—	—	8 ^a	2 ^b	4	2	2
<i>Solanum elaeagnifolium</i>	4	2	5	3	2	—	2	3	9	7	14 ^a	6 ^b	3	2	10 ^a	5 ^b	6	4	4
<i>Gutierrezia sarothrae</i>	—	—	—	—	T	2	T	T	—	T	T	—	1	1	T	T	T	T	T
<i>Prosopis glandulosa</i>	—	—	2	2	4	2	T	T	T	1	—	T	10 ^a	3 ^b	—	—	2	1	1
Total ²	18 ^a	16 ^a	15 ^a	15 ^a	6 ^a	4 ^a	14 ^a	7 ^b	13 ^a	10 ^a	15 ^a	9 ^b	14 ^a	6 ^b	19 ^a	10 ^b	14 ^a	10 ^a	10 ^a
Species	Jackrabbits																		
	Summer 1988		Fall 1988		Winter 1989		Spring 1989		Summer 1989		Fall 1989		Winter 1990		Spring 1990		Mean		
	GC	FC	GC	FC	GC	FC	GC	FC	GC	FC	GC	FC	GC	FC	GC	FC	GC	FC	
	----- (% dry weight) -----																		
<i>Astragalus</i> spp.	3	1	7	3	3	1	3	1	2	1	3	2	1	T	2	—	3	1	1
<i>Baileya multiradiata</i>	4	3	2	2	4	1	8	2	1	2	2	1	3	1	7	6	4	2	2
<i>Cassia bouhinioides</i>	1	T	2	2	1	—	3	1	2	1	2	—	T	—	1	T	2	1	1
<i>Psilostrophe tagetina</i>	2	—	2	T	10 ^a	T ^b	10 ^a	1 ^b	T	—	1	T	4	T	5	4	4	1	1
<i>Salsola australis</i>	2	1	3	3	T	—	1	T	3	2	1	1	—	4	1	T	1	1	1
<i>Solanum elaeagnifolium</i>	6	6	9	6	2	T	2	3	6	7	6	4	4	4	3	4	5	4	4
<i>Gutierrezia sarothrae</i>	1	4	5	8	10	14	4	7	4	6	5	7	8 ^a	15 ^b	2	3	5	8	8
<i>Larrea tridentata</i>	1	3	1	2	5	10	4	8	1	2	1	1	4	8	2	4	2	5	5
<i>Prosopis glandulosa</i>	2 ^a	9 ^b	12 ^a	16 ^a	9 ^a	12 ^a	5 ^a	11 ^b	10 ^a	12 ^a	13 ^a	16 ^a	7 ^a	17 ^b	6 ^a	10 ^a	8 ^a	13 ^b	13 ^b
Total ²	22 ^a	27 ^a	43 ^a	42 ^a	44 ^a	38 ^a	39 ^a	34 ^a	29 ^a	33 ^a	34 ^a	32 ^a	31 ^a	45 ^b	29 ^b	31	34	34	36

Row means within period with different superscripts differ ($P < 0.05$) using least significant difference (LSD) test.

Row means without superscripts had no analysis.

T = trace amount less than 1%.

(1986), Wansi (1989), and Schneberger (1990) in the Chihuahuan desert. Grass consumption was greatest in summer, shrub consumption was greatest in winter and forb consumption was generally similar between spring, summer, and fall with a decline in winter. Our data parallel that from southern Idaho (Anderson and Shumar 1986) and southern Nevada (Hayden 1966).

Jackrabbit diets on the 2 range condition classes showed a mean total similarity of 80% (Table 4). Similarities varied from 73% in winter to 84% in fall. We attribute the reduced winter similarity to lower forb availability on the fair than good condition range. During drought we would expect diets of jackrabbit on the 2 range condition classes to become more similar because they would be more dependent on shrubs.

Cattle Diets

Cattle diets on both the good and fair condition ranges were dominated by grasses (Table 3). Dominant grasses in the diet from most to least important were dropseed, black grama, bush muhly (*Muhlenbergia porteri* Scribn.), and threeawn (*Aristida* sp.). Increased consumption ($P < 0.05$) of black grama on good condition range is likely a result of greater % cover compared to the fair condition range.

The amounts of grasses consumed by cattle on both range condition classes appeared to be influenced by availability of preferred forbs. Our findings are consistent with Squires and Siebert (1983), who demonstrated that cattle will select the highest quality herbage available. Actively growing forbs in the Chihuahuan desert have higher protein, phosphorus, and cell soluble levels than grasses during active growth (Nelson et al. 1970).

Cattle on good condition range consumed up to 55% forbs compared to 43% on fair condition range (Table 3). The major

forbs eaten were leatherweed croton, silverleaf nightshade, Russian thistle, and globemallow. Overall, forbs were used most in summer and fall, intermediate in spring and least in winter. Forb cover was higher ($P < 0.05$) on good than fair condition range (Table 2), which accounts for the higher amounts in cattle diets on this range.

Shrub consumption was higher (19%) on the fair condition range compared to that (6%) on good condition ($P < 0.05$) (Tables 2, 3). Soaptree yucca and fourwing saltbush (*Atriplex canescens* Pursh [Nutt.]) were the most important shrubs in cattle diets, and received greatest use in winter and spring. Cattle made considerable use of the blooms on the soaptree yucca in spring.

Higher dietary shrub content by cattle on fair condition range was probably a function of decreased cover of grasses and forbs, and increased cover of shrubs, especially soaptree yucca (Table 2). Although fourwing saltbush was not abundant on either range, there was more fourwing saltbush growing on the fair than good condition range. Despite the fact that most of the shrubby cover on both ranges came from honey mesquite and snakeweed, these 2 shrubs received little use probably because of their toxicity (Holechek et al. 1989, Allison 1991).

The overall diet of cattle reported in our study generally agrees with Galt et al. (1982) on the Santa Rita Experimental Range in Arizona and other studies from the Chihuahuan desert (Rosiere et al. 1975, Hakkila et al. 1987). However, Galt et al. (1982) did report slightly higher levels of grasses and shrubs and lower levels of forbs in steer diets than in our study. Forbs were less available on their study area.

Diets of cattle on the 2 range condition classes showed mean total similarity of 74% (Table 4). Similarities varied from 69% in winter to 80% in summer. The divergence of cattle diets in winter

resulted from elevated shrub consumption on the fair condition range.

Comparative Jackrabbit and Cattle Diets on Good Condition Range

Primary factors that determine forage selection by range animals are body size, size of digestive system relative to body weight, type of digestive system, and mouth size and shape (Hanley 1982). Based on Holechek et al. (1989) cattle would be classified grazers and jackrabbits intermediate feeders. Studies by Arnold (1942), Lechleitner (1958), Dabo (1980), and Schneberger (1990) also depict jackrabbits as intermediate feeders.

Several more forbs were eaten by jackrabbits than by cattle. This was apparently because cattle avoided those forbs that are poisonous such as locoweeds (*Astragalus* sp.), desert marigold, wooly paperflower, and twinleaf (*Cassia bauhinioides* Gray). Unlike cattle, jackrabbits evolved with these forbs and may be capable of detoxifying them or limiting intake to subclinical levels. Also, jackrabbits have a small body and mouth, and therefore, greater capability to feed selectively on nonpoisonous parts of these forbs.

Jackrabbits readily used all available shrubs with the most important being prickly pear, honey mesquite, soap tree yucca, and mormon tea. Soap tree yucca was the only shrub important in cattle diets. For jackrabbits, maximum use of shrubs occurred in winter and minimum use occurred in summer. Cattle diets also followed this same pattern. Use of honey mesquite and soap tree yucca by jackrabbits was somewhat limited by height. Soap tree yucca and honey mesquite heights averaged 67.2 and 72.6 cm on good condition range and 78.7 and 93.6 cm on fair condition, respectively (Daniel 1991).

Cattle showed strong avoidance for the majority of the shrubs possibly because most are high in volatile oils (Nelson et al. 1970). According to Holechek et al. (1989), cattle avoid shrubs high in volatile oils because they lack mechanisms to reduce the toxic effect of these substances.

Diets of jackrabbits and cattle tended to diverge in winter probably because of reduced availability of forbs and green grasses. Schneberger (1990) also found jackrabbit and cattle diets diverged in winter on the College Ranch. We would expect the diets of the 2 animal species to become more similar when there is a prolonged drought. A drought would reduce forb and grass availability so the 2 animal species would depend on shrubs such as soap tree yucca, fourwing saltbush, mormon tea, and honey mesquite. Also, a high stocking rate that removed more than one-third of the perennial grass production each year would probably increase dietary overlap between the 2 animals. Under heavier grazing intensities the grass component would be reduced causing more dependence on shrubs by both cattle and jackrabbits.

Based on this study, we conjecture jackrabbit feeding activities may advance succession and favor establishment of grass-dominated communities in the Chihuahuan desert. It is important to recognize during the growing season jackrabbits used the perennial grasses when they were most vulnerable to damage. In years of high jackrabbit numbers, grass use by jackrabbits could be destructive. On the other hand, cattle grazing (particularly heavy grazing during the growing season) could cause retrogression to shrub-dominated communities. Under appropriate stocking, grazing jackrabbits and cattle together should maintain a mixture of grasses, forbs and shrubs. Jackrabbit numbers were about 40% higher on the fair condition compared to good condition range (Daniel 1991). These data indicate jackrabbits would have more impact on vegetation of ranges in low compared to high ecological condition. Jackrabbit populations during our study were considered to be at near average levels below highs (1985–1987) but

above 1980–1983 lows.

Poisonous Plants in Cattle and Jackrabbit Diets

Jackrabbit consumption of poisonous plants was over twice that of cattle when data were pooled across years, seasons, and range condition classes (Table 4). High occurrence of poisonous plants has traditionally been equated with poor range condition (Cronin et al. 1978). Tembo (1990) noted that the standing biomass of poisonous plants was higher on the fair condition range than good condition range. However, the overall levels of poisonous plants eaten by cattle did not differ ($P < 0.05$) on good and fair condition ranges, although there was a tendency for higher use on the good condition range. Both range condition classes were considered to be moderately stocked during the period of study and use of key forage plants averaged around 30–35% (Tembo 1990). Levels of poisonous plants consumed by the cattle were probably a reaction to stocking rate rather than to range condition classes. On both range condition classes cattle had adequate opportunity to graze selectively as shown by their tendency either to avoid or consume only minor amounts of poisonous plants, including the most abundant ones, broom snakeweed and honey mesquite, similar to Ralphs (1987). He found that cattle in northwestern Utah would not consume significant amounts of locoweed leaves, flowers, or mature pods when adequate forage was available. Avoidance was not shown for Russian thistle and silverleaf nightshade; however, cattle possibly selected these species as diet constituents when toxins were at safe levels, and it is probable other forages (grasses) in the diet diluted their toxic effect.

The relatively high consumption of poisonous plants by jackrabbits compared to cattle merits discussion. According to Laycock (1978) a varied diet would reduce the probability of eating lethal amounts of any poisonous species. However, jackrabbits may have consumed a more generalized diet to insure a balanced nutrient intake rather than to defend against plant poisons. Another explanation for the higher levels of poisonous plants in jackrabbit diets may be their ability to select the less-toxic portions of the plant. According to Hayden (1966), jackrabbits feed randomly and may pause to sample a plant and then move to another plant. This feeding behavior may be either to detect and avoid poisonous plants, and/or select parts high in water and nutrient content. We observed jackrabbits feeding on young creosotebush and silverleaf nightshade stems while leaves in most cases were avoided. This may be because the small twigs and leaves have higher levels of toxic substances. Another explanation is that jackrabbits may have the ability to detoxify some plant poisons. Laycock (1978) and Holechek et al. (1989) speculated native animals may have the ability to detoxify those poisonous plants with which they evolved. White et al. (1982) analyzed ingesta from stomachs of pygmy rabbits for volatile oils. They reported a loss of 77% of volatile oils had occurred, which they presumed was due primarily to mastication. Based on studies with hares (Reichardt et al. 1984), jackrabbits could have capability for digestive detoxification of volatile oils and tannins.

Our data suggest that jackrabbits may influence the dynamics of poisonous plant populations on Chihuahuan desert rangelands. Under moderate stocking rates, jackrabbits appear to positively affect Chihuahuan desert ranges by their consumption of poisonous plants. Because jackrabbits consume increased amounts of shrubs and poisonous plants, they have concurrent minimal forage competition with cattle. Hence, cattle and jackrabbits grazing may reduce cattle losses from poisonous plant consumption.

Management Implications

Our study showed cattle and black-tailed jackrabbits selected diets with different key forage species on moderately stocked good

and fair condition Chihuahuan desert ranges. Key forage species in cattle diets were primarily mesa dropseed and black grama across years, seasons and ranges. In contrast, poisonous forbs and unpalatable shrubs dominated jackrabbit diets. Honey mesquite and cactus were the 2 primary species consumed by jackrabbits across years, seasons, and ranges. Under moderate stocking rates cattle and jackrabbit diets were complementary rather than competitive. Based on Holechek (1991) the best approach to minimizing livestock losses from poisonous plants is to use a moderate stocking rate. This would involve removal of about one third the current year's growth of the key forage grasses (mesa dropseed, black grama, threeawn) by livestock. On the good condition range, this type of stocking has resulted in total cattle death losses of under 1% per year over a 25-year period (Holechek 1991). In contrast, annual cattle death losses on surrounding more heavily stocked ranges have averaged 4%. Programs geared towards eradication of jackrabbits through poisoning or shooting appear to be counter-productive on properly stocked Chihuahuan desert ranges.

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Mass-diameter regressions for moose browse on the Copper River Delta, Alaska

JAMES G. MacCRACKEN AND VICTOR VAN BALLEMBERGHE

Authors were graduate research assistant, Department of Fish and Wildlife Resources, University of Idaho, Moscow 83843; and research wildlife biologist, USDA, Forest Service, Pacific Northwest Research Station, Institute of Northern Forestry, 201 E. Ninth Ave., Suite 206, Anchorage, Alaska 99501. MacCracken is currently research scientist, Policy Analysis Group, College of Forestry, Wildlife, and Range Sciences, University of Idaho.

Abstract

Regression equations were developed to predict 3 mass components of 7 browse species important to moose (*Alces alces gigas*) on the Copper River Delta in southcentral Alaska. The accuracy of model predictions was the criterion for model selection. Model accuracy was evaluated using data splitting or jackknife procedures. Annual production of twigs and leaves and available twig mass on a stem were most accurately predicted from stem basal diameter with zero intercept models, zero intercept log-linear models, or log-log models. Twig mass eaten by moose was most accurately predicted from the diameter at the point of browsing of a twig with zero intercept or full linear models. Heteroskedasticity was significant ($P < 0.05$) in most of the data sets and could not be significantly reduced with log transformations or use of weighted least squares models. Heteroskedasticity appeared to have a relatively minor effect on model predictions. Most of the models gave mean predictions within $\pm 20\%$ of the actual values, particularly for the most ubiquitous species that were also the most important to moose. For each species, there were few differences ($P < 0.05$) in model coefficients between years and among habitat types. Differences in coefficient estimates appeared to be related to differences in stem morphology that were related to both site conditions and past browsing by moose.

Key Words: Alaska, *Alces alces*, browse, Copper River Delta, mass estimates, moose, predictive regression equations

A common procedure to estimate the mass (i.e., weight/unit area) of browse (i.e., trees and shrubs) is to relate an easily measured attribute of a plant or plant part to its weight using regression equations (Shafer 1963, Peek et al. 1971, MacCracken and Viereck 1990). The objective is to predict plant mass from the measured attribute.

A variety of measurements have been used as the independent variable in regression equations. These include twig basal diameter (Telfer 1969, Ruyle et al. 1983, Roundy et al. 1989), twig diameter at the point of browsing (Telfer 1969, Peek et al. 1971, MacCracken and Viereck 1990), canopy area and volume (Peek 1970, Uresk et al. 1977, Yarie and Mead 1989), basal stem diameter (Brown 1976, Alaback 1986), and basal stem circumference and number of twigs/stem (Oldemeyer 1982).

Most investigators have used simple least squares linear regression models to predict browse mass components (Basile and Hutchings 1966, Lyon 1970, Ferguson and Mardsen 1977, Thilenius 1988). These models often contain significant negative intercept coefficients that could result in negative predictions. Negative

intercepts may result from fitting a straight line to exponentially distributed data, or be a function of measurement imprecision and a limited sample for small y and x values, or a linear distribution that is truncated at a minimum threshold for both y and x . Methods to deal with an exponential distribution are well known, but the latter cases have not been adequately addressed.

Heteroskedasticity, in the form of increasing variation with increasing values of the independent variable, is a common problem when relating plant mass to other characteristics (Baskerville 1972). Formal tests have been developed to determine whether heteroskedasticity is significant (Glejser 1969). Logarithmic data transformations and weighted least square models are often used to reduce heteroskedasticity (Koutsoyiannis 1977). Few authors have examined their data for heteroskedasticity (Oldemeyer 1982, Ruyle et al. 1983, Rumble 1987) and the effect of heteroskedasticity on the predictive ability of regression equations is not well documented.

Many researchers have found that regression equations differ among species of browse (Telfer 1969, Peek 1970, Alaback 1986). In addition, equation coefficients may differ for a species among sampling sites (Peek et al. 1971, Ruyle et al. 1983, Roundy et al. 1989), with the size of the plant (Lyon 1970), by vegetation type (Yarie and Mead 1989), and with twig location on a plant (Basile and Hutchings 1966). Some authors suggested that small, statistically significant differences in equation coefficients had no practical implications (Basile and Hutchings 1966, Lyon 1970), while others stated that separate equations may need to be developed (Peek et al. 1971, Ruyle et al. 1983). What effect differences in coefficients for the same species have on the predictive ability of regression equations has not been objectively evaluated.

Few studies have formally evaluated the accuracy of regression models when used to predict plant mass (Thilenius 1988, 1990, Yarie and Mead 1989). A large r^2 (Brown 1976, Ruyle et al. 1983), small standard errors of coefficient estimates (Roundy et al. 1983), or decreased variance in mass estimates (Uresk et al. 1977) are not accurate indicators of predictive ability. In studies where regressions were used to estimate browse use it has been common to compare use estimates between regression techniques and other methods (Ferguson and Mardsen 1977, Provenza and Urness 1981, Ruyle et al. 1983). These are not tests of a models predictive ability either.

Snee (1977) discussed 4 methods for validating regression models. Two were based on theoretical expectations and 2 were data-based. The 2 data-based methods were the collection of new data and a data splitting or cross-validation approach. Jackknife and bootstrap resampling techniques (Krebs 1989) can also be used to generate model validation data sets. However, there is currently no formal method that we know of to objectively compare y and \hat{y} of validation data sets.

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The objectives of this study were to develop regression equations to predict the current annual growth of twigs and leaves (annual production), over-winter available mass, and mass eaten for browse used by moose on the Copper River Delta, Alaska. Our goal was to use 1 equation/mass component/species. We also assessed the predictive ability of the equations and examined the effects of yearly variation and habitat type on equation coefficient estimates.

Study Area and Methods

The Copper River Delta is located in coastal southcentral Alaska and is the largest contiguous wetland ($\approx 3,000 \text{ km}^2$) remaining on the Pacific coast of North America. The study area was described in detail by MacCracken (1992). Wetland herbaceous and shrub-dominated plant communities are abundant in lowland areas, with drier upland sites occupied by tall shrub communities, spruce [*Picea sitchensis* (Bong.) Carr.], or cottonwood (*Populus trichocarpa* Torr. & Gray) forest.

Preliminary results indicated that 4 browse-dominated habitat types (plant communities) were used the most by moose and that the study area could be divided into 5 sections unique in physiographic features, climate, vegetation development, and use by moose (MacCracken 1992). In each of those 5 sections, 4 permanent sampling sites (0.25 ha) were established representing each of the 4 habitat types used by moose. Habitat type classification followed Viereck et al. (1986).

Samples used to estimate regression equations to predict annual production of twigs and leaves and available mass of 7 browse species were collected at each site twice during 1988 and 1989. Sites were sampled in mid-April to mid-May, prior to leaf flush and during July–August, at peak mass. At each site, 5–10 individual stems of each browse species were harvested after the basal diameter was measured. A stem was a single shoot originating below the soil/moss/litter surface and the basal diameter was measured (mm) above the soil/moss/litter surface and the root crown. Stems were selected for sampling with a stratified random design, insuring that the full range of basal diameters for each species at a site was sampled. The strata were 10-mm basal diameter classes and the number of strata and stems sampled/strata varied with site characteristics. Harvested stems were separated into mass components in the lab, dried for 48 hours at 60° C, and weighed to the nearest 0.1 g.

For over-winter available mass estimates, twigs had 2 components: current annual growth and older portions (Telfer 1969). The limit of a twig was defined as the maximum diameter at the point of browsing (DPB) measured at a site for each species. If a species had not been browsed at a site, the average maximum diameter at the point of browsing of all other sites was used to define a twig.

Samples for developing regression equations to predict twig mass eaten were collected during October–December 1988 from 6 of the permanent sampling sites. All 4 habitat types were sampled plus an additional site in each of the 2 most important foraging habitats. At each site, up to 10 twigs were randomly clipped from 10 different stems for each species. Some stems had evidence of past browsing, but none had been recently browsed. Clipped twigs included all current annual growth and older material to insure that the full range of diameters at the point of browsing were sampled. In the lab, the twigs were clipped at 1–3 points along their length. The diameter at the point of clipping (= DPB) was measured with a pair of calipers to the nearest 0.1 mm. The samples were oven-dried for 48 hours at 60° C then weighed to the nearest 0.1 g. Twig mass posterior to the point of clipping (y) was related to the diameter at the point of browsing (x).

Data plots were examined to estimate the form (linear, curvilinear, exponential, etc.) of the mass-diameter relationships. If the

plots indicated that nonlinear relationships existed, appropriate data transformations were applied and linear models were estimated with ordinary least squares regression.

The predictive ability of most of the equations was evaluated using the data splitting method (Snee 1977). Prior to the development of the models, 10% of each data set was set aside as a validation data set (y_v, x_v). Observations for the validation data set were chosen with a stratified random sampling procedure to insure that all year and habitat type categories were represented. Sample sizes for felleaf willow [*Salix alaxensis* (Anderss.) Cov.] and cottonwood were too small to generate adequate validation data sets by splitting the data. For these species, jackknife procedures were used to validate the models (Krebs 1989). Comparisons between y_v and \hat{y}_v were made by calculating the mean of each and determining the percent deviation (Thilenius 1988). Retransformation bias was corrected for log-log models (Baskerville 1972, Sprugle 1982). The models that resulted in the smallest deviation between the means of y_v and \hat{y}_v were the models of choice. In addition, minimum root mean square error and maximum r^2 were also used as criteria to choose the best model. However, if these 3 criteria conflicted, prediction accuracy had priority.

Most statistical packages report an r^2 statistic that is appropriate only for full linear models (Kvalseth 1985). We report that R_1^2 ($1 - \frac{\sum (y - \hat{y})^2}{\sum (y - \bar{y})^2}$) of Kvalseth (1985) when models other than full linear models were estimated.

Once the best model was obtained, residual plots were examined to decide if testing for heteroskedasticity was warranted. Procedures outlined by Glejser (1969) were used to test if heteroskedasticity was significant. If it was, a weighted least squares model was estimated and tested to determine if heteroskedasticity had been significantly reduced (Koutsoyiannis 1977).

The effect of habitat type and year on equation coefficient estimates was examined by restructuring the data matrix using dummy variables so that 1 equation contained coefficients for each variable of interest. Comparisons of both intercept and slope coefficients between years and 2 habitat types were done with t -tests. Comparisons involving >2 habitats were made with F-tests, followed by all pairwise comparisons to determine which habitat produced a significant F (Koutsoyiannis 1977). Statistical significance was accepted at $P \leq 0.05$.

Table 1. Sample sizes for developing and testing regression equations to predict browse mass components on the Copper River Delta, Alaska.

Species	Production and available mass				
	Spring		Summer		Validation sample
	1988	1989	1988	1989	
	----- (Number of stems sampled) -----				
<i>Alnus sinuata</i>	108	129	104	92	43
<i>Myrica gale</i>	70	70	70	70	23
<i>Populus trichocarpa</i>	16	31	12	30	*
<i>Salix alaxensis</i>	20	20	20	20	*
<i>S. barclayi</i>	127	169	127	112	60
<i>S. commutata</i>	29	39	49	40	10
<i>S. sitchensis</i>	66	110	88	81	37
	Mass eaten				
	total		validation sample		
	----- (Number of twigs sampled) -----				
<i>A. sinuata</i>	110		21		
<i>M. gale</i>	126		13		
<i>P. trichocarpa</i>	53		10		
<i>S. alaxensis</i>	84		10		
<i>S. barclayi</i>	155		21		
<i>S. sitchensis</i>	141		16		

*models validated with the jackknife procedure.

Results

Browse Production and Availability

The number of stems sampled to estimate equations to predict production and available mass ranged from 80–535 (Table 1). For each species, all mass-basal diameter relationships were either linear or log transformed. Significant ($P < 0.05$) equations were obtained for each species-mass component with r^2 ranging from 0.16–0.76 (Table 2). Linear or log-linear models resulted in the most accurate predictions for 85% of the data sets. Log-log models

were most appropriate for the remaining 15%. However, full linear and log-linear models had negative intercepts resulting in negative predictions. Zero intercept linear and log-linear models were used for the data sets in which log-log models were inappropriate.

Eighty-five percent of the models overestimated browse mass components (Table 2). Deviation of the means of y_v and \hat{y}_v ranged from -9% to 35%. Seventy-three percent of the equations gave mean predictions within $\pm 20\%$ of the actual values. The predictive

Table 2. Mass-diameter regressions for browse used by moose on the Copper River Delta, Alaska. Equations estimate annual production of twigs and leaves, available mass, and mass eaten by moose/twig browsed during winter.

Species-mass component models	r^2 *	Model validation			
		y_v (SE)	\hat{y}_v (SE)	% Deviation [†]	
Annual production and available mass					
<i>Alnus sinuata</i>					
twig (winter)	= 1.21 (BD)	0.42	27.0(12.5)	30.3(5.8)	11
available mass (winter)	= 2.33(BD)	0.49	58.4(27.2)	58.3(11.2)	-1
twig (summer)	= -3.97(BD ^{1.77}) ²	0.76	6.1(1.6)	5.0(0.3)	-19
leaf	= 4.53(BD)	0.63	37.8(11.8)	86.7(16.3)	56
total (leaf+twig CAG)	= 5.14(BD)	0.63	43.9(13.0)	98.3(18.5)	55
<i>Myrica gale</i>					
twig (winter & summer)	= 1.20(BD)	0.16	2.5(0.5)	2.5(0.1)	0
available mass (winter)	= -3.33(BD ^{2.15})	0.61	5.1(0.7)	4.9(0.2)	-4
leaf	= 3.65(BD)	0.36	6.8(1.7)	7.4(0.8)	8
total (leaf+twig CAG)	= 4.52(BD)	0.36	9.3(2.2)	9.1(1.0)	-2
<i>Populus trichocarpa</i>					
twig (winter)	= 1.33(BD)	0.72	33.3(6.2)	38.4(4.1)	13
available mass (winter)	= 2.37(BD)	0.58	56.5(12.8)	71.0(7.2)	20
twig (summer)	= 0.98(BD)	0.75	16.5(5.0)	22.8(3.2)	28
leaf	= 4.82(BD)	0.69	73.4(26.6)	111.4(15.3)	34
total (leaf+twig CAG)	= 5.79(BD)	0.70	90.0(31.5)	134.4(18.5)	33
<i>Salix alaxensis</i>					
twig (winter)	= 0.42(BD)	0.38	6.7(1.3)	7.0(0.7)	4
available mass (winter)	= 1.00(BD)	0.54	13.4(3.2)	15.4(1.5)	13
twig (summer)	= 0.51(BD)	0.64	11.4(2.7)	12.5(2.2)	19
leaf	= 2.52(BD)	0.55	50.4(15.7)	62.3(11.3)	19
total (leaf+twig CAG)	= 3.03(BD)	0.57	61.8(22.8)	75.1(13.4)	18
<i>S. barclayi</i>					
twig (winter & summer)	= 0.36(BD)	0.62	7.4(0.8)	7.7(1.0)	4
available mass (winter)	= 1.51(BD)	0.44	34.7(7.8)	33.5(5.6)	-4
leaf	= 1.43(BD)	0.52	26.1(6.0)	29.5(3.6)	12
total (leaf+twig CAG)	= 1.76(BD)	0.52	32.6(7.6)	36.3(4.4)	10
<i>S. commutata</i>					
twig (winter)	= -4.39(BD ^{1.92})	0.65	5.1(2.3)	5.2(0.4)	2
available mass (winter)	= 0.55(BD)	0.48	8.6(2.7)	8.7(1.5)	1
twig (summer)	= 0.16(BD)	0.37	1.7(0.6)	1.9(0.3)	11
leaf	= 0.94(BD)	0.50	10.3(3.3)	11.2(1.6)	8
total (leaf+twig CAG)	= 1.10(BD)	0.49	12.0(3.9)	13.1(1.9)	8
<i>S. sitchensis</i>					
twig (winter)	= -3.74(BD ^{1.77})	0.34	4.8(1.4)	5.2(0.3)	8
available mass (winter)	= 11.07(lnBD)	0.20	21.0(7.1)	30.4(5.6)	31
twig (summer)	= -5.29(BD ^{2.36})	0.56	6.6(1.6)	6.7(0.3)	1
leaf	= 10.69(lnBD)	0.28	24.2(5.7)	30.6(1.5)	21
total (leaf+twig CAG)	= 13.04(lnBD)	0.28	30.7(7.1)	37.3(1.8)	18
Mass eaten regressions					
<i>Alnus sinuata</i>	= 0.34(DPB ⁴)	0.67	1.7(0.4)	1.7(0.4)	0
<i>Myrica gale</i>	= 0.12(DPB ²)	0.79	0.7(0.3)	0.7(0.3)	0
<i>Populus trichocarpa</i>	= 0.04(DPB ^{2.6})	0.92	1.2(0.5)	1.8(0.6)	33
<i>Salix alaxensis</i>	= 0.08 + 0.01 (DPB ^{3.4})	0.95	1.9(0.7)	2.0(0.8)	5
<i>S. barclayi</i>	= 0.05 + 0.03 (DPB ^{2.7})	0.81	1.1(0.4)	1.2(0.4)	8
<i>S. sitchensis</i>	= 0.03 + 0.06 (DPB ^{2.5})	0.80	1.4(0.6)	1.4(0.5)	0

[†] $100 \times (\hat{y}_v - y_v) / \hat{y}_v$.

²analyzed as $\ln y = b_0 + b_1(\ln x)$.

*see Methods for calculation for zero intercept and log-log models.

†the independent variable. Mass eaten equations use DPB as the independent variable. All mass predictions are in g/stem or g t/twig.

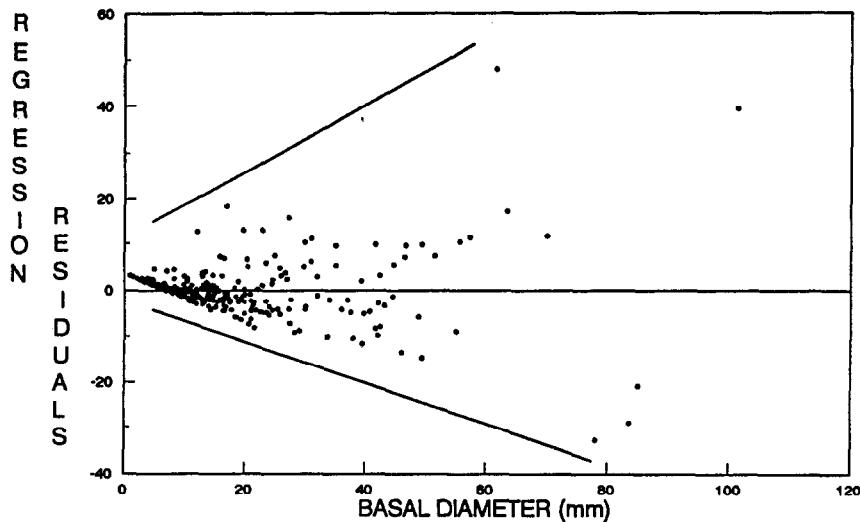


Fig. 1. A plot of residuals against the independent variable from the regression of current growth twig mass on stem basal diameter for Barclay willow. The funnel shaped distribution of the residuals suggested that heteroskedasticity in the data was a problem. The significance of heteroskedasticity was tested using procedures suggested by Glejser (1969).

ability of the models was not related to their r^2 value ($r_s = 0.19$, $P > 0.05$).

Heteroskedasticity was significant ($P < 0.05$) in 77% of the mass-basal diameter data sets, taking the form of increasing variance with increasing basal diameter (Fig. 1). Weighted least squares or log transformations did not significantly reduce heteroskedasticity in any data set and were not used.

Differences ($P < 0.05$) between years and habitat types in equation coefficients occurred in only 39% and 37% of all comparisons, respectively (Table 3). A majority of those differences were for the basal diameter coefficient. Significant differences ($P < 0.05$) for equation coefficients among habitat types occurred most often when contrasting habitats used by moose for foraging with those used for bedding.

Mass Eaten

The number of twigs sampled to estimate the mass of browse eaten by moose ranged from 53–155 (Table 1). Only 6 species were sampled since there was no evidence of moose eating undergreen willow (*S. commutata* Bebb). All mass-diameter at the point of browsing relationships were linear, but diameter at the point of browsing raised to a power resulted in the most accurate predictions with r^2 ranging from 0.67–0.92 (Table 2). Each model was significant ($P < 0.001$), and zero intercept models were used for 2 species. Of the 4 models with a positive intercept, only 1 was significantly different from zero ($P < 0.05$) (Table 2).

Fifty percent of the predictions were overestimates (Table 2). The mean deviation ranged from 0%–33%, and was greatest for cottonwood. The predictive ability of these models was weakly related to their r^2 value ($r_s = 0.76$, $P = 0.05$).

Heteroskedasticity was significant ($P < 0.05$) for each species, taking the form of increasing variance with increasing diameter at the point of browsing. Log transformations and weighted least squares models did not significantly reduce heteroskedasticity and were not used.

Differences ($P < 0.05$) in equation coefficients among habitat types occurred in 55% of all possible comparisons (Table 4). Sixty percent of those differences were due to the diameter at the point of browsing coefficient. Seventy percent of the habitat type differences were associated with comparisons of habitats used by moose for foraging vs. bedding.

Discussion

Numerous investigators have used regression equations to predict browse mass, but few have attempted to evaluate the accuracy of those predictions (Thilenius 1988, 1990; Yarie and Mead 1989). The lack of a formal summary statistic to compare y_v and \hat{y}_v makes models validation difficult and subjective. The χ^2 goodness-of-fit test is appropriate only for categorical data. Furthermore, most statistical methods that could be applied (e.g., t -test) test the hypothesis that a function of a parameter of the 2 data sets is not different from zero, not each other (e.g., $\bar{x}_1 - \bar{x}_2 = 0$).

Linear models resulted in the most accurate predictions for most of the mass-diameter relationships we examined. However, full linear models often contained significant negative intercepts, resulting in negative predictions for small diameters. In these situations, log-log models accurately represented only the lower portion of the data distribution and the predictions of those models were consistently poor due to large variation in the data at the upper end of the distribution (Fig. 2). The magnitude of prediction errors for large values accounted for the overall poor performance of log-log models. These results suggest that a minimum threshold in mass-diameter relationships may be the primary cause of negative intercepts in linear relationships.

We used zero intercept models when linear equations resulted in negative intercepts and log-log models resulted in poor predictions. Zero intercept models are theoretically justified since zero mass occurs at zero diameter. In addition, minimum threshold linear relationships provide a data-based justification. Furthermore, we found that zero intercept models either improved or did not alter the accuracy of mass predictions in 64% of the data sets in which a full linear or log-linear model was appropriate. We conclude that zero intercept models adequately solved the problems associated with data sets that were essentially linear, but truncated at a minimum threshold. Yarie and Mead (1989) also used zero intercept models and reported predictions of -11, -40, and -55% of mass estimates derived from plot clipping methods.

Thilenius (1988, 1990) reported a deviation of <1% between predicted and actual mass of current annual growth twigs of Barclay willow (*S. barclayi* Anderss.) on the Copper River Delta. Our predictions were a 4% overestimate. Differences between predictions of twig current annual growth from actual values for sweetgale (*Myrica gale* L.) reported by Thilenius (1990) ranged from

Table 3. Significant differences in regression equation coefficients between years and among habitat types for browse used by moose on the Copper River Delta, Alaska. For year comparisons, positive *t* statistics indicate that 1988 > 1989, and vice-versa.

Species and mass component	Year		Habitat type ¹	
	b ₀	b ₁	b ₀	b ₁
<i>Alnus sinuata</i>				
twig (winter)		<i>t</i> =3.69***		
available mass		NSD ²		NSD
twig (summer)	NSD	NSD	NSD	NSD
leaf		NSD		NSD
total		NSD		NSD
<i>Myrica gale</i>				
twig (winter-summer)		NSD		NSD
available mass	NSD	NSD	NSD	NSD
leaf		<i>t</i> = 3.17***		NSD
total		<i>t</i> = 2.81**		NSD
<i>Populus trichocarpa</i>				
twig (winter-summer)		<i>t</i> =-3.53***		NSD
available mass		<i>t</i> =-3.19***		<i>t</i> = 4.14*** OAW>CAW
twig (summer)		<i>t</i> =-3.01***		NSD
leaf		<i>t</i> =-2.79**		NSD
total		<i>t</i> =-2.92**		NSD
<i>Salix alaxensis</i>				
twig (winter)		NSD		<i>t</i> =2.90** CAW>OAW
available mass		<i>t</i> = 2.10*		NSD
twig (summer)		NSD		<i>t</i> =6.17*** CAW>OAW
leaf		<i>t</i> =-2.63**		<i>t</i> =4.90*** CAW>OAW
total		<i>t</i> =-2.46**		<i>t</i> =5.08*** CAW>OAW
<i>S. barclayi</i>				
twig (winter-summer)		NSD		<i>F</i> =15.0*** CAW>MS; CAW, OAW, MS>WS
available mass		NSD		NSD
leaf		NSD		<i>F</i> =3.7* CAW, OAW>MS
total		NSD		NSD
<i>S. commutata</i>				
twig (winter)	NSD	<i>t</i> =2.79*	<i>F</i> =18.6***	NSD
available mass		<i>t</i> =-4.50***		<i>t</i> =-3.59*** WS>MS
twig (summer)		<i>t</i> = 3.50***		<i>t</i> =-2.00* WS>MS
total		NSD		NSD
<i>S. sitchensis</i>				
twig (winter)	NSD	NSD	<i>F</i> =5.6** OAW, CAW>MS	NSD
available mass		NSD		<i>F</i> =41.5*** CAW, OAW>MS
twig (summer)		NSD		NSD
leaf		NSD		NSD
total		NSD		NSD

¹CAW = closed alder-willow, OAW = open alder-willow, MS = sweetgale-willow, and WS = woodland spruce habitat types.

²NSD = no significant difference (*P*>0.05).

* = *P*<0.05, ** = *P*<0.01, *** = *P*<0.001.

-42% to 16%. When averaged, our predictions were equal to the actual values. Thilenius (1988, 1990) collected Barclay willow and sweetgale samples from 2 adjacent sites, in 1 habitat type. In contrast, we sampled all habitat types where these species occurred with a replicated sampling scheme. Our equations should have broader application and greater accuracy in a variety of habitat types.

Raising diameter at the point of browsing to the power indicated (Table 2) is justified by the fact that twig mass is closely related to twig volume. Volume is a 3-dimensional measure and for most species, diameter at the point of browsing raised to a power very close to the volumetric expectation of 3 resulted in the most accurate predictions. Only Sitka alder [*Alnus sinuata* (Reg.) Rydb.] deviated from this trend, presumably due to the fact that alder

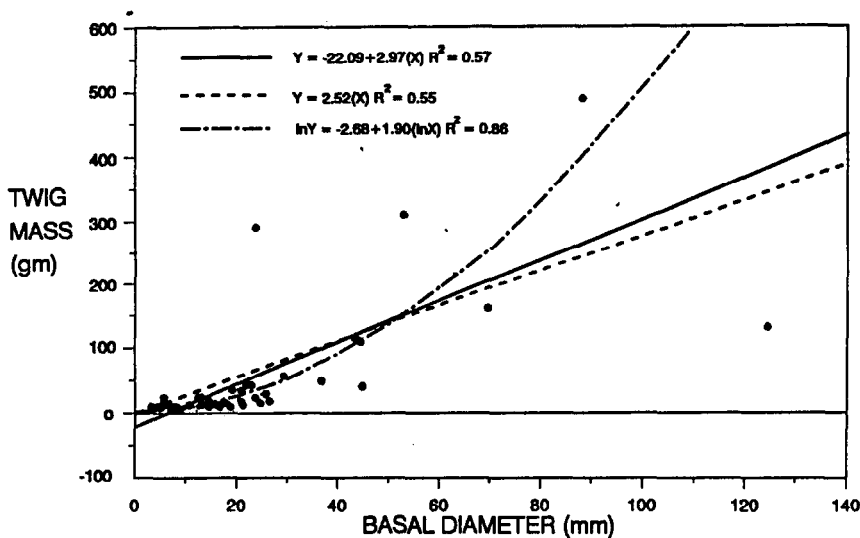


Fig. 2. A plot of 3 regression models fit to data for leaf mass (y) and stem basal diameter (x) for feltleaf willow. The full linear model produced a significant ($P < 0.05$) negative intercept, resulting in negative predictions for basal diameters ≤ 7.4 mm and a deviation of 6% between y_v and \hat{y}_v . The log-log model resulted in a deviation of -48% between y_v and \hat{y}_v , despite the high r^2 . The zero intercept model resulted in a deviation of 20% between y_v and \hat{y}_v . This example was typical for a majority of the mass-diameter relationships examined in this study.

Table 4. Significant differences in regression equation coefficients among habitat types for equations that predicted browse mass eaten by moose on the Copper River Delta, Alaska.

Species	Equation coefficient	
	b_0	b_1
<i>Alnus sinuata</i>	NSD ¹	NSD
<i>Myrica gale</i>		$t = -5.00^*$ WS > MS ²
<i>Populus trichocarpa</i>		NSD
<i>Salix alaxensis</i>	NSD	NSD
<i>S. barclayi</i>	$F = 6.60^*$ CAW, WS, OAW > MS; WS > CAW	$F = 6.66^*$ MS > WS; OAW > WS
<i>S. sitchensis</i>	$F = 204.4^*$ WS > OAW	$F = 106.8^*$ WS > CAW, OAW

¹NSD = no significant difference.

²CAW = closed alder-willow, OAW = open alder-willow, MS = sweetgale-willow, and WS = woodland spruce habitat types.

* = $P < 0.001$.

twigs were oblong in circumference, and the other species were round.

We identified a number of factors that could influence equation predictions. Heteroskedasticity was significant in most of the data sets we analyzed. Heteroskedasticity results in inefficient estimates of the model coefficients and biased standard errors and test statistics (Koutsoyiannis 1977). Our analysis produced variable results: some models with significant heteroskedasticity gave accurate predictions and others not. None of equations in which heteroskedasticity was insignificant ($P > 0.05$) resulted in predictions that deviated by more than 16% from the actual values. The predictions of log-log models were influenced the greatest by heteroskedasticity. The effects of heteroskedasticity on linear model predictions appear to be minimal as suggested by Rumble (1987), but more formal testing is needed. The failure of the data transformations to significantly reduce heteroskedasticity suggests that it may be related to some variable other than basal diameter or diameter at the point of browsing. The fact that variation was relatively large at large diameters at the point of browsing and large basal diameters suggests that stem or twig age may be important.

Differences in equation coefficients for a species between years and among habitats were significant in some instances, suggesting that the goal of using 1 equation to predict browse mass components may be unrealistic. Those differences could influence the predictive ability of an equation when these data subsets are pooled. Even though some coefficients differences were large, model predictions did not suffer substantially when the data were pooled and 1 equation was used for prediction, particularly for the most ubiquitous species that were also the most important to moose (MacCracken 1992). Presumably, predictions would be improved if separate equations were estimated for each different factor. Our data sets were not large enough to adequately assess the predictive ability of equations for each habitat type occupied by a species. Furthermore, such a procedure may be beyond the ability of most projects due to time and budget constraints.

Differences in equations among habitat types are likely due to differences in stem or twig morphology that reflect varying environmental conditions or use by herbivores (Peek et al. 1971). A majority of the differences in equations occurred when contrasting habitats used by moose for foraging with those used primarily for bedding. This suggests that browsing significantly altered shrub morphology and mass distribution on a twig or stem; a fact that was apparent in the field and discussed by Oldemeyer (1982:55). However, shrub morphology also varied with the physical environment of a specific site, independent of moose foraging. In fact, plant morphology influenced the ability of moose to forage on specific stems. In closed alder-willow stands, Barclay willow (the most abundant and important species) had large stem diameters and were about 3-5 m tall; characteristics that inhibited foraging by moose.

The use of predictive regression equations outside of the time frame or area from which the equations were developed should be undertaken with caution. If predictive regressions are used in this manner, validation samples should be collected in order to check the accuracy of the predictions. Furthermore, this information could be used to correct any consistent bias that may be present in the predictions.

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Genotype and planting depth effects on seedling vigor in sericea lespedeza

J. QIU AND J.A. MOSJIDIS

Authors are former graduate research assistant and associate professor, Dept. Agronomy and Soils and Alabama Agr. Exp. Sta., Auburn University 36849-5412.

Abstract

Sericea lespedeza [*Lespedeza cuneata* (Dumont de Courset) G. Don.] is a small-seeded forage legume that can improve forage quality and nitrogen content of interseeded pasturelands. Poor seedling vigor has caused interseeding failure. This study was conducted to determine the effects of genotype, planting depth, and their interaction on seedling vigor of sericea lespedeza in the field, and to determine if seedling traits measured in a growth chamber can be used to predict seedling growth in the field. Substantial variability was found among 54 sericea lespedeza genotypes for traits that can be used in a breeding program to improve seedling vigor. All seedling traits were correlated with each other, indicating a high proportionality existed among plant parts. Thus, any of the seedling traits measured could be used to represent seedling vigor. Genotypes 73-162-16, AU L2, AU L13, and 'Serala 76' outperformed other genotypes for most seedling traits under field and growth chamber conditions. Planting to a depth of 3 cm did not reduce seedling vigor, and therefore, may be recommended when there is insufficient moisture in the upper layer of sandy loam soils at planting. Although measurements taken in the growth chamber did not reliably predict field performance, information gathered in the growth chamber provides a good means of increasing the frequency of superior plants to be tested in the field.

Key Words: seedling growth, legumes, growth prediction, *Lespedeza cuneata*, seed weight

Successful stand establishment of forage species is highly dependent on seedling vigor as measured by seedling height or dry weight (Black 1957, Townsend 1979, Carren et al. 1987a, Carren et al. 1987b). Seed weight is a major plant determinant of seedling vigor (Beaveridge and Wilsie 1959, Wulff 1986) and planting depth is an environmental factor that may affect vigor in some species (Peiffer et al. 1972, Townsend and McGinnies 1972, Tischler and Voigt 1983) or may not have any effect in others (Black 1956, Williams 1967).

Sericea lespedeza [*Lespedeza cuneata* (Dumont de Courset) G. Don.] is a small-seeded forage legume that is often difficult to establish and displays poor seedling growth (Mosjidis 1990). Moore (1943) observed that as planting depth increased from 0.6 to 2.5 cm, emergence decreased from 83 to 35% at 49 days after planting in a greenhouse study and from 58 to 18% at 30 days after planting in a field experiment. Seed size of 10 inbred lines had a significant and positive correlation with seedling height in a greenhouse study but was not consistently correlated with seedling height or forage yield in field studies (Cope 1966). Little is known regarding effect of planting depth or plant depth-genotype interactions on seedling vigor as measured by seedling traits such as stem, leaf or shoot dry weight in sericea lespedeza.

Selection for seedling vigor could be facilitated by laboratory procedures that provide a rapid and reliable prediction of seedling vigor under field conditions in forage breeding programs. Twamley (1967) found that forage yield of birdsfoot trefoil (*Lotus corniculatus* L.) measured at 42 days after planting in a greenhouse provided a good prediction of seedling dry matter in the field. Cooper et al. (1980) reported that seedling height of birdsfoot trefoil measured at 3 days after planting in a growth chamber was highly correlated with field seedling vigor rating and forage yield. No information is available for sericea lespedeza regarding prediction of seedling growth in the field by seedling traits measured in controlled environments. The objectives of this study were to determine the effects of genotype, planting depth, and their interaction on seedling vigor of sericea lespedeza in the field, and to determine if seedling traits measured in the growth chamber can be used to predict seedling growth in the field.

Materials and Methods

Seeds of 54 sericea lespedeza genotypes, harvested at Tallassee, Ala., in 1988, were mechanically scarified with a Forsberg sample seed electric huller/scarifier (Forsberg Inc., Thief Rivers Falls, Minn. 56701)¹. Seeds were placed in the huller/scarifier for 7 seconds, cleaned, and placed again in the huller/scarifier for 2 additional seconds. Seed weight of each genotype was determined by weighing 5 samples of 1,000 scarified seeds counted by an electronic counter (Model 850-2, The Old Mill Company, Savage Industrial Center, Savage, Md. 20763)¹. A wide range of 1,000-seed weights (1,333 to 2,045 mg) was measured among the genotypes.

Field Experiments

Field experiments were conducted at Tallassee, Ala., on Hiwassee sandy loam soil (clayey, kaolinitic, thermic, typic Rhodudults). Seventy scarified seeds of each of the 54 genotypes were planted in a single row (4.6 m long and 0.5 m wide) at planting depths of 1 or 3 cm using a single-row cone seeder equipped with a packer wheel on 20 July 1990 and 18 April 1991. Emerged seedlings were counted at 14, 28, and 42 days after planting. For most genotypes maximum emergence was observed at 42 days after planting and final emergence was therefore considered to be percent emergence at 42 days after planting. At 60 days after planting 5 random seedlings per genotype were harvested to ground level. Traits measured on each seedling were height and stem and leaf dry weights. Stem and leaf weights were added to give shoot weight. The study was conducted in a split plot arrangement of treatments in a randomized complete block design with 4 replications in each year. Main plots were the planting depths and the split plots were the genotypes.

Growth Chamber Experiment

Two scarified seeds of each of the 54 genotypes were planted 1

Table 1. Mean squares for emergence and seedling traits of 54 field-grown sericea lespedeza genotypes at 2 planting depths (1 and 3 cm) at Tallahassee, Ala., 1990 and 1991.

Source	df	Emergence	Height	Shoot weight	Stem weight	Leaf weight
Years (Y)	1	32,609	6	628,182	30,930	380,328
Rep/Y	6	1,011	16,250	259,591	23,902	143,080
Depth (D)	1	1,607	14,786	145,968	11,842	74,657
Y × D	1	776	1,623	68,620	15,510	18,168
Error (a)	6	1,749	13,910	125,902	18,411	55,180
Genotypes (G)	53	176**	1,721**	27,006**	1,865**	15,474**
Y × G	53	106**	1,060**	12,242**	1,157**	6,147**
D × G	53	59	578	6,430	561	3,503
Y × D × G	53	57	567	4,512	411	2,541
Error (b)	596	61	561	6,296	621	3,285

**, **Significant at $P < 0.05$, and 0.01 , respectively.

cm deep in each of 7 Cone-tainers (Ray Leach Cone-Tainer Nursery, Canby, Ore. 97103)¹, 4 cm diameter by 21 cm deep, filled with 0.16 liter potting soil (13% peatmoss, 57% fine sandy loam soil, and 30% sand). After emergence, each individual Cone-tainer was thinned to 1 seedling. Trays containing the Cone-tainers were placed in growth chambers with temperature maintained at 26/22°C (13/11 hours). A mixture of fluorescent and incandescent lamps provided a photosynthetic flux photon density during daylight of $380 \mu\text{mol m}^{-2} \text{s}^{-1}$. Water was added only when the soil surface became dry.

The study was conducted in a split plot arrangement of treatments in a randomized complete block design with 3 replications (chambers). Main plots were the genotypes and the split plots were 2 sampling dates (17 and 31 days after planting). Three random seedlings per replicate from each genotype were harvested at each date. Height and stem and leaf weights were measured on each seedling. Stem and leaf weights were added to get shoot weight.

Data from field and growth chamber experiments were subjected to analysis of variance. Seedling growth under field conditions was related to seedling traits observed in the growth chamber by simple regression as a means of evaluating the growth chamber measurements as predictors. Correlations among seed weight and seedling variables were also obtained.

Results and Discussion

Field Experiments

Main effect of planting depth and year × planting depth interaction were not significant for emergence, height, shoot weight, stem weight, and leaf weight (Table 1). These results indicate that the 3-cm planting depth in sericea lespedeza did not reduce emergence or other seedling traits when compared to those at 1 cm, thus, contradicting the report by Moore (1943). The difference may be due to the improved sericea lespedeza genotypes used in this experiment or to some environmental factors. Lack of planting depth effects on seedling vigor has also been reported in other forage legumes (Black 1956, Williams 1967).

All seedling traits differed among the genotypes ($P < 0.05$) and year × genotype interactions ($P < 0.01$) indicated that the genotypes differed somewhat between the 2 years (Table 1). Genotypes 'Serala', 73-162-16, AU L2, AU L13, and 'Serala 76', however, consistently ranked among the top 20% for shoot and leaf weights in both years (Table 2). Although seedling vigor for some genotypes differed over years, other genotypes were relatively insensitive to changes in environmental conditions (data not presented) and, therefore, could be expected to produce consistent results over a variety of planting conditions.

Seed weight was not correlated with any seedling traits in the 1990 experiment, but was correlated ($P < 0.05$) with height ($r = 0.32$), shoot weight ($r = 0.51$), stem weight ($r = 0.48$), and leaf weight

Table 2. Average height and shoot, stem, and leaf weights of selected genotypes of sericea lespedeza measured at 60 days after planting at Tallahassee, Alabama, in 1990 and 1991.

Genotype	Height	Shoot weight	Stem weight	Leaf weight
	- mm -	----- mg -----		
1990 Experiment				
Serala	131	260	84	177
73-162-16	122	168	111	57
AU L2	120	204	53	151
AU L13	113	194	54	140
Serala 76	103	182	53	129
1991 Experiment				
Serala	118	270	77	193
73-162-16	132	349	99	249
AU L2	126	292	78	214
AU L13	142	391	110	280
Serala 76	121	276	70	206

($r = 0.51$) in the 1991 experiment. Although the relationship of seed weight to seedling traits in sericea lespedeza was neither close nor consistent over years, seedlings from larger-seeded genotypes may have advantages over those from smaller-seeded genotypes for seedling vigor (Wulff 1986).

Growth Chamber Experiment

Differences were found among 54 genotypes for 3 of 4 seedling traits (Table 3). Sampling date accounted for most of the variability, however, none of the interactions between genotypes and

Table 3. Mean squares for seedling traits of 54 sericea lespedeza genotypes measured at 17 and 31 days after planting in a growth chamber.

Source	df	Height	Shoot weight	Leaf weight	Stem weight
Replications	2	1,795	621	362	35
Genotypes (G)	53	324**	107*	64*	7
Error (a)	106	129	73	38	6
Dates (D)	1	132,126**	33,488**	17,516**	2,560*
G × D	53	119	71	41	4
Error (b)	108	95	63	34	5

***Significant at $P < 0.05$, and 0.01 , respectively.

sampling date were significant. These results indicate that seedling traits were consistent between 17 and 31 days after planting, and seedling trait variables could be measured at either date.

Seed weight was correlated ($P < 0.05$) with all seedling traits at both 17 and 31 days after planting (Table 4). The correlation coefficients for seed weight obtained at 17 days after planting were larger than those at 31 days after planting. These results indicate

Table 4. Correlation coefficients (r) between mean seed weight and mean seedling traits of 54 sericea lespedeza genotypes measured at 17 and 31 days after planting in a growth chamber.

Seed or seedling variables	Variables in field			
	Height	Shoot weight	Stem weight	Leaf weight
17 days after planting				
Seed weight	0.32*	0.64**	0.54**	0.66**
Height		0.68**	0.80**	0.60**
Shoot weight			0.92**	0.98**
Stem weight				0.85**
31 days after planting				
Seed weight	0.27*	0.43**	0.42**	0.42**
Height		0.75**	0.87**	0.70**
Shoot weight			0.94**	0.99**
Stem weight				0.94**

*Significantly differs from zero at $P < 0.05$ and 0.01, respectively.

that genotypes with heavier seeds produced more vigorous seedlings, and the relationship between seed weight and seedling vigor was more pronounced in the earlier growth stage. The positive relationship between seed weight and seedling growth found in this experiment was similar to the finding reported by Cope (1966).

All seedling traits were correlated ($P < 0.01$) with each other (Table 4), indicating a high proportionality existed among plant parts especially for leaf and stem weights and, therefore, shoot weight. We conclude that any of the seedling traits measured could be used to represent seedling vigor.

Prediction of Field Performance

Height of seedlings of genotypes measured at 17 days after planting in the growth chamber were significantly ($P < 0.05$) correlated with seedling height measured in the 1990 field experiment, and were correlated with all seedling traits measured in the 1991 field experiment (Table 5). Stem weight measured at 17 days after planting in the growth chamber was not correlated with any seedling trait measured in the 1990 field experiment but was correlated with all seedling traits measured in the 1991 field experiment. Leaf weight and shoot weight measured at 17 days after planting in the growth chamber were correlated ($P < 0.05$) with most seedling traits measured at 60 days after planting in both 1990 and 1991 field experiments, with the exception of seedling height measured in the 1990 field experiment. No seedling traits measured at 31 days after planting in the growth chamber were correlated with any of those measured in the 1990 field experiment, but all seedlings traits measured at 31 days after planting in the growth chamber were correlated with those measured in the 1991 field experiment.

Table 5. Correlation coefficients (r) between height (H), stem weight (SDW), leaf weight (LDW) and shoot weight (SHDW) measured at 17 and 31 days after planting in the growth chamber experiment and at 60 days after planting in the 1990 and 1991 field experiments.

Chamber variables	Field 1990				Field 1991			
	H	SDW	LDW	SHDW	H	SDW	LDW	SHDW
Chamber								
17 days after planting								
H	0.29*	0.23	0.17	0.20	0.43*	0.36*	0.32*	0.33*
SDW	0.21	0.24	0.19	0.21	0.40*	0.41*	0.43*	0.43*
LDW	0.24	0.28*	0.37*	0.35*	0.49*	0.54*	0.66*	0.64*
SHDW	0.25	0.27*	0.33*	0.32*	0.49*	0.53*	0.62*	0.61*
31 days after planting								
H	0.20	0.03	0.05	0.05	0.50*	0.35*	0.30*	0.32*
SDW	0.16	0.03	0.09	0.08	0.46*	0.39*	0.38*	0.39*
LDW	0.16	0.07	0.21	0.18	0.38*	0.40*	0.49*	0.47*
SHDW	0.16	0.06	0.18	0.15	0.41*	0.41*	0.47*	0.46*

*Significantly differs from 0 at $P < 0.05$.

Table 6. Coefficients of determination (R^2) from single and multiple regressions used to predict seedling traits of sericea lespedeza measured at 60 days after planting in the 1991 field experiment.

Variables in growth chamber†	Variables in field			
	Height	Shoot weight	Stem weight	Leaf weight
SW‡	0.129	0.298	0.278	0.293
H	0.188	0.112	0.128	0.101
SDW	0.161	0.186	0.170	0.185
LDW	0.236	0.409	0.297	0.436
SHDW	0.240	0.367	0.283	0.385
SW, H	0.242	0.326	0.318	0.316
SW, SDW	0.191	0.327	0.303	0.323
SW, LDW	0.238	0.436	0.347	0.456
SW, SHDW	0.243	0.410	0.342	0.421
H, SDW	0.196	0.187	0.172	0.187
H, LDW	0.267	0.412	0.299	0.445
H, SHDW	0.259	0.378	0.283	0.404
SW, H, SDW	0.242	0.330	0.318	0.323
SW, H, LDW	0.273	0.437	0.352	0.462
SW, H, SHDW	0.267	0.414	0.345	0.431
H, SDW, LDW	0.238	0.465	0.327	0.506
SW, H, SDW,	0.312	0.490	0.380	0.522

†Measured at 17 days after planting in the growth chamber experiment.

‡Seed weight (SW), height (H), stem weight (SDW), leaf weight (LDW), and shoot weight (SHDW).

Seed weight and seedling traits measured 17 days after planting in the growth chamber experiment were used as independent variables in multiple regressions to predict seedling traits measured in the 1991 field experiment (Table 6). Shoot weight in the growth chamber experiment provided the best single-variable estimate of height and leaf weight at 60 days after planting in the 1991 field experiment. Leaf weight measured in the growth chamber was the best single independent variable to estimate both shoot weight and stem weight in the field. When 2 or more independent variables were included in the equations, there were only small increases in R^2 values (Table 6). Seed weight and seedling traits measured in the growth chamber could be used to give an estimation of field performance; however, the variables measured accounted for a maximum of only 52% of the variation. Therefore, measurement of seedling traits under the growth chamber conditions may not provide a reliable estimate of seedling vigor under field conditions in sericea lespedeza. However, genotypes 73-162-16, AU L2, AU L13, and 'Serala 76' consistently ranked among the top 20% for shoot weight in the growth chamber and in both years in the field.

Summary and Conclusions

There is substantial variability among sericea lespedeza genotypes for traits that can be used in a breeding program to improve seedling vigor. Genotypes 73-162-16, AU L2, AU L13, and 'Serala 76' outperformed other genotypes for most seedling traits under field and growth chamber conditions. Planting at 3 cm deep did not reduce emergence and seedling growth compared to 1 cm and, therefore, may be recommended in sandy loam soils when there is insufficient moisture in the upper soil layer at planting time. Although measurements taken in the growth chamber did not reliably predict field performance, information gathered in the growth chamber provides a good means of increasing the frequency of superior plants to be tested in the field.

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Effects of sericea lespedeza root exudates on some perennial grasses

K.L. KALBURTJI AND J.A. MOSJIDIS

Authors are lecturer, Lab of Ecology, Faculty of Agriculture, Aristotelian University of Thessaloniki, 540 06 Thessaloniki, Greece; and associate professor, Dept. of Agronomy and Soils and Ala. Agr. Exp. Sta., Auburn University, Auburn 36849-5412.

Abstract

Root exudates are substances released into the surrounding medium by healthy and intact plant roots. Research on root exudates has shown that root exudates can reduce seed germination and plant growth. There is no information on the effect of sericea lespedeza [*Lespedeza cuneata* (Dum. de Cours) G. Don.] root exudates on other plants. In a series of greenhouse experiments we studied (1) if sericea root exudates affect seed germination and seedling growth of the perennial grasses tall fescue (*Festuca arundinacea* Schreb.), bermudagrass [*Cynodon dactylon* (L.) Pers.], and bahiagrass (*Paspalum notatum* Flugge); and (2) if any such responses were cultivar dependent. The effects of the root exudates were measured in 2 experiments. In the first one, coarse perlite was used as a medium to measure seed germination and radicle and

coleoptile growth. In the second experiment, soil was used as a medium to measure emergence and biomass. Root exudates from sericea lespedeza had no effect on germination and emergence of tall fescue and bahiagrass but reduced their radicle and coleoptile length and biomass. Germination, radicle, and coleoptile length, and emergence of bermudagrass decreased when exposed to the root exudates; however, biomass was not affected. Cultivars of the grass species differed in their response to the root exudates of sericea lespedeza. Thus, establishment of tall fescue in mixture with sericea lespedeza is not likely to be affected; however, its growth is likely to be decreased. Therefore, tall fescue contribution to total yield will be reduced. Conversely, establishment of bermudagrass is likely to be affected, but once established, its growth is expected to be similar to its grown alone.

Key Words: allelopathy, *Lespedeza cuneata*, tall fescue, *Festuca arundinacea*, bermudagrass, *Cynodon dactylon*, bahiagrass, *Paspalum notatum*

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Root exudates are substances released into the surrounding medium by healthy and intact plant roots (Rovira 1969). They have been implicated in interactions among plants and soil microorganisms (Rovira 1969, D'Arcy Lameta and Jay 1987, Richardson et al. 1988) and plant-plant interactions (Rovira 1969). Research on root exudates has shown that they can reduce seed germination and plant growth (Pope et al. 1985a, b; Kalburtzi et al. 1989). Hence, root exudates may be of importance in intercropping and crop rotation.

Sericea lespedeza [*Lespedeza cuneata* (Dum. de Cours) G. Don.] is a perennial legume well adapted to infertile soils which has been grown in association with grasses to extend the production season of pastures (Hoveland and Donnelly 1985). *Sericea lespedeza* residues incorporated into the soil have been reported to reduce growth of corn (*Zea mays* L.) (Langdale and Giddens 1967); rye (*Secale cereale* L.), ryegrass (*Lolium multiflorum* Lam.), tall fescue (*Festuca arundinacea* Schreb.), bermudagrass [*Cynodon dactylon* (L.) Pers.] and bahiagrass (*Paspalum notatum* Flugge) (Kalburtzi and Mosjidis 1992). There is no information about the interactions of *sericea lespedeza* with other plants at the root level.

The objectives of this study were: (1) to find if *sericea lespedeza* root exudates affected seed germination and seedling growth of tall fescue, bermudagrass, and bahiagrass; and (2) to determine if any such response were cultivar dependent.

Materials and Methods

The effects of *sericea lespedeza* root exudates on percentage germination and emergence and plant growth of tall fescue, bermudagrass, and bahiagrass were examined in a series of greenhouse experiments. Root exudates obtained from the low-tannin cultivars 'AU Donnelly' and 'AU Lotan' and from the high-tannin cultivar 'Serala' were tested on 3 cultivars of tall fescue ('AU Triumph', endophyte-infected 'Ky-31', and endophyte-free 'KY-31') and of bermudagrass ('CD-6.69', 'Arizona Common', and 'Guymon'), and 2 of the bahiagrass ('Pensacola' and 'Tifton 9').

Root exudates were obtained by using a modification of the technique described by Papadakis (1977). One hundred seeds of each *sericea lespedeza* cultivar were planted in separate containers (65-cm long × 50-cm wide × 35-cm deep) filled with coarse perlite. The bottom and both side panels of the containers were perforated with holes 0.4 cm in diameter. Each container was placed inside a separate tub (100-cm long × 60-cm wide × 51-cm deep) filled to a height of 35 cm with full strength Hoagland No. 2 nutrient solution (Hoagland and Arnon 1950) which was vigorously aerated. The containers were suspended 17.5 cm from the bottom of the tubs. Thus, the nutrient solution could wet the perlite, and root exudates from the plants in the containers could diffuse into the nutrient solution in the tub. The space between the container and the tubs was covered with black plastic to reduce water evaporation from the nutrient solution. An additional container filled with perlite but not planted was immersed in a tub with nutrient solution and used as a control. The pH and electrolytical conductivity were determined for the nutrient solution of each tub in all experiments once a week.

Thirty days after planting the *sericea lespedeza* cultivars, 2 experiments for each of the 3 grass species were started. In the first experiment, 28 seeds of each cultivar of tall fescue, bermudagrass, and bahiagrass were germinated in coarse perlite (Horticultural Products, W.R. Grace & Co., Cambridge, Mass.)¹ placed in separate boxes (27 length × 20 width × 6 depth cm). In the second experiment, 10 seeds of each grass cultivar were planted in 3,399-cm³ pots (17 cm in diameter) filled with potting soil [13% peatmoss,

57% Bassfield loamy fine sand soil (coarse-loamy, siliceous, thermic, Typic Hapludults), and 30% sand]. This potting soil (pH = 5.6) contained 1.9% organic matter, 1.4 g total N kg⁻¹, and 72 g P kg⁻¹. Exchangeable cations were 3.8, 1.2, and 0.4 cmol kg⁻¹ of Ca²⁺, Mg²⁺, and K⁺, respectively. The plants in the pots were thinned to 5 per pot 20 days after emergence.

Treatments were imposed by watering the plants with nutrient solution taken from the tubs where each of the 3 *sericea lespedeza* cultivars were growing, as well as nutrient solution from the control (no plants). Each container or pot was watered with 100 ml of the nutrient solutions whenever needed to maintain adequate soil moisture. The pots were leached with tap water every 15 days to avoid salt accumulation in the soil.

Percentage germination and radicle and coleoptile length were measured 7 days after planting in perlite. In soil, the plants were allowed to grow for 50 days. At the end of this period, shoots were cut at soil level, oven dried at 65° C for 72 hours and weighed.

Within each species, data were analyzed as a factorial experiment in a split plot design where cultivars were the main plots and treatments (*sericea lespedeza* root exudates) were the subplots. There were 6 replications with 1 container or pot per treatment per replication. Comparison between treatment means were done according to the least significant test (Gomez and Gomez 1984).

Results and Discussion

Germination of tall fescue and bahiagrass grown in perlite was not affected by root exudates (Table 1). Germination of bermudagrass was reduced from 7 to 12% by root exudates compared to

Table 1. Effect of *sericea lespedeza* root exudates on percentage seed germination of tall fescue, bermudagrass, and bahiagrass grown in perlite, averaged over cultivars.

Exudate source	Tall fescue	Bermudagrass	Bahiagrass
	----- (%) -----		
Control	76	93	82
Serala	72	86	80
AU Lotan	71	85	79
AU Donnelly	71	82	78
LSD(0.05)	ns	5	ns

the control (Table 1). The latter results agree with the reduced germination measured in beet (*Beta vulgaris* L.) and okra (*Abelmoschus esculentus* L.) when exposed to root exudates from several crops and weeds (Pope et al. 1985a).

Radicle length of bermudagrass and bahiagrass was reduced by root exudates from *sericea lespedeza* (Table 2). Similar effects of crop root exudates on the radicle elongation of other plants have been reported by Pope et al. (1985a) and Kalburtzi et al. (1989). The cultivar-treatment interaction was significant (P = 0.01) for

Table 2. Effect of *sericea lespedeza* root exudates on radicle length of tall fescue cultivars and bermudagrass and bahiagrass, averaged across cultivars.

Exudate source	Tall Fescue				
	AU Triumph	KY-31 endophyte infected	KY-31 endophyte free	Bermudagrass	Bahiagrass
	----- (cm) -----				
Control	2.9	3.1	2.8	5.5	2.8
Serala	2.9	2.5	1.9	3.6	2.1
AU Lotan	2.5	2.4	2.3	3.6	2.0
AU Donnelly	2.7	2.7	2.1	3.6	2.1
LSD (0.05)	ns	0.3	0.3	0.3	0.2

¹Names of products are included for the benefit of the reader and do not imply endorsement or preferential treatment by the Alabama Agricultural Experiment Station, Auburn University.

radicle length of tall fescue. AU Triumph was not affected by the root exudates whereas both KY-31 had a shorter radicle. Radicle length of endophyte-infected KY-31 was equally reduced by all the root exudates, whereas endophyte-free KY-31 was reduced more by exudates from Serala than from the other sericea lespedeza cultivars. Radicle length was reduced 35% in bermudagrass and 25–28% in bahiagrass (Table 2).

Coleoptile length of all grass species was reduced by root exudates of sericea lespedeza (Table 3). Wheat and favabean root

Table 3. Effect of sericea lespedeza root exudates on coleoptile length of tall fescue, averaged across cultivars, bermudagrass, and bahiagrass cultivars.

Exudate source	Tall fescue	Bermudagrass			Bahiagrass	
		CD-6.69	Arizona common	Guymon	Pensacola	Tifton 9
Control	5.0	7.4	9.3	9.0	4.5	4.9
Serala	4.6	6.4	7.3	7.1	3.6	3.8
AU Lotan	4.8	6.5	7.9	6.6	3.5	3.9
AU Donnelly	4.6	6.8	7.8	6.2	3.5	4.5
LSD (0.05)	0.3	0.6	0.8	0.6	0.5	0.2

exudates had similar effects on the growth of each other (Kalburtzi et al. 1989). Coleoptile length of tall fescue was reduced 8%. Cultivar-treatment interaction was significant ($P < 0.01$) for coleoptile length of bermudagrass. Coleoptile length of CD-6.69 was reduced by exudates of Serala and AU Lotan, but it was not affected by exudates of AU Donnelly. Coleoptile length of Arizona Common was equally affected by the root exudates of the sericea lespedeza cultivars whereas that of Guymon was more affected by AU Lotan and AU Donnelly than by Serala (Table 3).

Cultivar-treatment interaction was significant ($P = 0.03$) for coleoptile length of bahiagrass. Coleoptile length of Pensacola was equally affected by all the root exudates whereas that of Tifton 9 was reduced more by exudates from Serala and AU Lotan than from AU Donnelly (Table 3).

The experiments conducted with soil indicated that percentage of emergence of tall fescue, bermudagrass, and bahiagrass were reduced 5.4, 2.0, and 4.3% by the root exudates, respectively; however, these reductions were not significant ($P > 0.05$). These results correspond with our previous experiment on the effect of root exudates on percentage of germination of tall fescue and bahiagrass in perlite, but differ from those on bermudagrass (Table 1).

Aboveground biomass of tall fescue and bahiagrass was reduced by root exudates, whereas biomass of bermudagrass was not affected (Table 4). Similar effects of crop root exudates on biomass of other plants have been reported by Pope et al. (1985b) and Kalburtzi et al. (1989).

Cultivar-treatment interaction was significant ($P = 0.04$) for aboveground biomass of tall fescue. AU Triumph was not affected by any of the root exudates. Aboveground biomass of KY-31 endophyte-infected was reduced between 11 and 16% by all root exudates and aboveground biomass of KY-31 endophyte-free was reduced (19–22%) by root exudates of AU Lotan and AU Donnelly, but was not affected by Serala root exudates (Table 4).

Bahiagrass cultivars also responded differently to sericea lespedeza root exudates. Aboveground biomass of Pensacola plants was reduced by all root exudates, however, exudates from AU Donnelly decreased biomass of Pensacola plants 40% whereas Serala and AU Lotan reduced its biomass 13–17%. Plants of Tifton 9 had 21 to 23% less biomass when exposed to root exudates from AU Lotan and AU Donnelly, but were not affected by Serala (Table 4).

Table 4. Effect of sericea lespedeza root exudates on above-ground biomass of tall fescue, bermudagrass averaged across cultivars, and bahiagrass.

Exudate source	Tall fescue					
	AU Triumph	KY-31 endophyte infected	KY-31 endophyte free	Bermudagrass	Bahiagrass	
					Pensacola	Tifton 9
Control	4.1	3.8	3.2	10.8	5.2	5.3
Serala	3.9	3.4	3.2	10.3	4.5	5.2
AU Lotan	4.1	3.2	2.6	10.8	4.3	4.2
AU Donnelly	3.6	3.4	2.5	10.7	3.1	4.1
LSD (0.05)	ns	0.4	0.3	ns	0.6	0.6

The overall response of tall fescue and bahiagrass aboveground biomass is similar to the response of their radicle and coleoptile length, respectively, whereas the response of bermudagrass radicle and coleoptile length were not representative of the effects of sericea lespedeza root exudates on the biomass of this species.

The pH of the solution containing sericea lespedeza root exudates ranged from 5.4 to 6.5 for the experiments with tall fescue, from 5.4 to 6.4 for the experiments with bermudagrass, and from 6.0 to 6.8 for the experiments with bahiagrass. Electrolytical conductivity of the solution containing root exudates for the experiments with tall fescue, bermudagrass, and bahiagrass ranged from 0.12, 0.10, and 0.14 to 0.21, 0.23, and 0.26 Sm^{-1} , respectively. No relationship was observed between pH or electrolytical conductivity and seedling emergence or growth response. These findings agree with Tang and Young (1982), who found that pH and concentration of salts were not causative factors in the observed inhibition of lettuce (*Lactuca sativa* L.) radicle length by bigalta limpo-grass [*Hemarthia altissima* (Poir.) Stapf. and Hubb] root exudates.

Summary

Root exudates from sericea lespedeza had no effect on germination and emergence of bahiagrass but reduced its radicle and coleoptile length and aboveground biomass. Germination, radicle, and coleoptile length, and emergence of bermudagrass decreased when exposed to the root exudates; however, aboveground biomass was not affected. Tall fescue cultivars differed in their response to the root exudates of sericea lespedeza. Establishment of tall fescue in mixture with sericea lespedeza is not likely to be affected; however, the growth of some cultivars is likely to be decreased. Therefore, bahiagrass and some tall fescue cultivars contribution to total yield will be reduced. Conversely, establishment of bermudagrass is likely to be affected, but, once established, its growth is expected to be similar to when grown alone.

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Effects of sericea lespedeza residues on cool-season grasses

K.L. KALBURTJI AND J.A. MOSJIDIS

Authors are lecturer, Lab. of Ecology, Faculty of Agriculture, Aristotelian University of Thessaloniki, 540 06 Thessaloniki, Greece; and associate professor, Dept. Agronomy and Soils and Alabama Agr. Exp. Sta., Auburn University, Auburn, Ala. 36849-5412.

Abstract

Incorporation of crop residues into the soil prior to planting has been shown to reduce the growth of subsequent crops. Information is limited on the allelopathic effect of sericea lespedeza [*Lepedeza cuneata* (Dum. Cours) G. Don.] residues on multiple cropping and rotational systems. Experiments were conducted to determine: (1) if sericea lespedeza residues affected seed germination and plant growth of rye (*Secale cereale* L.), ryegrass (*Lolium multiflorum* Lam.), and tall fescue (*Festuca arundinacea* Schreb.); (2) if cultivars of these species varied in response to phytotoxins from sericea lespedeza residues; and (3) if N fertilization nullified the effects of residues. Germination experiments were conducted by using water extracts from low- or high-tannin sericea lespedeza residues, distilled water (control), and topsoil and subsoil obtained from areas in which low- or high-tannin sericea lespedeza plants had grown for 4 years. Greenhouse experiments showed that germination, emergence, seedling growth, above-ground biomass, and N concentration of rye and tall fescue were reduced by sericea lespedeza residues. Although ryegrass germination was not affected by the residues, biomass and N concentration were reduced. Rye and tall fescue germination were not affected by soils where sericea lespedeza previously had grown, but ryegrass germination and seedling growth of all 3 species were reduced. Immobilized N was the main factor limiting plant growth. Fertilizer-N more than compensated for the negative effects of the residues on all species. Establishment

of rye and tall fescue in a sericea lespedeza field is likely to require higher seeding rates than normal to compensate for reduced germination, whereas ryegrass would not be affected. Fertilizer-N may be needed to enhance growth of grasses that otherwise would be curtailed by sericea lespedeza residues.

Key Words: allelopathy, legumes, plant litter, *Lepedeza cuneata*, rye, *Secale cereale*, ryegrass, *Lolium multiflorum*, tall fescue, *Festuca arundinacea*

Incorporation of crop residues into the soil has been shown to reduce growth of subsequent crops (Miller 1983, Hicks et al. 1989). This effect was associated with the release of phytotoxic substances from some crop residues (Rice 1984, Barnes et al. 1987). Guenzi and McCalla (1962) found that seed germination and seedling growth of corn (*Zea mays* L.) and sorghum [*Sorghum bicolor* (L.) Moench] were affected by water residue extracts of other crop species. Rye residues inhibited seed germination and growth of several crops and weeds (Barnes and Putnam 1986). Kalburtzi et al. (1989) reported allelopathy of wheat [*Triticum aestivum* (L.) Em. Tell] and favabean (*Vicia faba* L.) water extracts from their residues on seed germination and seedling growth.

Sericea lespedeza [*Lepedeza cuneata* (Dum. Cours) G. Don.] is a long-lived perennial used for forage production and soil conservation. Because sericea lespedeza is dormant during winter, it is recommended to overseed it with cool-season grasses to extend the productive season (Hoveland et al. 1990).

Information on allelopathic effect of sericea lespedeza residues in multiple cropping and rotational systems is limited. Langdale

and Giddens (1967) found that sericea lespedeza stem residues incorporated into the soil depressed corn growth. Logan et al. (1969) reported autoallelopathy in seed germination and seedling growth from a sericea lespedeza seedcoat inhibitor. Cope (1982), however, detected no allelopathy of sericea lespedeza seed leachates to germination and seedling growth of 7 forage species, or to sericea lespedeza itself. Kalburtji and Mosjidis (1992) reported that sericea lespedeza residues had a minor negative effect on above-ground biomass of bermudagrass [*Cynodon dactylon* (L.) Pers.] and bahiagrass (*Paspalum notatum* Flugge) in contrast to the positive effect of N fertilization.

The objectives of this study were to determine if sericea lespedeza residues affected seed germination and seedling growth of rye, ryegrass, and tall fescue; if variability existed in the degree of tolerance among cultivars of rye, ryegrass, and tall fescue to phytotoxic compounds present in sericea lespedeza residues; and if an interaction existed between soil incorporation of sericea lespedeza residues and nitrogen (N) fertilization that influences rye, ryegrass, and tall fescue emergence and establishment.

Materials and Methods

The effects of sericea lespedeza plant residues on seed germination, seedling development, and growth of rye, ryegrass, and tall fescue were examined in a series of laboratory and greenhouse experiments. Included were 4 cultivars each of rye ('Bonel', 'Forager', 'Winter Grazer 70', and 'Gurley's Grazer 2,000') and ryegrass ('Urbana', 'Penploid', 'Gulf', and 'Marshall') and 3 tall fescues ('AU Triumph', 'KY-31' 45% endophyte infected, and KY-31 endophyte-free). In December of 1989, sericea lespedeza residues and soil samples were obtained from nurseries of high- or low-tannin genotypes that were grown for 4 years in Tallahassee, Ala. High-tannin genotypes have between 270 and 304 g kg⁻¹ of tannin whereas low-tannin genotypes have between 139 and 228 g kg⁻¹ (Petersen et al. 1991). The nurseries were located on soil classified as Bassfield loamy fine sand (coarse-loamy, siliceous, thermic, Typic Hapludults).

Seed Germination

Two experiments were conducted on each of the 3 grass species. In the sericea lespedeza residue extract experiment, 20 seeds of each of the 4 cultivars of rye and ryegrass and of the 3 tall fescue cultivars were germinated in 3 treatments: 0, low-, and high-tannin residue extracts. The 0-tannin (control) treatment was distilled water. Low- and high-tannin treatments were water extracts from low- or high tannin sericea lespedeza residues. In the soil extract experiment, 20 seeds of the same 11 cultivars were germinated in distilled water (control) and water extracts from topsoil (0 to 10-cm depth) and subsoil (10 to 30-cm depth) obtained from soil in which low- or high-tannin sericea lespedeza plants had grown for 4 years.

Residue and soil extracts were obtained by grinding 50 g of residue or mixing the same amount of soil with 500 ml of distilled water in a blender for 10 min. The mixture was agitated for 2 hours, and filtered through Whatman No. 1 filter paper. Electrolytic

conductivity and pH were measured in each extract.

Seeds were germinated on Whatman No. 42 filter paper moistened with 5 ml extract or distilled water in petri dishes placed in an incubator in the dark at 22/15° C for 16/8 hours. Percentage seed germination and radicle and coleoptile lengths were recorded after 7 days incubation. Seeds were considered germinated if the radicle had protruded and through the seed coat.

Data were analyzed by species as a factorial experiment in a split plot design with 5 replications where main plots were grass cultivars and subplots were treatments. In the residue extract experiment, treatments were tannin levels and, in the soil extract, soil depths and tannin levels.

Seedling Emergence and Growth

Ten grass seeds of each cultivar were planted in 1,890-cm³ pots filled with potting soil (13% peatmoss, 57% fine sandy loam soil, and 30% sand, pH 5.5) in the greenhouse. Prior to planting sericea lespedeza residues (11% stems, 85% leaves, and 4% seeds) were thoroughly mixed with the soil before placing in the pots. The potting soil contained 1.7% organic matter, 1.4 g total N kg⁻¹, and 63 mg P kg⁻¹. Exchangeable cations were 3.4, 1.1, and 0.2 cmol kg⁻¹ for Ca²⁺, Mg²⁺, and K¹⁺, respectively. Mean day and night temperatures during the time that the experiments were conducted were 28 and 15.5° C, respectively.

Treatments were a factorial combination of 3 rates of sericea lespedeza residues (0, 6, and 12 g pot⁻¹), 2 rates of N (0 and 30 mg kg⁻¹ of soil) applied 4 times during the growth of the grasses, and 2 types of sericea lespedeza residues (low- and high-tannin content) applied to 3 or 4 cultivars depending on the species. The rates of residue are representative of the amounts found in fields with no sericea lespedeza, with sericea lespedeza grown for hay production (3,800 kg ha⁻¹), and with sericea lespedeza grown for soil conservation or biomass production (7,600 kg⁻¹) for 4 years and cut once at the end of each summer. These rates were determined by sampling sericea lespedeza fields near Tallahassee, Ala. The N source was 135 mg of ammonium nitrate (33% N) in 50 ml of water applied to each pot at the beginning of the experiment and every 15 days thereafter.

Seedling emergence was recorded 7 days after sowing. Fifteen days after sowing, the plants were thinned to 5 plants pot⁻¹. Plants were harvested 55 days after sown, dried at 65° C for 72 hours, and weighed. This material was ground to pass an 18-mesh sieve and analyzed for total N on a Leco N analyzer.

Within each species, data were analyzed as a factorial experiment in a split plot design where cultivars were the main plots and treatments (sericea lespedeza residue rates, N rates, and type of sericea lespedeza residue) were the subplots. There were 4 replications (pots) of each treatment. Comparison between treatment means were done according to the least significant test and single degree of freedom contrast (Gomez and Gomez 1984).

Results and Discussion

Seed Germination

Sericea lespedeza residue extracts did not affect either germina-

Table 1. Effects of low- and high-tannin sericea lespedeza residue extracts on rye, ryegrass, and tall fescue seed germination and seedling length, averaged across cultivars.

Treatment	Seed germination			Radicle length			Coleoptile length		
	Rye	Ryegrass	Tall fescue	Rye	Ryegrass	Tall fescue	Rye	Ryegrass	Tall fescue
	----- (%) -----			----- (cm) -----					
Control	85	96	79	6.1	5.4	3.2	3.2	3.5	2.4
Low tannin	82	94	77	5.5	5.5	1.6	2.8	3.6	2.3
High tannin	79	94	75	5.2	5.5	1.6	2.7	3.6	1.9
LSD (0.05)	3	ns	ns	0.2	ns	0.2	0.2	ns	0.3

Table 2. Means of seed germination and seedling growth after 7 days of rye, ryegrass, and tall fescue as affected by soil extracts, averaged across cultivars.

Treatment	Seed germination			Seedling growth					
	Rye	Ryegrass	Tall fescue	Rye	Ryegrass	Tall fescue	Rye	Ryegrass	Tall fescue
		(%)		(cm)					
Control	ns	99	ns	7.6	7.2	2.7	5.7	4.3	1.9
All extracts	ns	96	ns	6.5	5.7	2.4	4.4	3.4	1.7
Soil depth									
0-10 cm	— ¹	97	—	6.1	—	ns	3.9	—	ns
10-30 cm	—	95	—	6.8	—	ns	4.9	—	ns
Tannin level									
Low	—	96	—	6.6	—	2.5	4.6	—	1.7
High	—	95	—	6.3	—	2.4	3.9	—	1.6

All comparisons within soil depths and tannin levels are significant ($P = 0.05$).

¹No data.

tion or seedling growth of ryegrass when compared to the control (Table 1). They also had no effect on tall fescue seed germination, but reduced germination of rye and seedling growth of both rye and tall fescue. Similar effects have been observed on bermudagrass and bahiagrass by Kalburtji and Mosjidis (1992).

Extracts from high-tannin sericea lespedeza residues decreased rye seed germination by 7% compared to the control, whereas extracts from low-tannin residues had no effect (Table 1). Rye radicle length was reduced 10 and 15% by extracts from low- and high-tannin, respectively. There was a significant ($P < 0.01$) cultivar-extract interaction for radicle length in rye, but this accounted for only a small portion (3.8%) of the variability. Low-tannin residue extract reduced rye coleoptile length, averaged over cultivars, by 13%, whereas high-tannin extract diminished rye coleoptile length by 16%.

Tall fescue was more sensitive to residue extracts than rye (Table 1). Its seedlings had a 50% reduction in radicle length in the presence of high- or low-tannin residue extracts, whereas coleoptile length was reduced 21% but only in the presence of high-tannin residue extract. These results can be explained by the reported reduction of cell elongation or division due to phytotoxins released by plant material into the environment (Rice 1984).

Soil extracts had no effect on rye and tall fescue seed germination, whereas ryegrass germination was reduced slightly (Table 2). Rye and tall fescue had radicle and coleoptile lengths reduced by the soil extracts. Topsoil extracts reduced rye radicle and coleoptile length more than subsoil extracts.

Extracts from soil in which high-tannin plants previously had grown reduced ryegrass germination as well as rye and tall fescue radicle and coleoptile length more than from soils in which low-tannin plants had grown (Table 2).

There was a significant ($P < 0.01$) soil depth by tannin level interaction on ryegrass seedling growth. Extracts from subsoil samples where high-tannin plants had grown reduced radicle and coleoptile length more than those from where low-tannin plants had grown (Table 3). Topsoil extracts inhibited ryegrass radicle and coleoptile length more than subsoil, regardless of the tannin level.

Analyses of soil extracts indicate that soils where sericea lespedeza had grown for 4 years contained inhibitors of plant growth regardless of the soil depth or the tannin level in the residues. Overall, topsoil and high-tannin residues had a more pronounced effect than subsoil and low-tannin residues. This suggested that sericea lespedeza plants and their residues released phytotoxic compounds to the surrounding environment. Guenzi and McCalla (1966) reported that compounds produced during crop residue and soil organic matter decomposition reduced the yield of several crop species. Also, living plants can release substances that accumulate in the soil in amounts that are harmful to other species (Kil and Lee

Table 3. Effects of sericea lespedeza soil extracts on early seedling growth of ryegrass, averaged across cultivars.

Treatment	Radicle length	Coleoptile length
	(cm)	
Subsoil		
Low	6.8	4.0
High	6.0	3.6
Topsoil		
Low	ns	ns
High	ns	ns
Low-tannins		
0-10 cm	5.1	3.0
10-30 cm	6.8	4.0
High-tannins		
0-10 cm	5.1	3.0
10-30 cm	6.0	3.6

All comparisons within soil depths and tannin levels are significant ($P = 0.05$) unless otherwise indicated.

1987, Dornbos et al. 1990). This could explain why ryegrass was affected by soil extracts and not by the residue extracts.

Although the interaction between tall fescue cultivars and treatments was not significant in the experiments conducted, cultivar KY-31 endophyte infected had better germination (91 vs. 51%) than KY-31 endophyte free. The endophyte-infected cultivar had radicle (2.7 vs. 1.6 cm) and coleoptile (2.3 vs. 1.4 cm) length longer than endophyte free KY-31.

The pH of residues and soil extracts ranged from 5.2 to 5.6 and from 5.2 to 6.2, respectively. Electrolytic conductivities of the residue and soil extracts ranged from 0.24 to 0.42 and 0.23 to 0.31 dS m⁻¹, respectively. No relationship was observed between pH or electrolytic conductivity and seed germination or growth response. These findings agree with other reports (Yakle and Cruse 1984, Martin et al. 1990).

Seedling Emergence and Growth

Cultivar and amount of residue accounted for most of the variability in emergence of rye and tall fescue. Sericea lespedeza residues incorporated into the soil reduced rye and tall fescue emergence, but had no effect on ryegrass. When compared to the control (0 g pot⁻¹), rye and tall fescue emergence were reduced 5 and 6%, respectively, by 6 g of residue per pot and 8 and 12%, respectively, by 12 g of residue per pot (Table 4). Differences in emergence between the 2 levels of residues were not significant. These results are consistent with our germination experiments where rye germination and radicle and coleoptile length were reduced by extracts from sericea lespedeza residues. Similarly, radicle and coleoptile length of tall fescue were reduced by the residues. Nitrogen rate and

Table 4. Effects of sericea residues with low or high tannin content and N fertilization on rye, ryegrass, and tall fescue seedling emergence and biomass, averaged across cultivars.

Treatment	Emergence			Biomass		
	Rye	Rye-grass	Tall fescue	Rye	Rye-grass	Tall fescue
	----- (%) -----			----- (g pot ⁻¹) -----		
Nitrogen rate						
0 mg kg ⁻¹	93	99	89	0.71	0.83	0.95
30 mg kg ⁻¹	94	99	92	2.72	1.95	2.35
LSD (0.05)	ns	ns	ns	0.12	0.09	0.13
Tannin level						
Low	93	100	92	1.77	1.40	1.65
High	94	99	89	1.66	1.38	1.64
LSD (0.05)	ns	ns	ns	ns	ns	ns
Residue rate						
0 g pot ⁻¹	98	100	96	1.99	1.56	1.93
6 g pot ⁻¹	93	99	90	1.72	1.39	1.51
12 g pot ⁻¹	90	99	85	1.44	1.22	1.49
LSD (0.05)	4	ns	5	0.14	0.11	0.15

tannin level had no effect on emergence of any species.

Most interactions among cultivars, residue rates, tannin levels, and N rates were not significant for emergence. The rye cultivar-residue rate interaction was significant ($P < 0.01$) for emergence. Bonel and Winter Grazer 70 were the least affected cultivars, while Forager and Gurley's Grazer 2000 were the most affected (Fig. 1).

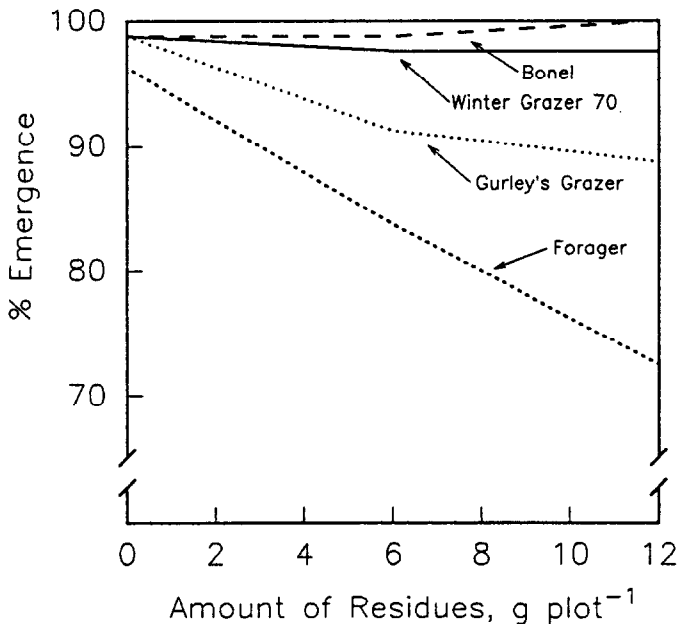


Fig. 1. Effect of sericea lespedeza residues on seedling emergence of 4 rye cultivars.

For all species studied, main effects of cultivars, N application, and amount of residue were significant for above-ground biomass. Nitrogen application accounted for most of the variability in dry weight. Nitrogen application increased biomass dry weight of rye, ryegrass, and tall fescue 74%, 57%, and 60%, respectively. Tannin level had no effect on growth (Table 4).

Above-ground biomass production of all species decreased in the presence of sericea lespedeza residues. Rye biomass dry weight was reduced 14% by the low and 28% by the high amount of residue, when compared to the control, whereas reductions in ryegrass biomass dry weight were 11% and 22% and in tall fescue

22% and 23%, respectively (Table 4). Ryegrass was the species least affected by sericea lespedeza residues. With the exception of tall fescue, we found that the greater the amount of residue the lower the above-ground plant dry weight. Sericea lespedeza residues had similar effects on bermudagrass and bahiagrass (Kalburtji and Mosjidis 1992).

Regardless of the species, most interactions among cultivars, residue rates, tannin levels, and N rates were not significant for above-ground biomass. The only significant interactions were N-residue rate for rye biomass and cultivar-N for dry weight of the species studied; however, these interactions accounted for only a small portion (0.8 to 1.7%) of the total variability.

As in the germination experiments, endophyte-infected tall fescue out-performed endophyte-free in greenhouse experiments. It had greater emergence (95 vs. 80%) and biomass (1.6 vs 1.3 g pot⁻¹) than endophyte-free tall fescue.

For all species studied, there were significant main effects of cultivars, N application, and amount of residue on shoot N concentration. Nitrogen application increased shoot N concentration 104%, 143%, and 43% in rye, ryegrass, and tall fescue, respectively (Table 5), and accounted for most of the variability observed.

Table 5. Effects of sericea lespedeza residues with low or high tannin content and N fertilization on content of N in shoots of rye, ryegrass, and tall fescue, averaged across cultivars.

Treatment	Shoot-N		
	Rye	Ryegrass	Tall fescue
	----- (g kg ⁻¹) -----		
Nitrogen rate			
0 mg kg ⁻¹	21.7	21.4	17.7
30 mg kg ⁻¹	44.2	51.9	25.3
LSD (0.05)	0.9	1.1	0.9
Tannin level			
Low	32.8	36.9	21.4
High	33.1	36.5	21.6
LSD (0.05)	ns	ns	ns
Residue rate			
0 g pot ⁻¹	34.7	39.5	23.9
6 g pot ⁻¹	32.7	36.1	21.2
12 g pot ⁻¹	31.5	34.4	19.4
LSD (0.05)	1.2	1.3	1.1

Shoot nitrogen concentration in all species was reduced as the amount of sericea lespedeza residue incorporated in the soil increased (Table 5). When compared to the control the reduction in N concentration caused by the low level of residue applied to the pots was 6, 9, and 11% for rye, ryegrass, and tall fescue, respectively. The high residue rate reduced N concentration 9, 13, and 19% for rye, ryegrass, and tall fescue, respectively. Tannin level had no effect on shoot N concentration. Although the interactions N-residue rate in rye and ryegrass, cultivar-residue rate in tall fescue, and cultivar- N-tannin level in ryegrass were significant, they accounted for only a small portion (0.3 to 2.6%) of the variability in N content.

Results reported in this paper agree with those of Kalburtji and Mosjidis (1992) in warm-season forage grasses and Langdale and Giddens (1967) who observed that incorporation of different rates of sericea lespedeza stem residue into the soil reduced corn growth. Langdale and Giddens (1967) related this response to the release of phenolic compounds from sericea lespedeza residue.

In conclusion, reductions in seed germination of rye and seedling growth of rye and tall fescue by extracts from sericea lespedeza residues; reductions in ryegrass germination and in seedling growth of the 3 grass species by extracts from soils where sericea lespedeza had grown for 4 years; and reductions in emergence,

above-ground biomass, and N concentration of rye and tall fescue by incorporation of sericea lespedeza residues in the soil indicate that establishment of rye and tall fescue in a sericea lespedeza field is likely to require higher seeding rates than normal to compensate for reduced emergence. Although ryegrass emergence was not reduced by the soil incorporation of the residues, its above-ground biomass and N concentration were. Immobilization of N appeared to be the main factor limiting plant growth and N fertilization more than compensated for the negative effects of the residues on all species. Hence, N fertilization is needed to enhance growth of the 3 grasses that otherwise would be curtailed by sericea lespedeza residues.

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Influence of litter on herbage production in the mixed prairie

WALTER D. WILLMS, SEAN M. MCGINN, AND JOHAN F. DORMAAR

Authors are range ecologist, meteorologist, and soil scientist, respectively, Agriculture Canada Research Station, Lethbridge, Alberta, Canada T1J 4B1.

Abstract

Litter (dead plant material) increases production in xeric environments but the nature of this effect is uncertain. The purpose of this study was to determine the relationship between litter quantity and herbage production over a 4-year period as well as to determine the effect of repeated removal of litter on production. The study was made in a *Stipa-Bouteloua-Agropyron* faciation of the Mixed Prairie association, near Lethbridge, Alberta, Canada. Litter quantity was altered by mechanical removal before spring growth and the residue separated into coarse and fine components. In Experiment 1, the effect of litter on herbage production was tested by removing litter at 0, medium, and high levels that resulted in an average residue of coarse litter of 1,171, 787, and 377 kg ha⁻¹. Coarse litter was related to an increase in herbage production ($P < 0.05$) in 3 of the 4 years studied. The effects of litter were related to the growing conditions of each year. The linear regression coefficients describing the response (herbage production related to litter) ranged from 0.114 to 0.802 with the smallest effect under either very dry or very wet conditions. In Experiment 2, litter was removed at high levels in either 0, 1, 2, or 3 successive years. These treatments resulted in an average residue of coarse litter of 1,300, 164, 149, and 188 kg ha⁻¹. Herbage production was not affected by removing litter for more than 1 year but plant height, tiller weight, and herbage yield of some plant species were.

Key Words: yield, *Agropyron smithii*, *Stipa comata*, *Bouteloua gracilis*, *Stipa viridula*, *Koeleria cristata*, *Carex* spp., soil degree-days

The litter (dead plant material) component of native grasslands affects the structure and function of the plant community through its impact on the chemical and physical environment (Facelli and Pickett 1991). Litter also acts as a physical barrier to heat and water flow at the soil surface, altering the micro-environment of the plant and soil (Weaver and Rowland 1952). Litter conserves soil moisture by reducing evaporation from the soil but reduces input from rainfall by intercepting water equivalent to about twice the weight of litter (Naeth et al. 1991). Frequent litter removal stimulates production in the mesic tallgrass prairie (Weaver and Rowland 1952) but impairs production on the xeric mixed prairie (Willms et al. 1986).

Litter reduction has serious implications for grazing management since it is independent of range condition (i.e., successional stage). Range in good condition likely has more litter and the effect of its removal will be more dramatic. Since litter reduction is generally an inherent aspect of grazing, a better understanding of the relationship between litter and production is imperative. Therefore, a study was made to define the relationship between litter quantity and herbage production as well as the effects of repeated annual litter removal on productivity. To help in interpretation of these results, we also studied the effect of litter removal on soil temperature and moisture and herbage species composition.

Materials and Methods

Site Description

The study area was located at the Agriculture Canada, Animal Diseases Research Institute, near Lethbridge, Alberta. The soils are Orthic Dark-Brown Chernozems (Typic Haploboroll) and with a loamy texture. The species were characteristic of the *Stipa-Bouteloua-Agropyron* faciation of the Mixed Prairie (Coupland 1961). However, porcupine grass (*Stipa spartea* var. *curtiseta* Hitchc.) is replaced by green needle grass (*S. viridula* Trin.) as an associated species (Table 1). The climate is continental with average daily temperatures of -9.0 and 18.1° C in January and July, respectively. Average annual precipitation is 404 mm with 32% occurring in May and June (Grace and Hobbs 1986). Average pan (Class A) evaporation during the summer months is at least double, and often triple, the average precipitation while average annual wind velocity is 20.4 km hr⁻¹ (Grace and Hobbs 1986).

Four of 5 sites selected for study had been grazed by cattle until 1985 when an enclosure (0.5 ha) was constructed at each site. The enclosure at the fifth site was constructed before 1975. The species composition among sites was similar with several exceptions (Table 1). Range condition, defined in terms of the species composition relative to that of a stable climax community (Wroe et al. 1988), was above 80% in sites B to E but only 67% in site A. Site A had more June grass (*Koeleria cristata* (L.) Pers.) and pasture sage (*Artemisia frigida* Willd.) but less wheatgrass (*Agropyron* spp.) and green needle grass. Site E, which had the longest period of protection from grazing, had considerably less blue grama (*Bouteloua gracilis* (H.B.K.) Lag.) than the others (Table 1).

Experimental Procedure

The effect of litter removal was examined in 2 experiments over a 4-year period from 1987 to 1990. Experiment 1 was designed to estimate the relationship between litter and herbage production. Experiment 2 was designed to estimate the effect of repeated annual litter removal on production and species composition. Each experiment was repeated on 5 sites (A-E) within enclosures. The sites were distributed over an area of 6 km² and spaced about 1 km apart.

Experiment 1

Residual litter treatments at each site were established in a 3 × 3 Latin square design representing 3 levels of litter removal in 2 × 2-m quadrats. Litter was removed at 0, medium, or high levels using a rotary mower set at either 7 or 3-cm cutting height for the medium and high levels, respectively, and raking cut herbage without disturbing the soil surface. Neither cutting height disturbed the crown of plants. Litter was removed before the appearance of new leaves in late winter or early spring. The treatments were repeated on the same plots in each year from 1987 to 1990. Plant material was sampled on a different 0.25-m² subplot in each year after the growing season in late August by cutting with electric clippers at the soil surface and removing all herbage and pasture sage. The entire herbage sample, or a subsample, was hand-separated into components of current production, coarse and fine litter, and

Table 1. Composition (% basal area¹) of major species and range condition within study enclosures on 5 sites.

	Site				
	A	B	C	D	E

	----- (%) -----				
Northern wheatgrass (<i>Agropyron dasystachyum</i>)	1.3	6.6	1.9	4.0	3.7
Western wheatgrass (<i>A. smithii</i>)	5.2	9.1	10.7	11.7	17.6
Blue grama (<i>Bouteloua gracilis</i>)	22.0	22.0	21.4	22.2	1.7
June grass (<i>Koeleria cristata</i>)	15.8	5.8	11.3	7.1	5.1
Needle-and-thread (<i>Stipa comata</i>)	24.6	27.4	20.1	16.8	21.6
Green needle grass (<i>Stipa viridula</i>)	2.8	4.2	12.3	12.8	2.7
Sedges (<i>Carex</i> spp.)	6.2	16.6	10.0	17.1	27.0
Pasture sage (<i>Artemisia frigida</i>)	12.1	2.9	5.5	5.0	10.5
Winter fat (<i>Eurotia lanatum</i>)	0.5	0	0.6	0	3.4
Moss phlox (<i>Phlox hoodii</i>)	3.1	3.3	1.3	1.0	0
Scarlet mallow (<i>Sphaeralcea coccinea</i>)	2.8	0	0.6	0.7	1.7
Wild vetch (<i>Vicia americana</i>)	0.8	0.4	0.3	0	0.3

Range condition	67	86	82	86	89

¹Species composition, as a percent of basal area, was estimated by sampling 3,200 points using a 32-pin frame along a transect; only "hits" on live vegetation below 2-cm height were counted.

pasture sage and oven-dried at 70° C. Coarse litter, consisting of standing as well as fallen litter, was separated from fine litter using a 2-mm mesh screen. The fine litter component was ashed to account for mineral soil.

Soil temperatures were recorded at a single site using a data logger (Campbell Scientific, CR21X, Logan, Utah) fitted with thermocouples. Five thermocouples, connected in parallel 15 cm apart, were used to spatially average soil temperatures at 5 cm depth on 2 replications of each treatment. Measurements were begun in early April and continued throughout the growing season. Air temperatures at 1.5 m above ground were taken at 1-minute intervals and their averages output every hour. Estimates of soil moisture (0 to 10 cm-depth) were made gravimetrically on all plots at intermittent times before 1990 and using time domain reflectometry (Soil Moisture Equipment Corp., Trase 6050 XI, Santa Barbara, Calif.) at bi-weekly intervals in 1990. Soil moisture was not sampled during or immediately after a significant precipitation event.

Experiment 2

At each of the 5 sites, 4 treatments representing years of repeated annual litter removal (0, 1, 2, and 3) and 4 replications were arranged in a 4 × 4 Latin square design with 2 × 2-m quadrats. Litter was removed at the same time and in a similar manner to the high removal treatment in Experiment 1. Litter was removed in 1988, 1989, and 1990 on the 3, 2, and 1 repeated annual treatment, respectively. Herbage was sampled in August, 1990, by sampling tiller density, plant height (to the tip of extended leaves), and weight of dry matter for each grass species in 5 subplots (100 cm²) randomly located within a 0.5 × 1.0-m quadrat and harvesting the remainder of the herbage in a bulk sample. The bulk sample was separated into herbage components as in Experiment 1. Tiller weight was estimated as the weight of dry matter divided by tiller number.

Statistical Analysis

The relationship between litter and production (Experiment 1) was determined with regression analysis for each year, by analyzing site as a fixed factor and the quantity of fine and coarse litter as covariates; and calculating the solution for the covariates. From this analysis, it was determined that the quantity of fine litter, whether alone or in combination with coarse litter, made no contribution to production. Fine litter was, therefore, dropped from the analyses.

The effects of repeated litter removal on production and vegeta-

tion characteristics (Experiment 2) were evaluated with analysis of variance for a Latin square design with multiple sites (Steel and Torrie 1980). Specific treatment means were compared using single degree of freedom contrasts. All measurements made from the subplots in Experiment 2 were transformed either by the logarithmic scale for weight data or square-root scale for tiller density in order to remove dependency between means and variances (Steel and Torrie 1980). Standard error of means for data transformed by the logarithmic scale were back-transformed using the Delta method (Rao 1973). Significant ($P < 0.05$) site × treatment interactions were evaluated by examining the treatment effect on each site. The effect of residual litter on soil moisture (Experiment 1) was analyzed for each sampling date with analysis of variance as in Experiment 2. Soil temperature at 5-cm was used to determine soil degree-days (SDD) for a 5° C base. Soil degree days were related to litter quantity for each year using regression analysis.

Results

Experiment 1

Precipitation over the growing season was above average in 1987 and 1989 and below average in 1988 and 1990 (Table 2). Only 59% of average precipitation was recorded in 1988 with the greatest amount in August; that year also had the greatest pan evaporation. Although 1990 precipitation was below average, most rainfall occurred in spring when the plants' water demands are greatest.

Table 2. Precipitation and pan evaporation over a 4-year period at Lethbridge.

	Jan-Mar	Apr	May	Jun	Jul	Aug	Apr-Aug
Precipitation	----- (mm) -----						
1987	61	21	15	58	93	63	250
1988	34	0	22	45	12	63	142
1989	88	29	53	51	42	78	253
1990	42	38	76	40	33	36	223
Long-term average	59	32	54	72	42	42	242
Pan evaporation							
1987	—	215	247	304	242	169	1177
1988	—	231	288	315	309	238	1381
1989	—	142	233	252	266	200	1093
1990	—	151	169	247	235	238	1040
Long-term average	—	152	208	248	262	220	1090

Herbage production was lowest in 1988 and highest in 1990 (Table 3). Sites A and B produced about half as much forage as site E. The proportion of coarse litter in the high and medium treatments averaged 32 and 67% of the control (Table 3), respectively, but varied among years and sites. The amount of fine litter was not affected by the treatments.

Table 3. Herbage production and coarse litter yields (mean \pm 1 SD) summarized by year, site, and litter removal treatment in Experiment 1.

Year	----- (kg ha ⁻¹) -----	
	Herbage production	Litter
(n = 15)		
1987	688 \pm 168	555 \pm 298
1988	200 \pm 126	912 \pm 654
1989	854 \pm 401	824 \pm 371
1990	1406 \pm 652	820 \pm 578
Site		
(n = 12)		
A	540 \pm 318	603 \pm 243
B	607 \pm 455	590 \pm 298
C	815 \pm 519	793 \pm 402
D	767 \pm 597	671 \pm 348
E	1230 \pm 760	1233 \pm 784
Litter removal treatment		
(n = 20)		
Control	959 \pm 698	1171 \pm 614
Medium	812 \pm 237	787 \pm 237
High	604 \pm 394	377 \pm 143

Herbage production was positively correlated ($P < 0.05$) with coarse litter in each year except 1989 (Table 4). Significant linear regression coefficients ranged from 0.114 in 1988 to 0.802 in 1990. Although production generally differed among sites, the coefficients were similar as indicated by no interaction ($P < 0.05$) between site and litter quantities (Table 4).

Table 4. Effect of site and coarse litter (g 0.25 m⁻²) on forage production over a 4-year period at 5 sites on a *Stipa-Bouteloua-Agrophyron* community.

Year	P>F			Litter	
	Site	Litter	Site \times litter	Intercept	Coefficient
1987	<0.001	<0.001	0.930	15.71 (1.70) ¹	0.288 (0.065)
1988	<0.001	<0.001	0.319	5.13 (0.77)	0.114 (0.015)
1989	<0.001	0.127	0.586	31.23 (4.45)	0.192 (0.123)
1990	0.56	<0.001	0.279	28.16 (5.85)	0.802 (0.128)

¹Standard error of estimate.

Soil moisture estimates in the 0 to 10 cm depth were similar among treatments at each sampling time except one in 1987 when soil moisture in the control, medium, and high treatments averaged 25, 23, and 22%, respectively. The lowest soil moisture measurements were made in spring, 1988, during a prolonged dry period when estimates in each treatment averaged 8%. In 1990, soil moisture was greater than 30% for most of May when water demand is normally high.

Soil degree day was inversely ($P < 0.006$) related to litter quantity (Table 5). However, the effect was not the same among years ($P = 0.015$) with coefficients ranging from -1.796 in 1987 to -0.114 in 1990. The effect of litter was only significant ($P < 0.05$) in 1987 and 1990 but $P < 0.10$ in 1988.

Table 5. Effect of coarse litter (kg ha⁻¹) on soil (5 cm) degree-days (based on 5° C cumulated from 1 April to 9 July) in an analysis for all years combined as well as by year on a single site on a *Stipa-Bouteloua-Agrophyron* community.

Year	Effects (P>F)		Litter	
	Litter	Year \times litter	Intercept	Coefficient
0.005	0.006	0.015	1999 (166) ¹	-0.210 (0.053)
By Year				
1987	0.025		2714 (31)	-1.796 (0.071)
1988	0.079		2967 (88)	-0.348 (0.043)
1989	0.209		2134 (183)	-0.224 (0.076)
1990	0.014		1766 (7)	-0.114 (0.002)

¹SE of estimate.

Experiment 2

Removing litter reduced the production of herbage and pasture sage but removing litter for more than 1 year had no cumulative effect (Table 6). The effect of litter removal differed among sites only in magnitude rather than trend. At each site, yields on the control (0 litter removal) were greater ($P < 0.05$) than between each removal treatment but yields among removal treatments were similar ($P > 0.05$). Proportional yield reduction with litter removal ranged from 0.38 on site E to 0.72 on site D for current production, 0.76 on site C to 0.90 on site E for coarse litter, and 0.61 on site B to 0.82 on site D for pasture sage. The yield of fine litter was not affected by the litter removal treatment (Table 6).

Litter removal resulted in greater ($P < 0.05$) tiller density of grasses and sedges (*Carex* spp.) combined, but reduced tiller weights (Table 6). Tiller weights decreased with litter removal from 1 to 3 successive years.

Litter removal reduced plant height of sedges and all grass species (Table 7) but the effect of removing litter from more than 1 year was significant ($P < 0.05$) only in western wheatgrass (*A. smithii* Rydb.), blue grama, and sedge spp. Tiller density of western wheatgrass, green needle grass, blue grama, and sedge spp. were not affected by removing litter. Tiller density of needle-and-thread (*S. comata* Trin. + Rupr.) and June grass increased with number of years that litter was removed (Table 7). Tiller weights of all species, except green needle grass, were reduced by removing litter. Removing litter for more than 1 year had a cumulative effect on the tiller weights of needle-and-thread, blue grama, and sedge spp. The net effect of morphological changes was a significant ($P < 0.05$) reduction in weight only for western wheatgrass and sedge spp. (Table 7).

Discussion

The presence of litter had a significant positive effect on herbage production in 3 of 4 years of this study. Removing litter for more than 1 successive year had no effect on herbage yield but did influence plant height, tiller weight, and herbage yield of some plant species. The variable effects of litter among years appears to be related to the current growing conditions, with similar, small responses to removal in dry or wet conditions, as in 1988 and 1989, respectively, and a large response in more moderate moisture conditions, as in 1990 (Table 4).

Litter appears to increase herbage production by reducing evaporation and making more water available for plant growth. Therefore, litter might be expected to be more effective in promoting plant growth when soil water is limiting. This hypothesis is supported only by circumstantial evidence rather than by direct measurements of evaporation and transpiration. For example, the low effectiveness of litter in both 1988 and 1989 appeared related to insufficient water across all treatments in 1988, and sufficient water across all treatments in 1989. The xeric conditions in 1988 were

Table 6. Effect of successive annual litter removed on subsequent herbage components over 5 sites sampled either with macro-plots (0.5 m²) or sub-plots (500 cm²).

	Litter removal years					Factor effect		
	0	1	2	3	SEm	Site (S)	Litter removal (L)	S × L
Macro-plots								
Constituent	----- (g) -----					----- (P>F) -----		
Current production	2270 ^b	994 ^a	1049 ^a	956 ^a	67	<0.001	<0.001	<0.001
Coarse litter	1300 ^b	164 ^a	149 ^a	188 ^a	86	<0.001	<0.001	<0.001
Fine litter	343 ^a	258 ^a	313 ^a	201 ^a	62	0.001	0.420	0.271
Pasture sage (<i>Artemisia frigida</i>)	497 ^b	117 ^a	144 ^a	102 ^a	28	<0.001	<0.001	<0.001
Sub-plots								
Grass and Sedge								
Tiller density ² (No 500 cm ⁻²)	136 ^a	186 ^b	212 ^b	213 ^b	0.465 ⁴	0.008	<0.001	0.410
Tiller weight ¹ (mg)	40.8 ^c	26.3 ^b	21.1 ^a	20.8 ^a	0.030 ³	<0.001	<0.001	0.764

^{a-c}Means with the same letter within row do not differ ($P > 0.05$).

^{1,2}Back-transformed means from: ¹logarithmic and ²square-root transformations.

^{3,4}Standard errors of transformed means; to estimate standard errors of back-transformed means using the Delta method (Rao 1973) = ³SE of transformed means × back-transformed mean; ⁴SE of transformed means × 2 × √back-transformed mean.

Table 7. Species response to litter removal (means back-transformed; tiller densities from square root transformation and all others from logarithmic transformation) from 5 sites⁵.

	Litter removal (yrs)	Western wheatgrass	Needle-and-thread	Green needle grass	June grass	Blue grama	Sedge spp.
Height¹							
		----- (cm) -----					
	0	23.2 ^c	16.2 ^b	20.5 ^b	10.4 ^b	8.6 ^c	11.2 ^c
	1	16.5 ^b	10.1 ^a	17.1 ^a	7.0 ^a	6.6 ^b	8.4 ^b
	2	15.1 ^{ab}	9.2 ^a	17.9 ^a	6.8 ^a	5.5 ^{ab}	7.3 ^{ab}
	3	14.4 ^a	9.2 ^a	15.6 ^a	6.5 ^a	4.6 ^a	7.1 ^a
	SEm ³	0.016	0.024	0.017	0.021	0.020	0.016
Tiller density²							
		----- (number 500 cm ⁻²) -----					
	0	17.7 ^a	28.6 ^a	9.5 ^a	22.4 ^a	25.3 ^a	32.8 ^a
	1	20.0 ^a	43.4 ^{ab}	13.9 ^a	44.6 ^b	24.3 ^a	26.6 ^a
	2	13.7 ^a	49.0 ^{ab}	10.7 ^a	50.3 ^b	34.2 ^a	23.2 ^a
	3	15.9 ^a	67.4 ^b	13.9 ^a	45.7 ^b	27.3 ^a	31.1 ^a
	SEm ⁴	0.36	0.67	0.39	0.73	0.61	0.43
Tiller weight¹							
		----- (mg) -----					
	0	104 ^b	31 ^b	61 ^a	26 ^b	12 ^c	20 ^c
	1	62 ^a	22 ^{ab}	44 ^a	17 ^a	10 ^{bc}	16 ^b
	2	69 ^a	17 ^a	40 ^a	15 ^a	8 ^{ab}	14 ^{ab}
	3	66 ^a	17 ^a	43 ^a	17 ^a	6 ^a	12 ^a
	SEM ³	0.033	0.040	0.040	0.028	0.028	0.022
Weight¹							
		----- (g 500 cm ⁻²) -----					
	0	1.59 ^b	0.74 ^a	0.52 ^a	0.40 ^a	0.25 ^a	0.61 ^b
	1	1.16 ^{ab}	0.90 ^a	0.59 ^a	0.68 ^a	0.21 ^a	0.39 ^{ab}
	2	0.81 ^a	0.87 ^a	0.44 ^a	0.70 ^a	0.26 ^a	0.32 ^a
	3	0.82 ^a	1.02 ^a	0.57 ^a	0.67 ^a	0.17 ^a	0.38 ^a
	SEm ³	0.038	0.045	0.038	0.038	0.0176	0.022

^{a-c}Means with the same letter within subset of column do not differ ($P < 0.05$).

^{1,2}Back-transformed means from: ¹logarithmic and ²square-root transformations.

^{3,4}Standard errors of transformed means; to estimate standard errors of back-transformed means using the Delta method (Rao 1973) = ³SE of transformed means × back-transformed mean; ⁴SE of transformed means × 2 × √back-transformed mean.

⁵Site × treatment significant ($P < 0.05$) only for June grass (wt, till, tiller wt), western wheatgrass (ht), and sedges (wt).

attributed to low precipitation in winter and spring and a high evaporation potential during the growing season. Precipitation in 1989 was almost double that of the previous year with substantially lower pan evaporation (Table 2). Litter effectiveness was reduced when water was either not available for conservation or abundant water for growth made conservation irrelevant.

The effectiveness of litter was particularly pronounced in 1990 when precipitation was below average but the rainfall events were uniformly distributed over the growing season and each event produced substantial amounts of water. Litter intercepts rainfall and reduces the amount of water available for infiltration (Naeth et al. 1991), but it also reduces surface runoff and reduces evaporation between rainfall events.

The water conservation hypothesis was not supported by soil moisture estimates between litter removal treatments but was supported by soil heating as indicated by significant ($P < 0.05$) inverse relationships between litter quantity and soil degree days (Table 5). The soil degree days reflect evaporation potential and soil moisture and, therefore, provide another index of litter effectiveness. Since soil moisture was similar among treatments over most of the year, the soil degree day is chiefly a function of litter. The relationship between soil degree day and litter quantity supports the observation that litter was least effective in 1988 and 1989 and most effective in 1987 and 1990.

After year 1, repeated removal of litter did not affect any of the herbage components. We expected the quantity of fine litter to decline with repeated removal since litter inputs were stopped while decomposition continued. Lack of an effect may have been due to an incomplete removal of each year's production, since herbage produced in any year was harvested after the following winter during which shattering losses from standing herbage occurred. An alternate explanation is that decomposition was not substantial enough to produce a significant effect over 3 years.

Production was expected to decrease with repeated litter removal as reported in a previous study (Willms et al. 1986). In that study, conducted on a more xeric mixed prairie community, grass production declined by 25 to 56% following 1 to 3 years of litter removal while in the present study production was reduced by 56% regardless of the number of times litter was removed (Table 6). Some of the differences in response between the 2 studies may be due to the composition of the plant community, since species respond differently to repeated litter removal (Table 7).

The response of some species to repeated litter removal was not expected based on their response to summer grazing. Western wheatgrass, blue grama, and sedge spp. are all "increasers" (Wroe et al. 1988) but, in most cases, responded to litter removal with significantly ($P < 0.05$) reduced plant heights and tiller weight or yield (Table 7). Shorter plant heights of all species, as a result of litter removal (Table 7), may be the consequence of reduced water available for plant growth while greater tiller density in some species may be due to increased light intensity at the crown (Willms 1988).

Litter quantity may be as important to the productivity of the mixed prairie grasslands as is range condition. Although the production response to litter or range condition is highly variable and dependent on current moisture conditions, herbage production was reduced up to 60% with litter removal, which is comparable to a reduction of about 50% in yield (Unpublished data, Adams), and 68% in recommended stocking rate (Wroe et al. 1988), for range in poor condition.

The amount of residual litter is an index of grazing pressure which, over time, will affect range condition. Blue grama is associated with reduced range condition on the study site and is favored by the warmer and drier soil environment which is created when litter is removed (Weaver and Roland 1952) and infiltration reduced (Naeth et al. 1991). On the other hand, artificially increasing litter by adding straw reduced the cover of blue grama and increased needle-and-thread (Smoliak 1965), which is associated with better range condition.

The immediate effect of litter removal due to overgrazing can be overcome by reducing grazing pressure and allowing litter to accumulate. The amount of litter necessary for maximum production is impossible to define due to its variable annual effect and its linear effect on production. This study suggests that, in the arid mixed prairie, maximum production is achieved with maximum litter quantity. Therefore, grazing must be managed to conserve litter in order to stabilize livestock production and sustain range condition.

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Field stratification of antelope bitterbrush seeds

JAMES A. YOUNG, J. ROSS WIGHT, AND JAMES E. MOWBRAY

First author is range scientist, USDA-ARS, Landscape Ecology of Rangelands, 920 Valley Rd., Reno, Nev. 89512; second and third authors are range scientists, Northwest Watershed Research Center, 800 Park Blvd., Plaza IV, Suite 105, Boise, Ida. 83705.

Abstract

The germination ecology of antelope bitterbrush [*Purshia tridentata* (Pursh) Nutt.] seed has probably been investigated more than any other range shrub. Seeds of this valuable browse species are known to require moist prechilling before they will germinate. Our purpose was to investigate the nature of this dormancy breaking by placing packages (2 × 2-mm mesh screen) of seeds on the surface and buried in the seedbed at several locations in Idaho and Nevada and to recover the seeds monthly through the winter. The seeds were categorized based on their being: (a) capable of germinating; (b) dormant; or (c) dead at each recovery. The seedbeds of the 2 sites in Nevada, during 2 years of drought, were not sufficiently wet to bring large amounts of the antelope bitterbrush seeds out of dormancy. The seeds did not rot in the field, and being protected from predation, they remained dormant in the seedbed. The highest elevation site in Idaho had as high as 80% of the seeds lose dormancy. If seedbed microenvironmental conditions were satisfactory, the inherent seed dormancy was lost by midwinter. Snow cover, as it influences seedbed moisture and temperatures, apparently is an important factor in the prechilling of antelope bitterbrush seeds.

Key Words: browse regeneration, seed and seedbed ecology, microenvironment

Antelope bitterbrush [*Purshia tridentata* (Pursh) Nutt.] is one of the most important browse species on western rangelands in North America. Widely distributed in the more arid portions of the Sierra-Cascade and Rocky Mountains and the Intermountain area, antelope bitterbrush provides valuable browse for domestic and wild animals. Natural and artificial regeneration of this species, especially on winter ranges, is a major problem for range managers.

Hormay (1943) reported that seeds of antelope bitterbrush required a period of incubation under cool, moist conditions before they would germinate. This type of seed dormancy is known as a stratification requirement, from classical German forestry techniques required to break the dormancy. Modern seed technologists prefer the self-evident term prechilling requirement. Many economically important species of the rose family are known to have seed dormancy that requires moist prechilling for germination. There is a great deal of published information concerning the physiology of prechilling requirements, but little information concerning the field ecology of the natural process.

Since the discovery of the nature of dormancy of antelope bitterbrush seeds, a variety of chemical treatments have been offered to replace or modify the cool, moist stratification requirement. These include soaking the seeds in an aqueous solution of thiourea (Pearson 1957), or hydrogen peroxide (Everett and Meeuwig 1957), or enrichment of the germination substrate with gibberellic acid (McConnell 1960). Detailed laboratory experiments have

defined the temperature limits of the antelope bitterbrush requirement (0 to 5° C with 2° C optimum) (Young and Evans 1976).

Our purpose was to place seeds of antelope bitterbrush in field seedbeds at various geographic locations of the Intermountain area in the late fall and recover seeds periodically during winter and determine the germination characteristics of the seeds.

Materials and Methods

Seeds of antelope bitterbrush were obtained from commercial seed lots collected at the Boise Front, Ida. They were collected from the same stands and processed by the same commercial threshing and cleaning equipment. The experimental design consisted of 4 replications of 100 seeds each arranged in a randomized block design. Seeds were placed in the field in 10 × 10-cm packets made of galvanized screen with 2 × 2-mm openings. Packets were either placed on the soil surface or buried 2.5 cm deep in the surface soil. The natural surface soil at each location was used except at Reno, Nev., where greenhouse flats, 40 × 50 × 10 cm, were filled with surface soil from the Granite Peak, Nev., location. The flats were buried so their surface was the same level as the surrounding soil surface.

The packets of seeds were placed in the field in late October of 1987 and 1988. Packets were recovered monthly through 1 May of the following year. Packets were placed at 3 locations in the Reynolds Creek Watershed of the Northwest Watershed Research Center, located in the Owyhee Mountains, south of Boise, Ida. In Nevada, experimental locations were Reno and Granite Peak, located 50 km north of Reno (Tables 1 and 2).

The amount of snow cover on the seed packages in the field was ocularly estimated if discontinuous, and the snow depth measured. Soil frost was determined on plots without snow cover with frost tubes, and where snow depth made this impossible, with gypsum blocks buried at the soil surface. Frozen blocks produce high resistance.

Upon recovery, the seed packets were opened and the seeds classified as germinated if the radicle was emerged 2 mm. Ungerminated seeds were placed on germination paper in petri dishes and moistened with tap water. The seeds were incubated at 15° C for 2 weeks in dark incubators. Germinated seeds were counted weekly. At the end of the incubation period, seeds that were covered with fungal mycelium and were soft were considered dead. Seeds that remained firm and ungerminated were considered dormant.

Analysis of variance (ANOVA) was used on percentage germination with arc sin square root transformation after Hartley's F-max test of homogeneity of variance was performed to determine if it was appropriate.

Results and Discussion

In a very simple algorithm of what would be necessary to develop a model for the germination of seeds of antelope bitterbrush, the seeds are always in 1 or more of 3 categories: (a) capable

Table 1. Physical characteristics of sites where the field stratification was conducted in Nevada and Idaho.

Location	Soils			Mean annual precipitation (mm)
	Group	Surface texture	Elevation (mm)	
Reynolds Creek, Ida.				
Quonset	Xerollic Haplargids	gravelly loam	1195	230
Lower Sheep Creek	Pachic Argixerolls	silt loam	1660	340
Upper Sheep Creek	Pachic Cryoboroll	silt loam	1880	500
Reno, Nev.	Typic Haplargids ^a	sandy loam	1385	180
Granite Peak, Nev.	Typic Haplargids	sandy loam	1850	250

^aSoil collected at Granite Peak.

Table 2. Plant communities of the sites where the field stratification was conducted in Nevada and Idaho.

Location	Plant community	Natural antelope bitterbrush site
Reynolds Creek, Ida.		
Quonset	<i>Artemisia tridentata</i> ssp. <i>wyomingensis</i> / <i>Elytrigia spicata</i>	yes
Lower Sheep Creek	<i>Artemisia tridentata</i> ssp. <i>wyomingensis</i> / <i>Elytrigia spicata</i>	yes
Upper Sheep Creek	<i>Populus tremuloides</i> - <i>Artemisia tridentata</i> ssp. <i>vaseyana</i> / <i>Elytrigia spicata</i>	no
Reno, Nev.	No natural plant community	no
Granite Peak, Nev.	<i>Artemisia tridentata</i> ssp. <i>vaseyana</i> / <i>Stipa thurberiana</i>	yes

of germination if placed in a suitable environment; (b) dormant in any environment; (c) nonviable or dead (Table 3). Obviously the proportion of the seed populations in each of these categories changes over winter. The 3 seed parameters of germinable (capable of germinating), dormant, and dead appear very simple, but their interactions with year of seed production, site, and burial become complex.

Initial Seed Population

In this study we started with seed populations with 5 and 4% germination, and over 99% viability (as indicated on seed tag) for 1986 and 1987, respectively. Comparing the overall average results by recovery dates revealed no significant (P = 0.01) differences between the years for the 3 germination parameters (data not shown). As the data presentation develops it will be clear that this similarity in the overall averages between years is apparently a function of compensating variability rather than statistical precision.

In repeated experiments, the initial seed population never has the same physiological characteristics. Even in the most careful seed storage conditions, seeds from the same lot change over time. Kay et al. (1988) provides numerous examples of germination

declines, enhancement, and cyclic responses for seeds of native shrubs. There are so many environmental influences on seed production in native plant stands, germination responses for various parameters are seldom identical. Young and Evans (1989) provide detailed studies of this phenomena for seeds of basin big sagebrush (*Artemisia tridentata* ssp. *tridentata*) repeatedly collected from native stands and grown in reciprocal common gardens. After this study was completed, Susan Meyer (1989) demonstrated in an innovative study that incubation temperatures from maturity to the time of germination influenced the nature of cool-moist chilling requirements for seeds of antelope bitterbrush. Until they were placed in the field, the seeds in this study were stored in 1 lot, but once placed in the field variable temperatures dependent on the site came into play.

Seed Burial

Germination of seeds of antelope bitterbrush was significantly (P = 0.01) higher with seed burial versus on the surface of the seedbed at all recovery dates except December and March (Table 3). In December, the seeds did not have their prechilling requirements completely satisfied and March would be the optimum time for bitterbrush emergence in nature (Young and Evans 1981). The higher germination of the seeds recovered from the surface in the March recovery was due to the very high germination of seeds recovered from the surface of seedbeds at the Upper Sheep Creek site. Deep snow cover at this site apparently canceled the negative influence of the surface environment. The harshness of surface seedbeds in temperate desert environments has been well quantified both for extremes in fluctuating temperatures and moisture stress (Evans and Young 1970, 1972). Remember the seeds in this study were not naked on the soil surface, but were placed in screen packages that partially modified the harshness of the surface environment.

Lower Sheep Creek in the Reynolds Creek watershed is a natural site for antelope bitterbrush (Table 2). Detailed comparison of seed germination for surface and buried seeds illustrates how harsh the surface environment can be at this site (Fig. 1). Only in 1 monthly sample in the 2 years of the study did seeds placed in screen

Table 3. Changes over time in the characteristics of antelope bitterbrush seeds recovered from the field. Overall averages of surface and buried seeds at all sites and both years for monthly recoveries from December through May.^a

Seed characteristics	Initial seed	Recovery date					
		Dec.	Jan.	Feb.	March	April	May
----- % -----							
Germination							
Field	—	1 (7)	8 (6)	17 (5)	25 (5)	26 (8)	20 (5)
Laboratory	4 (2)	7 (6)	18 (3)	17 (3)	16 (8)	8 (4)	2 (5)
Total	4 (2)	8 (2)	26 (4)	34 (5)	41 (5)	34 (6)	22 (8)
Dormant	96 (6)	90 (9)	66 (11)	64 (9)	57 (10)	53 (12)	58 (14)
Dead	0 (3)	2 (5)	8 (10)	6 (9)	2 (10)	13 (6)	23 (5)

^aMeans given with confidence interval (0.01 level of probability) in parenthesis (Evans et al. 1982).

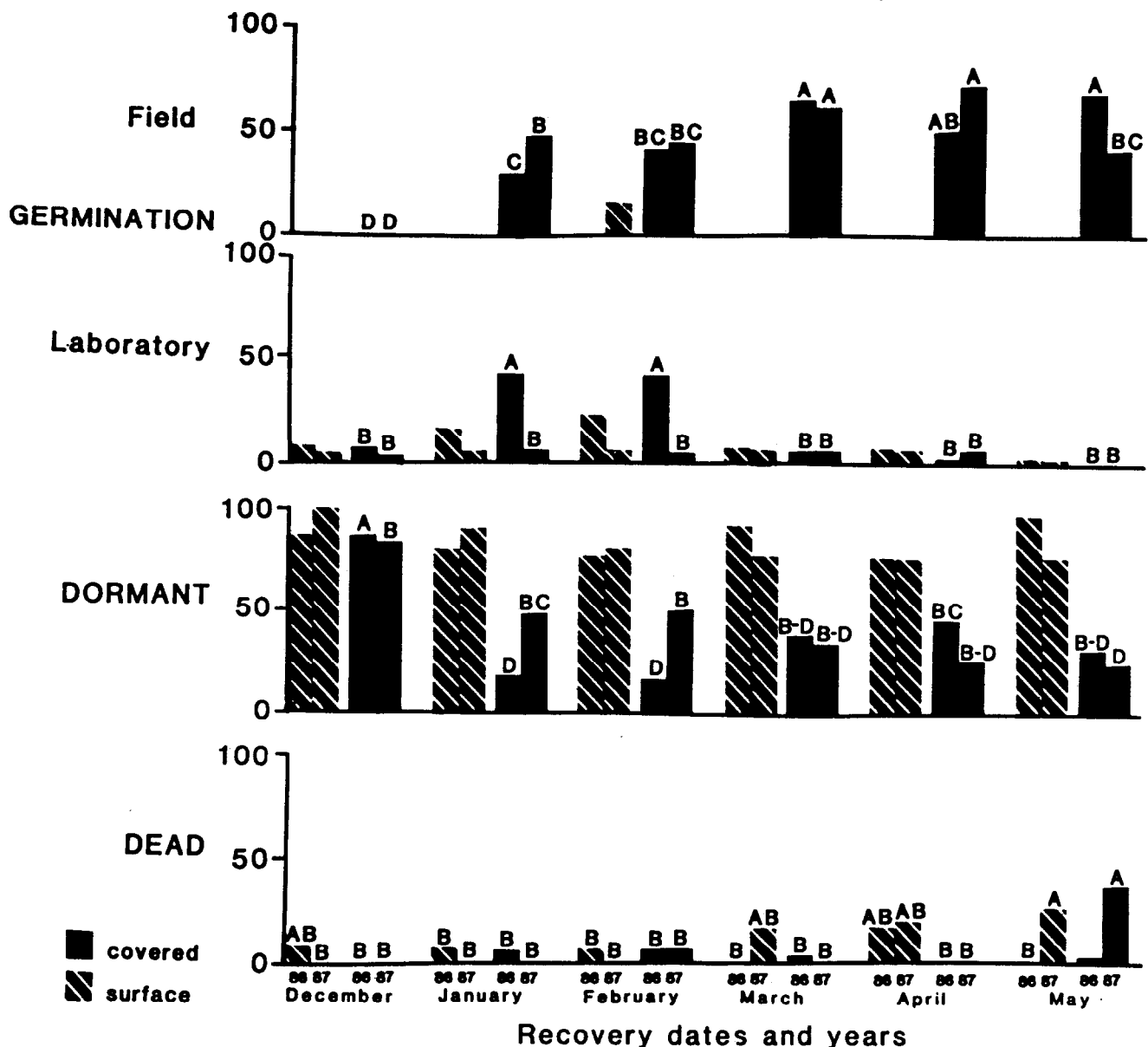


Fig. 1. Percentage field and laboratory germination, dormant and dead seeds of antelope bitterbrush at the Lower Sheep Creek locations of Reynolds Creek, Ida. Seeds recovered monthly from December to May 1986-87 and 1987-88. Seeds recovered from the surface of the soil or buried 2.5 cm deep. Columns within seed characteristics and burial types with the same letter are not significantly different at the 0.01 level of probability as determined by confidence intervals calculated from regression equations. No letters indicate no significant differences.

packages on the soil surface germinate in the field. Buried seeds had optimum field germination in the spring from March to May. Comparing field and laboratory germination over time at Lower Sheep Creek demonstrates that germination on the soil surface was not the primary problem for the seeds of antelope bitterbrush. The failure of the surface seeds to germinate was due to their unsatisfied cool-moist prechill requirements. Over the course of both winters, the seeds on the soil surface never had a significant ($P = 0.01$) reduction in the percentage of dormant seeds (Fig. 1). Buried seeds at Lower Sheep Creek had either germinated or were ready to germinate by January, at a rate of 70 and 50% for 1986-87 and 1987-88, respectively.

At both of the Nevada locations, the failure of the antelope bitterbrush seeds to meet cool-moist prechilling conditions on the soil surface was even more pronounced than at Lower Sheep Creek (data not shown). To obtain the proper perspective of these germination dynamics, remember that we are defining germination as the radicle emerged 2.0 mm. Germinated does not mean a leafy

antelope bitterbrush seedling waving in the breeze, but rather extremely slow root elongation under very cold conditions. Low seed mortality until late in the spring illustrates how slow the

Table 4. Comparison of seeds placed on surface or buried 2.5 cm deep. Average (%) of all sites and both years for the percentage of seeds of antelope bitterbrush that germinated in the field and laboratory for monthly recoveries from December through May.^a

Seed burial	Recovery date					
	Dec.	Jan.	Feb.	March	April	May
Surface	9	24 b	23 b	35	23 b	7 b
2.5 cm deep	18	35 a	40 a	45	41 a	37 a

^aMeans within recovery date are not significantly different when followed by the same letter as determined by Duncan's Multiple Range test. No letters indicate no significant differences.

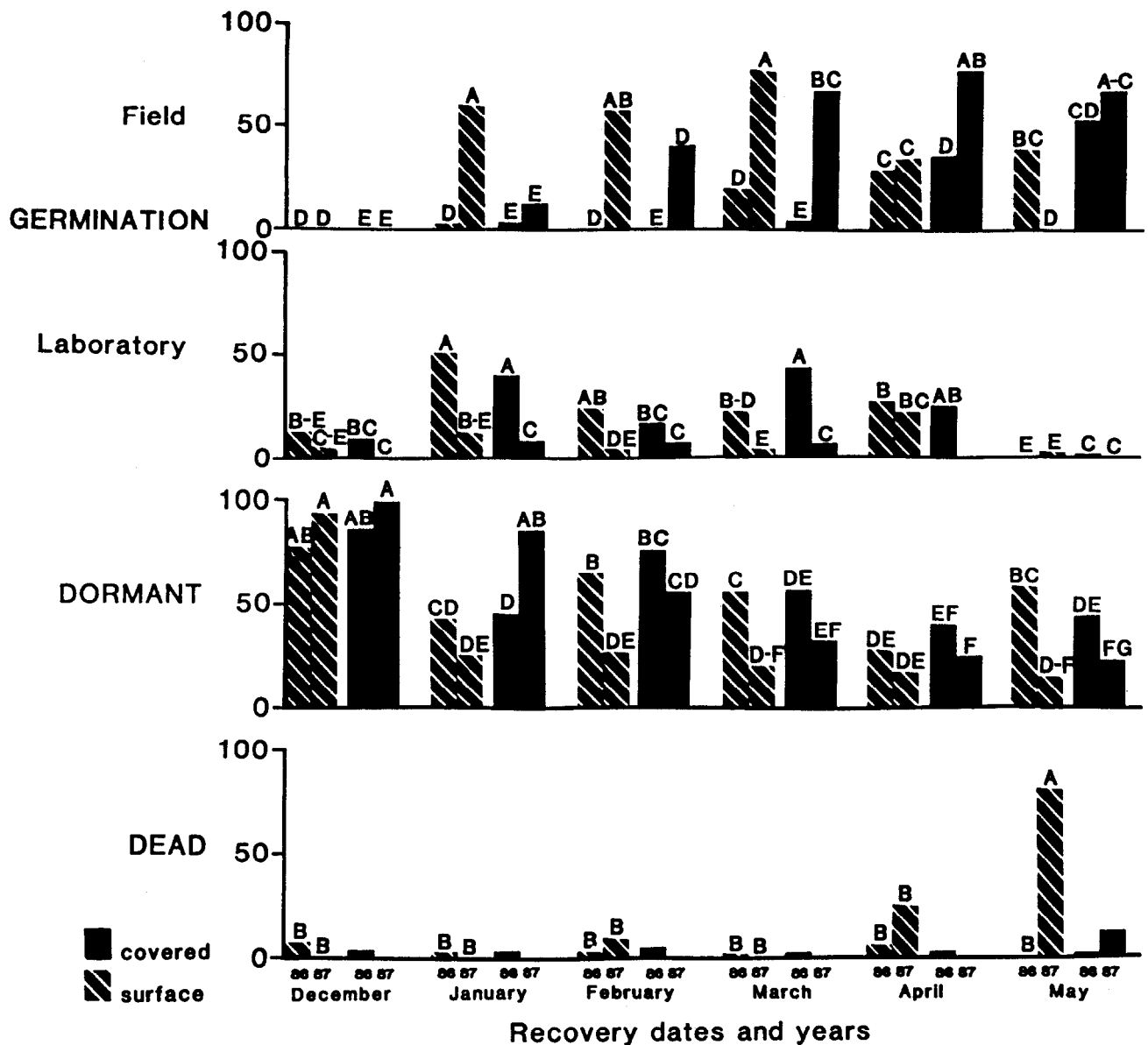


Fig. 2. Percentage field and laboratory germination, dormant and dead seeds of antelope bitterbrush at the Upper Sheep Creek locations of Reynolds Creek, Idaho. Seeds recovered monthly from December to May 1986-87 and 1987-88. Columns within seed characteristics and burial types with the same letter are not significantly different at the 0.01 level of probability as determined by confidence intervals calculated from regression equations (Evans et al. 1982). No letters indicate no significant differences.

germination process can be under cold conditions in the field.

Upper Sheep Creek in the Reynolds Creek Watershed is generally above the natural distribution of bitterbrush. The seed placement site was located on a north facing slope where snow drifts normally persist into late spring. The seedbed environment of the Upper Sheep Creek site allowed more than 75% of the antelope

bitterbrush seeds to come out of dormancy and be capable of germination (Fig. 2). This was the highest percentage of any location. The influence of the greater snow cover at Upper Sheep Creek is apparent in the extremes in soil temperatures at this location versus the lowest experimental site in the watershed, Quonset (Fig. 3). In 1987-88 it appeared that the persistent snow cover created a

Table 5. Precipitation during stratification period at field locations.

	Quonset		Lower Sheep Creek		Upper Sheep Creek		Reno		Granite Peak	
	1986-87	87-88	1986-87	87-88	1986-87	87-88	1986-87	87-88	1986-87	87-88
	(cm)									
November	1.2	0.8	1.4	2.1	3.0	3.8	0.9	1.1	1.4	1.6
December	0.7	3.3	0.7	2.4	2.6	5.8	0.2	0.3	0.4	1.0
January	2.2	2.0	2.0	2.4	5.8	7.6	0.3	0.8	0.6	0.9
February	0.7	1.4	5.4	0.7	6.4	0.8	0.1	0.4	0.4	0.8
March	5.9	1.7	2.4	2.5	4.3	3.4	0.4	0	0.7	0
Total	10.7	9.2	11.9	10.1	21.8	21.8	1.9	2.6	3.5	4.3

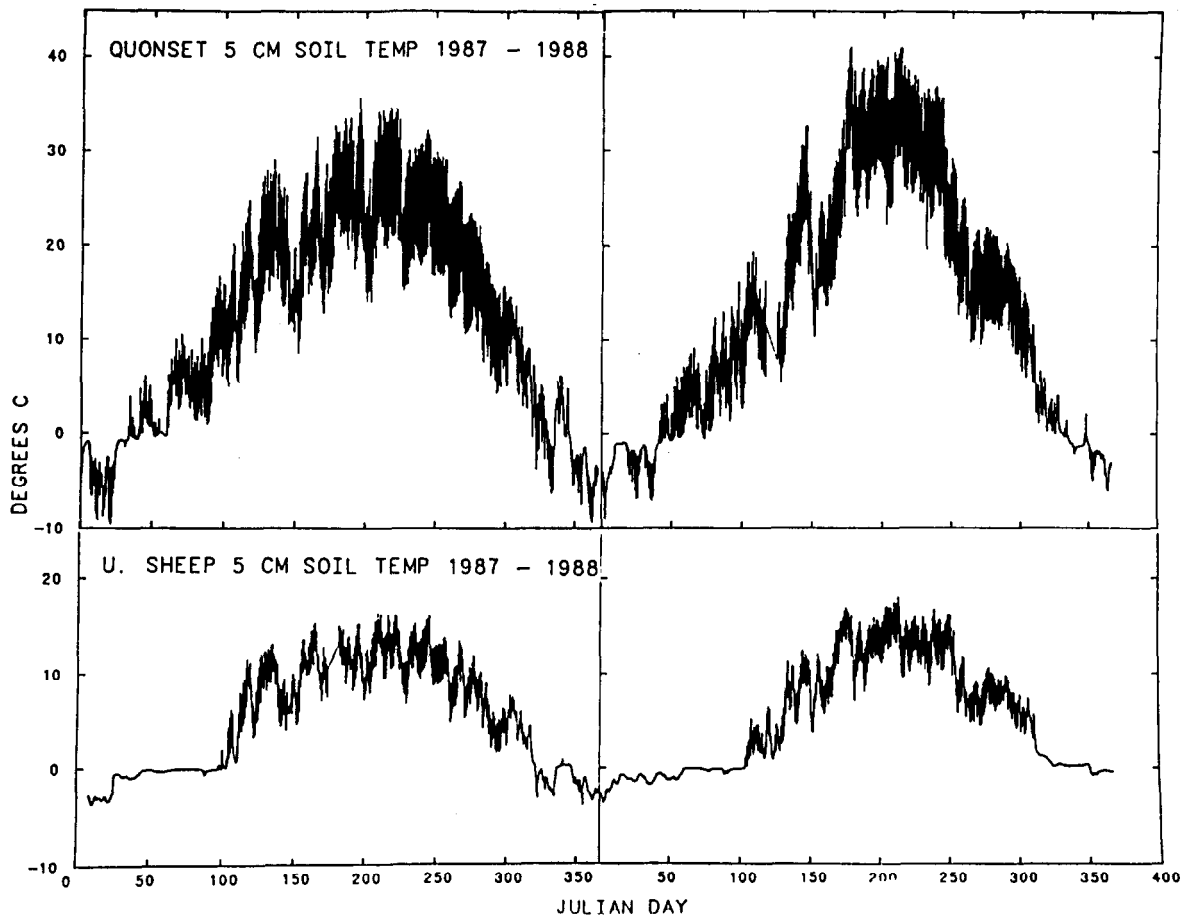


Fig. 3. Soil temperatures at 5 cm at the Quonset and Upper Sheep Creek locations in Reynolds Creek Watershed 1987-88.

problem because seed mortality reached 80% with seeds on the surface (Fig. 1). Apparently the germinating seedlings exhaust food reserves while still buried under the snow.

Microenvironmental Relations

Antelope bitterbrush seedling establishment is generally considered to be difficult to obtain, and especially difficult to attain in

the face of competition from such plants as cheatgrass (*Bromus tectorum* L.) and seed predation by granivores (Nord 1965). This competition is for soil moisture for growth. In the 2 years of this experiment there was not adequate moisture for cool-moist pre-chilling of antelope bitterbrush seeds during November and December at the 2 Nevada locations (Table 5). Seeds returned to Reno, Nev., had a maximum of 30% germination. This was in

Table 6. Snow and frost depth and snow cover at Lower Sheep Creek in the Reynolds Creek Watershed 1986-87 and 1987-88.

Month	Week	Snow depth		Snow cover		Frost depth	
		86-87	87-88	86-87	87-88	86-87	87-88
		(cm)		(%)		(cm)	
November	4	— ¹	0	—	0	—	0-11
December	1	0	1.3	0	100	0	—
	2	3.3	0	90	0	0-27	0-20
	3	3.8	2.5	6	100	frozen	0-27
	4	3.8	1.3	20	100	0-40	0-42
January	1	21.3	18.0	100	100	0-39	0-42
	2	30.0	16.3	100	80	0-50	0-5
	3	—	21.3	—	100	—	0-7
	4	drifts	11.3	75	95	—	0-16
February	1	—	16.3	15	100	0	0-17
	2	—	17.8	5	—	0-12	3-25
	3	2.0	0	100	0	0	0-18
	4	31.3	0	100	0	0-14	0-20
March	1	30.0	0	95	0	0-12	12-18
	2	0	0	0	0	0	0
	3	0	1.3	0	100	0	0
	4	0	2.0	10	90	0	0

¹Samples not collected.

February 1988, and it resulted in 4% germination in the field in March (data not shown). The dry November 1987 at the Quonset site in Reynolds Creek resulted in only 2% of the surface and 25% of the buried seeds being capable of germinating in January 1988.

Without the protective screen packages used in this study, the populations of antelope bitterbrush seeds would have been almost totally collected, a small portion consumed immediately and the majority cached in scatter hoards, by rodents. Rodent caches are usually about 2.5 cm deep in the surface soil. Considering the advantage of seed burial over the surface in obtaining the necessary moist prechilling to overcome dormancy, this is a most fortuitous situation and an apparent example of parallel evolution.

The dormancy of antelope bitterbrush seeds is broken by cool incubation of moist seeds, so obviously both temperature and moisture are important in the over-winter seedbeds. Obviously, at the high elevation of Granite Peak, Nev., mid-winter temperatures are very cold in bare seedbeds, but this did not break the dormancy of dry antelope bitterbrush seeds. In experimental studies of the moist prechilling requirements of antelope bitterbrush seeds, it was determined that temperatures below about -3° C were detrimental to breaking dormancy (Young and Evans 1976). Based on observations of comparative success in natural regeneration of antelope bitterbrush plants, it has long been thought that areas with continuous snow cover had better antelope bitterbrush establishment than lower elevation areas. This has been attributed to the environment for moist prechilling provided at the soil surface by the snow cover.

We have snow depth, cover, and frost depth data for the Lower Sheep Creek seed recovery (Table 6). For both years of the study there was no snow cover at the site for the first month the seeds were exposed in the field. For both years less than 10% of the seeds recovered had germinated or would germinate, and 4 to 6% of the seed population was germinable when the seeds were placed in the field. Snow depths for December ranged from 0 to 3.8 cm and 0 to 1.3 cm for 1986 and 1987, respectively. The spatial distribution of this snow cover was highly variable over the site (Table 6). The soil was frozen to a depth of 42 cm at certain locations and discontinuous times during December. With seed burial, this variable snow cover and these temperatures were sufficient to bring 70 and 50% of

the antelope bitterbrush seeds to a physiological state where they could germinate, for 1987 and 1988, respectively (Fig. 1). Seeds on the soil surface at Lower Sheep Creek only had 4 to 18% potential germination during the 2 years in question for January recoveries.

Obviously the breaking of dormancy of antelope bitterbrush seeds by moist prechilling in the field has very fragile safe site conditions controlling the process. If we add phenotypic and ecotypic variability among seed populations and the Meyer influence of pregermination incubation temperatures, the field model becomes potentially very complex, but still a necessary and most valuable area of research.

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Improvement of dry tropical rangelands in Hainan Island, China: 1. Evaluation of pasture legumes

DAVID L. MICHALK, FU NAN-PING, AND ZHU CHIN-MING

Authors are former director, former pasture technician, and production manager of Gaopoling Model Cattle Farm, Ba Suo, Dong Fang County, Hainan Island, People's Republic of China.

Abstract

During 1981-83, we studied some legumes for potential improvement of dry tropical (1,001 mm annual rainfall) rangelands in Hainan Island, China. The productivity and persistence of 16 pasture legumes were tested on sandy (<5 mg/kg available P) and loam (12-25 mg/kg) soils under cutting in a randomized block design with plots split for sequential sowings in 1981, 1982, and 1983. Dry matter yield, sward composition, and legume density were measured at the end of the wet and dry seasons each year. Thirteen legumes established with density averaged over 3 sequential sowings >1 plant/m² on 1 or both soils, but only 5 perennial stylos (*Stylosanthes*), *siratro* [*Macroptilium atropurpureum* (D.C.) Urban], and *centro* (*Centrosema pubescens* Benth) (loam soil only) persisted through 2 dry seasons and yielded more than 0.5 metric tonne (t)/ha in 3-year-old swards. *S. guianensis* (Aubl.) Sw. cv Cook yielded best on both soils, but proved less tolerant to fire than cv Graham, which is the common stylo recommended by this study as a companion for *siratro* for improvement of loam soil rangeland. *Siratro* was the only non-stylo to produce >2 t/ha and show relative stability with sward age, but careful grazing management and regular fertilization are needed to maintain *siratro* content above 40% in commercial sowings. Tolerance to fire, low P requirement, and high yield in 2- and 3-year-old stands makes *S. scabra* Vog. cv *Seca* the most suitable legume for sandy soil, but since it is slow to establish, a mixture of *S. scabra* and *S. hamata* (L.) Taub. cv *Verano* which is noted for its quick establishment and prolific seed production is recommended for range improvement of low P soils.

Key Words: China, dry tropical, legumes, *Stylosanthes*, superphosphate, anthracnose, fire tolerance

China has implemented a national program to rapidly increase the output of red meat from rangelands (Zhao 1981). Agricultural planners in the southern provinces of Guangdong and Hainan identified the dry tropics of western Hainan (Fig. 1) as a region suitable for range improvement on 2 counts: (1) unlike other parts of the island, the potential to boost agricultural income through increased production of food, field, and plantation crops is limited by low rainfall and poor soils; and (2) this region which covers 20%

of Hainan already has an abundance of native (Huang Niu) cattle numbering 70,000 or 25% of Hainan's herd and a large area of rangeland with potential for cattle production.

To increase beef production from these dry tropical rangelands, cattle nutrition must be improved. During the late wet season and protracted dry season, the nutritive value of native vegetation severely limits productivity of beef cattle. Studies on Yellow Ox cattle in south China show that low calving percentages, high mortality of lactating cows, and low turnoff rates of inferior quality animals are directly related to protein deficiency in native pasture (Ayres et al. 1983).

Based on studies in Australia and South America, livestock nutrition can best be improved by broadcasting legumes into grass-dominated rangelands to increase the quantity and quality of available forage (Hutton 1979, Walker 1983). For many years, *Stylosanthes humilis* H.B.K. (Townsville stylo) and superphosphate was the standard recommendation for improvement of native grassland throughout northern Australia (Humphreys 1967), and in monsoonal areas of south-east Asia, Latin America, and East Africa (Kretschmer 1965). However, because of its susceptibility to anthracnose (*Colletotrichum gloeosporioides* Penz.) fungus (Irwin and Cameron 1978), *S. hamata* (L.) Taub and *S. scabra* Vog. are not recommended as replacements for *S. humilis* in the dry tropics (Gillard et al. 1980), while *S. guianensis* (Aubl.) Sw. has proved to be more productive in areas where annual rainfall exceeds 1,000 mm (Bishop et al. 1981).

In addition to the *Stylosanthes* species, *Macroptilium atropurpureum* (DC.) Urban (*Siratro*) is a persistent and productive trailing legume adapted to a wide range of soil and vegetation types with annual rainfall as low as 750 mm ('t Mannelje 1974) including the dry tropics (Anning 1982b). *Centrosema pubescens* Benth., although more suited to the wet tropics (Hutton 1970), will persist in 1,100 mm rainfall areas when grown on clay soils with favourable moisture regimes (Anning 1982b).

While agricultural planners in Guangdong Province were aware of the value of these legumes for improving cattle production, they also recognized that a lack of local expertise in range science posed a serious limitation to progress in Hainan Island. Assistance was sought from New South Wales, Guangdong's sister state in Australia (Saville and Sheridan 1980), to develop a joint range improvement program with the following objectives: (1) to select forage species adapted to dry tropical Hainan; (2) to determine fertilizer requirements of different forage species; and (3) to develop methods of establishment and utilization (Michalk and Dunn 1984). Finance for the program was provided by Guangdong, and technical input by New South Wales. In this paper of a series focusing on range improvement in the dry tropics of China, we

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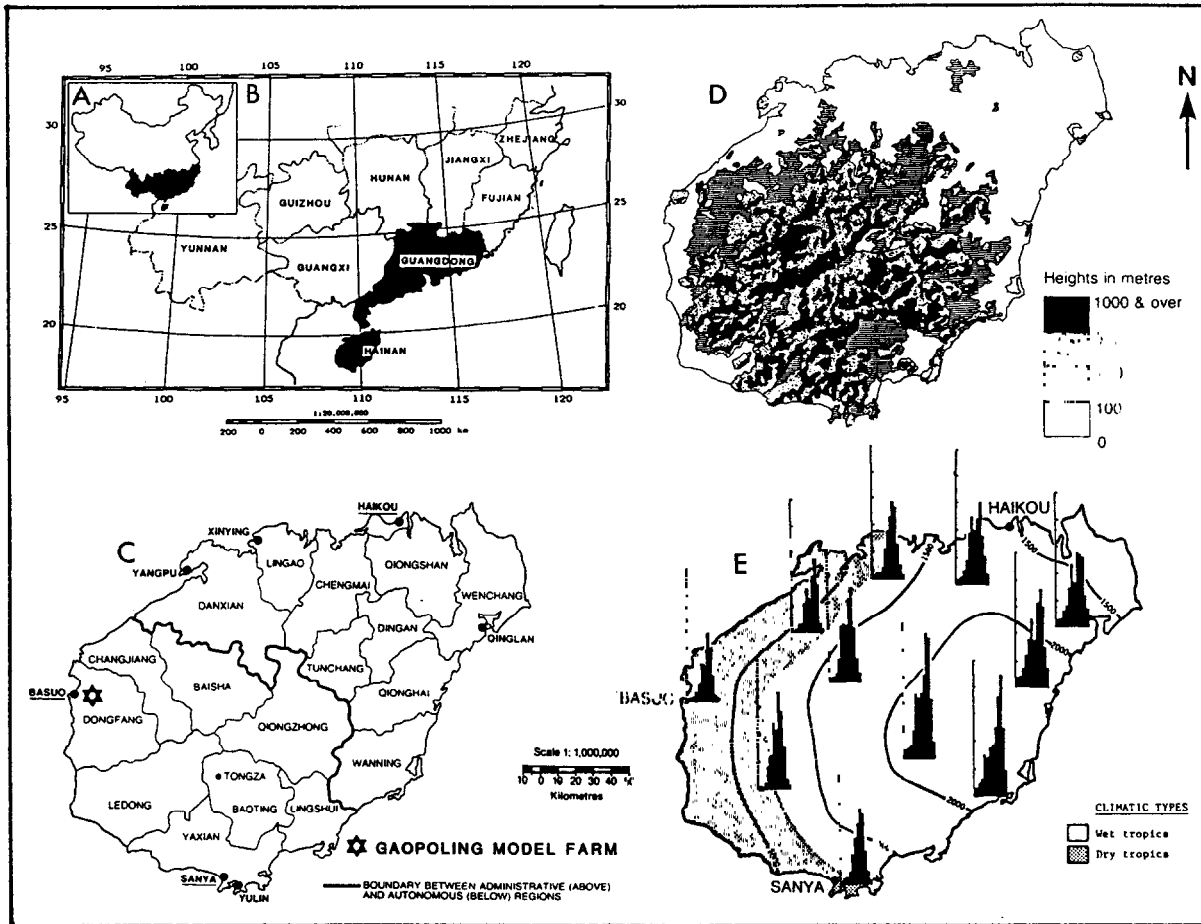


Fig. 1. (a) Location of China's tropical and subtropical region; (b) location of Guangdong and Hainan; (c) counties of Hainan and location of Gaopuling Model Cattle Farm; (d) topography of Hainan; and (e) dry tropical region delineated by rainfall isohyets.

report on our studies conducted between 1981 and 1983 at Gaopuling Model Cattle Farm which aimed to select pasture legumes that would: (1) grow and produce seed on sandy soil under phosphorus and water stresses; (2) persist under grazing; and (3) tolerate pests and diseases. No evaluation of pasture legumes had been undertaken in the dry tropics of Hainan prior to the reported studies.

Location and Environment of Hainan's Dry Tropical Rangelands

Location

Hainan Island, which lies between longitudes $108^{\circ}30'$ and 111° E, and latitudes 18° and $20^{\circ}31'N$ (Fig. 1), forms the extreme southern limit of the People's Republic of China, except for the disputed Parcel Reefs. With an area of $34,077 \text{ km}^2$ (Anon. 1982), the oval-shaped island ranks as the world's 26th largest island. Although it accounts for less than 1% of China's land area, its tropical climate, rich mineral and petroleum resources (Anon. 1982), and strategic location make Hainan an important, yet undeveloped, region of China (Michalk 1986).

Gaopuling Model Cattle Farm ($19^{\circ}09'N$; $108^{\circ}68'W$) is 14 km west of Ba Suo township on 2,000 ha of undulating coastal plain in Dong Fang County, Hainan Island (Fig. 1). This large area was chosen because Guangdong officials believed that demonstration of range improvement on a large, rather than on a small scale would serve as a better model for extension of the program to other state farms. The model farm is typical of dry tropical rangeland found in western Hainan where annual rainfall averages less than 1,400 mm (Fig. 1). It is representative of the 162,000 ha set aside by

the Hainan government for range improvement.

Climate

Lying in a rain-shadow cast by the Five-Finger and Red Mist Mountain Ranges (Fig. 1), Dong Fang county has a seasonally dry savanna-type climate with an average annual rainfall of 1,001 mm (Table 1), 85% of which falls during the 5-month wet season (mid-May to mid-October). Table 1 also shows the monthly rainfall recorded at Gaopuling Farm over the experimental period (1981-1983).

Year-to-year variability in rainfall is large with annual totals over the last 29 years (1955-83) ranging from 275 mm in 1969 to a maximum of 1,529 in 1980. The probability of a drought year occurring in Dong Fang county is 1 year in 7. Drought years occur when the anticyclone over Mongolia persists into late May or June, which delays the onset of the typhoon season, or when local synoptic patterns are such that typhoons curve towards Japan without entering the South China Sea.

Typhoons make a significant contribution to rainfall in western Hainan. Records from the Dong Fang County Weather Station show that over the 1955-83 period 46% of the annual total was associated with typhoons, two-thirds of which occurred in the July to September period. During the experimental period between 3 and 8 typhoons were recorded, accounting for 42 to 64% of total rainfall (Table 1). Typhoon rain occurs as intense, short duration storms with 417 mm (July 1983) being the highest fall recorded in a single day in Dong Fang County.

Mean monthly maximum/minimum temperatures for the experimental period ranged from $23/15^{\circ} \text{C}$ in January to $32/26^{\circ} \text{C}$ in

Table 1. Average climatic parameters for Dong Fang County (1955 to 1981) and Gaopoling Farm rainfall for 1981-1983.

	Rainfall			Evaporation	Average temperature	Solar radiation
	Mean	1981	1982			
	----- (mm) -----			(mm)	(°C)	(cal/cm ² day)
January	7	3	0	17	127	258
February	13	2	33	5	109	286
March	17	0	1	101	140	323
April	32	63	25	11	185	400
May	63	30	147	33	247	468
June	143	143	195	77	224	467
July	138	128	126	565	234	484
August	254	181	33	244	186	419
September	203	57	190	64	148	367
October	101	200	199	141	157	355
November	22	20	128	0	146	333
December	8	0	8	8	136	258
Total	1001	827	1085	1266		
Number of typhoons	5	6	8	3		
% total rain	46	42	50	64		

July, similar to the long-term temperature regime for the county (Table 1). Dong Fang has the hottest summer recorded in Hainan, even though the hottest maximum temperature ever recorded in the county is only 35.4° C. During the study period, the highest temperature (35° C) was recorded on 13 May 1983, while minimum temperature did not fall below 9° C.

Soils

Rangeland soils of Hainan's dry tropics are mapped as "dry red earths" in the Chinese classification system, which equates with Usttorroxs in *Soil Taxonomy* (Zhao and Shi 1986). Soil texture ranges from deep siliceous sands on the coastal plain to red loam in the undulating hinterland (Xiong and Tang 1986). The phosphorus infertile (<5 mg/kg available P) sandy soil (Table 2) covers 60% of the area of Gaopling Farm (Michalk and Dunn 1984) interspersed with small areas of moderately fertile red loam (Table 2) which is more typical of the "dry red earths" described by Zhao and Shi (1986).

Unimproved Rangeland Vegetation

Vegetation ranges from monsoonal scrub with tall bunchgrasses from the genera *Heteropogon*, *Dichanthium*, *Chrysopogon*, and *Themeda* forming the understory on better loam soil to degraded grassland dominated by blady grass (*Imperata cylindrica* (L.) Beauv. var. *major* (Nees.) C.E. Hubbard) and prostrate, grazing-tolerant grasses on sandy soil. Scrub species on the coastal plain include: *Grewia* spp. (14%); *Helicteres* spp. (11%); *Aglaia dasyc-lada* How & T.C. Chen (5%); *Quercus helferana* (Yu) L. Menitski (4%); and a number of shrubby *Desmodiums*.

Forage production ranges from 1.1 t/ha on degraded grassland to 2.2 t/ha on low density (<5,000 shrubs/ha) scrubland (Michalk and Fu 1988). Native legumes, mostly from the genera *Desmodium* and *Alysicarpus*, which account for less than 10% of total herbaceous biomass on unimproved rangeland, are not very responsive to superphosphate (Michalk and Fu 1988).

Materials and Methods

To select suitable legumes, 16 species/cultivars which included types with erect and trailing growth form (Table 3) were chosen for study based on their performance in Australia. Legumes were sown at recommended seeding rates (Table 3) into weed-free, cultivated seedbeds in sequential plantings in 1981 (1 August), 1982 (15 June), and 1983 (12 July) on sandy and red loam soils. Study subplots were 21 m² (3 m x 7 m) and replicated 3 times. Legume seed was scarified using hot water treatment, inoculated with commercial *Rhizobia* in peat, and pelleted with rock phosphate or lime prior to planting.

A newly cleared red loam site was stick-raked and ploughed between April and planting for the 1981 sowing, but old cultivation areas were used for the 1982 and 1983 sowings. Heavily grazed sites were selected for sandy soil studies. All plots were fertilized with local Grade 4 superphosphate (28 kg P/ha) at sowing, but no maintenance fertilizer was applied to 2- or 3-year-old swards.

To test the ability of sown legumes to compete with companion grasses, plots were oversown with 6 kg/ha of Brownseed grass (*Paspalum pilcatulum* Michx.) cv. Rodd's Bay at the 1982 sowing. Brownseed grass was chosen because experience in the dry tropics

Table 2. Chemical analyses for sandy and red loam soils at Gaopoling Farm, Hainan Island.

Depth (cm)	pH		Organic matter (%)	Total N (%)	Exchangeable cations (meq/100 g)					Available P (mg/kg)	Available trace elements (mg/kg)						
	H ₂ O	KCl			Ca	Mg	K	Na	Al		Cu	Zn	Fe	Mn	Mo	B	Co
Deep sandy soil																	
0-10	5.8	5.4	0.63	0.04	1.78	0.58	0.20	0.63	na ¹	3	0.1	1.1	1.8	68	<0.1	na	na
10-20	5.7	5.4	0.46	0.03	1.65	0.55	0.16	0.03	na	2	0.2	0.5	16	56	na	na	na
20-40	5.9	5.5	0.20	na	0.72	0.31	0.05	na	na	3							
>40	6.1	5.5	0.09	na	0.90	0.32	0.05	na	na	6							
Red loam soil																	
0-10	5.8	5.4	1.36	0.09	7.58	2.55	0.42	0.07	na	25	0.3	1.2	32	136	<0.1	0.2	0.4
10-20	6.1	5.6	1.01	0.08	6.43	2.54	0.31	0.06	na	8	0.4	1.4	29	66	na	na	na
20-40	6.3	5.6	0.34	na	1.64	1.35	0.12	na	na	na							
>40	6.4	5.6	0.15	na	2.07	1.94	0.14	na	na	na							

¹na = data not available

Table 3. Name, sowing rate, germination percentage, and first year establishment of tropical legumes tested at Gaopoling Farm, 1981-1983.

Botanical name	Common name & cultivar	Growth form ¹	Sowing rate	Germination ²	Establishment ³	
					Sand	Loam
			(kg/ha)	(%)	--- (plants/m ²) ---	
<i>Macroptilium lathyroides</i> (L.) Urban	Phasey bean cv Murray	E	6	59	3.3c	10.7b *
<i>M. atropurpureum</i> (DC.) Urban	Siratro	T	3	85	3.4c	5.1cd
<i>Stylosanthes humilis</i> H.B.K.	Townsville stylo cv Lawson	E	6	86	4.0c	3.1d
<i>S. guianensis</i> (Aubl.) Sw.	Common stylo cv Cook	E	6	83	24.2a	18.7a *
<i>S. guianensis</i> (Aubl.) Sw.	Common stylo cv Endeavour	E	6	83	23.3a	21.6a
<i>S. guianensis</i> (Aubl.) Sw.	Common stylo cv Graham	E	6	83	23.3a	21.6a
<i>S. hamata</i> (L.) Taub	Caribbean stylo cv Verano	E	6	93	10.0b	8.7bc
<i>S. scabra</i> Vog.	Shrubby stylo cv Seca	E	6	85	22.3a	17.8a *
<i>Desmodium intortum</i> (Mill.) Urban	Desmodium cv Greenleaf	T	3	89	F	F
<i>D. uncinatum</i> (Jacq.) DC.	Desmodium cv Silverleaf	T	3	85	F	F
<i>Neonotonia wightii</i> (Wight & Arn.) Lackey	Glycine cv Tinaroo	T	4	76	0.4c	2.7d
<i>Macrotyloma axillare</i> (E. Mey) Verdc.	Axillaris cv Archer	T	4	94	F	F
<i>Centrosema pubescens</i> Benth.	Centro	T	4	80	1.3c	2.7d
<i>Pueraria phaenoloides</i> (Roxb.) Benth.	Puero or tropical kudzu	T	3	85	F	F
<i>Trifolium semipilosum</i> Fres.	Kenya clover cv Safari	P	4	85	F	F
<i>Trifolium repens</i> L.	White clover cv Haifa	P	4	94	F	F

Legume density means within soil type followed by the same letter are not significantly different at $P < 0.05$; * indicates a significant difference ($P < 0.05$) in legume density due to soil type; ¹Growth form code: E = erect; T = trailing; P = prostrate; ²Germination of seed scarified with hot water treatment; ³Establishment for legumes averaged over the 3 sequential sowings (1981, 1982, 1983); F = failed to establish.

of northern Australia had indicated that if left ungrazed this grass will produce a dense stand which was too competitive for legumes (Anning 1982a).

To estimate establishment and persistence, legume plants were counted in two 0.5-m² quadrats/plot at the end of the wet (November) and dry seasons (May/June) of each establishment year. Pasture production was estimated by harvesting forage from four 0.25-m² quadrats at a height of approximately 2 cm above the ground surface using hand shears. Estimates were made at the end of the wet and dry seasons each year. Harvested material was weighed in the field and subsamples taken to determine botanical composition by hand sorting and dried at 100° C for 24 hours to determine dry matter content of sown legumes, grasses, and forbs. All yields are expressed in metric tonnes (t)/ha.

At the end of the dry season each year, plots were grazed with cattle to remove carry-over production from the previous wet season to a level of about 500 kg/ha. Although legumes remained green for at least part of the dry season, little additional growth was measured during this period and so legumes were evaluated on their wet season performance only.

Statistical Analyses

Analyses of variance split in time were set up in the Genstat program (Payne et al. 1988) to analyze density and production data from the randomized block design for establishment year performance of legumes in the 3 sequential sowings with soil types (2), establishment years (3), and species (7) as main effects. Least significant differences based on error terms from the appropriate stratum of the analyses of variance for pasture parameters were used to differentiate between significant and nonsignificant means.

Similar analyses were used to test significance of legume and grass production in 1- (mean of sequential sowings in 1981, 1982, and 1983); 2- (mean of 1981 sowing cut in 1982 and 1982 sowing cut in 1983); and 3- (1981 sowing cut in 1983) year-old pasture swards. A linear regression model with fitted terms for year, soil type, pasture age, species, and all significant ($P < 0.05$) second- and third-order interactions was used to predict yield of sward components and verify analyses of variance. The high degree of variability in legume ($R^2 = 0.97$), native grass ($R^2 = 0.90$), and total ($R^2 = 0.88$) yields explained by these models implied that there was no confounding between sites and years within soil types due to pooling data for the analysis of variance.

Linear and nonlinear regressions were used to examine relationships between sown legume performance, rainfall, plant density, and age of pasture.

Results

A. Establishment Year

Plant Density

Only 10 legumes established successfully with mean density > 1 plants/m² on one or both soils (Table 3). Perennial stylos (*S. guianensis* and *S. scabra*) had the highest density, especially on sandy soil except for the cultivar Graham, which established better on loam soil (Table 3). Density of *S. hamata*, an annual/perennial stylo, was half that of the other perennial ecotypes, while establishment of the annual *S. humilis* was only half that of *S. hamata* (Table 3).

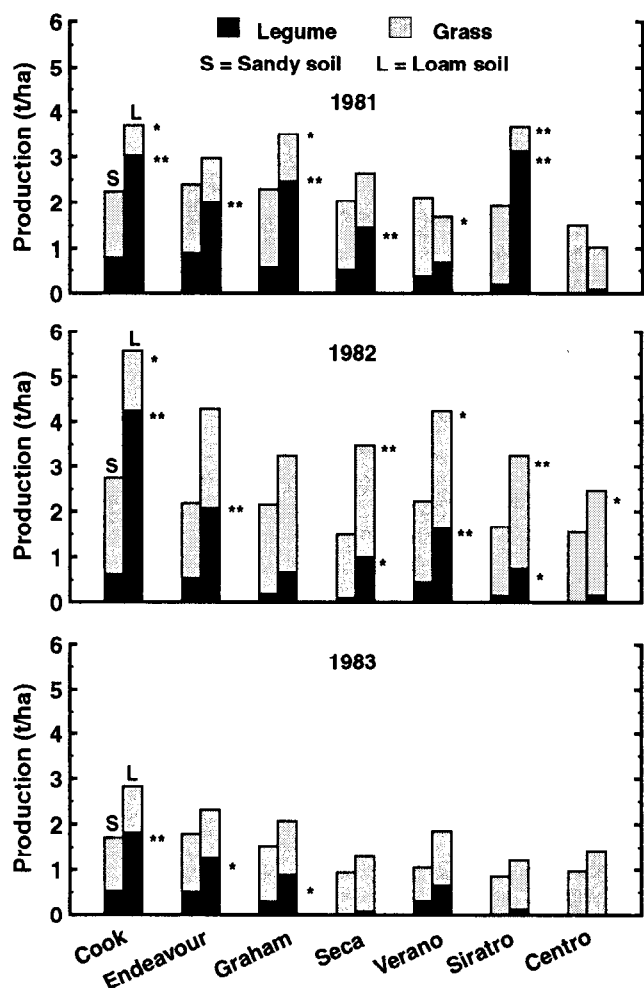
In contrast to stylos, legumes with a trailing growth form (siratro, glycine and centro) established better on fertile loam soil (Table 3). Siratro established better than glycine or centro, but was not as dense as swards of *M. lathyroides*. Year of sowing affected ($P < 0.01$) perennial stylo density with more plants establishing in 1981 than in 1982 and 1983. Density of *S. humilis*, *S. hamata*, and the trailing legumes was not affected by year of establishment even though the growth season was longer and wetter in 1982 and 1983 (Fig. 2; Table 5).

Density of brownsed grass (11 plants/m²) sown with legumes in the 1982 sowing did not impact significantly on legume establishment.

Production

Soil type affected ($P < 0.01$) establishment year legume production (Table 5). Legume yield on the loam soil exceeded yield on sand soil by 3 or more times, depending on species (Fig. 2; Table 5). Cook stylo was the most productive legume on loam soil, followed by Endeavour stylo, with Graham stylo and Siratro equal third (1.3 t/ha). On sandy soil there was little difference between legumes in establishment year production (Fig. 3).

Year of establishment did not affect legume production on sandy soil, but did impact on legume yield in newly sown pastures on loam soil (Fig. 2): Cook and Verano yielded significantly more when sown in 1982, Graham and Siratro produced highest yield in the 1981 sowing, while Endeavour and Seca performed well in both 1981 and 1982. Except for Graham, production measured for the



* and ** indicates significant differences in legume or grass yield due to soil type at $P < 0.05$ and $P < 0.01$

Fig. 2. Establishment year production (t DM/ha) for tropical legumes sown on sand and loam soils at Gaopoling Farm.

Table 4. Legume density (plants/m²) at the end of the wet and dry season for sand and loam at Gaopoling Farm, 1981–1982.

Legume name	Soil type			
	Sand		Loam	
	Wet ¹	Dry	Wet	Dry
	----- (plants/m ²) -----			
Common stylo cv Cook	29.5a	24.0c *	21.5bc	19.8b
Common stylo cv Endeavour	26.0a	29.3ab	20.0b	18.2b *
Common stylo cv Graham	16.8b	27.0bc*	30.3a	30.0a
Shrubby stylo cv Seca	26.0a	34.2a *	18.7c	23.0b *
Caribbean stylo cv Verano	12.3b	8.3d	9.2de	7.2c
Townsville stylo cv Lawson	4.0c	0e *	4.7ef	0.2d *
Siratro	4.2c	3.2e	5.5ef	7.2c
Phasey bean cv Murray	1.3c	0e	12.2d	0.2d *
Glycine cv Tinaroo	0.3c	0e	3.3f	0.2d
Centro	1.7c	0.2e	3.8f	2.5d

Legume density means followed by the same letter are not significantly different at $P < 0.05$ within seasons; * indicates a significant difference ($P < 0.05$) in legume density within soil types due to season; ¹ Density for sown legume measured at end of wet season and end of dry season averaged over to years (1981 & 1982).

Table 5. Significant main effects for establishment year production (tDM/ha) for 3 sequential sowings of tropical legumes sown on sand and loam soils at Gaopoling Farm.

Main effect	Comparison	Parameter	
		Legume	Grass
Soil type	Sand	0.34b	1.45a
	Loam	1.35a	1.46a
Year	1981	1.16a	1.25b
	1982	0.90b	2.00a
	1983	0.47c	1.10b
Sown legume	Cook	1.84a	1.29a
	Endeavour	1.22b	1.44a
	Graham	0.85c	1.62a
	Seca	0.53d	1.46a
	Verano	0.69d	1.52a
	Siratro	0.74cd	1.38a
	Centro	0.05e	1.45a

Main effect means within parameters followed by the same letter are not significantly different at $P < 0.05$.

	Sowing to harvest		
	1981	1982	1983
Growth period (days)	130	172	159
Rainfall (mm)	458	879	1022

1983 sowing was lowest for all legumes (Fig. 2; Table 5).

Year of establishment had no effect on yield per plant on sandy soil, but reduced ($P < 0.05$) plant size on loam soil with smaller plants present in 1983 compared with 1981 and 1982. Yield per plant of siratro, for example, declined from 47 g/plant for 1981–2 to 4 g/plant for 1983, while stylo size was reduced from 13 to 7 g/plant. Excessive leaching of nutrients by 417 mm of rainfall received 2 weeks after sowing may explain in part poor legume performance in the 1983 sowing (Table 5), and the significant negative correlation between rainfall received during the sowing to harvest period (Table 5) and legume yield on sand ($R^2 = 0.99$) and loam ($R^2 = 0.76$) soils.

First year legume production was correlated with legume density on sandy ($R^2 > 0.77$) and loam soil ($R^2 > 0.86$) soils for all legumes except for Cook, Endeavour, and Seca stylos. However, production/plant was significantly higher ($P < 0.05$) on loam soil, with individual plants producing between 32% and 974% more than those on sandy soil, depending on species and/or year of establishment.

Siratro produced the largest dry matter yield per plant (32 g/plant) averaged over the 3 sowings on loam soil, followed by Cook stylo (23 g/plant), with Verano (11 g/plant) and Endeavour stylo (10 g/plant) equal third. By comparison, production per plant averaged only 3 and 4 g/plant, respectively, for siratro and the stylos growing on sandy soil. Larger plant size on loam soil was attributed to a combination of higher fertility (Table 2) and superior water-holding capacity of soil.

Grass standing crop in legume swards was similar on both soils and was not affected by legume species (Fig. 2, Table 5). However, year of establishment and its interaction with soil type did impact ($P < 0.01$) grass production. Higher grass yield on loam soil in 1982 was due mainly to production of brownseed grass, which accounted for 72% of the grass component, while 1981 grass yield on loam was reduced to 57% of sand soil grass production by high legume yield (Table 4). For sand soil, 1981 and 1982 grass yields were similar (Fig. 2) due to poor production of sown brownseed grass, which contributed only 10% to grass yield at the 1982 sowing. There was no difference in grass yield between soil types in the 1983 sowing, which was lower ($P < 0.05$) than yield for the 1982 sowing for both

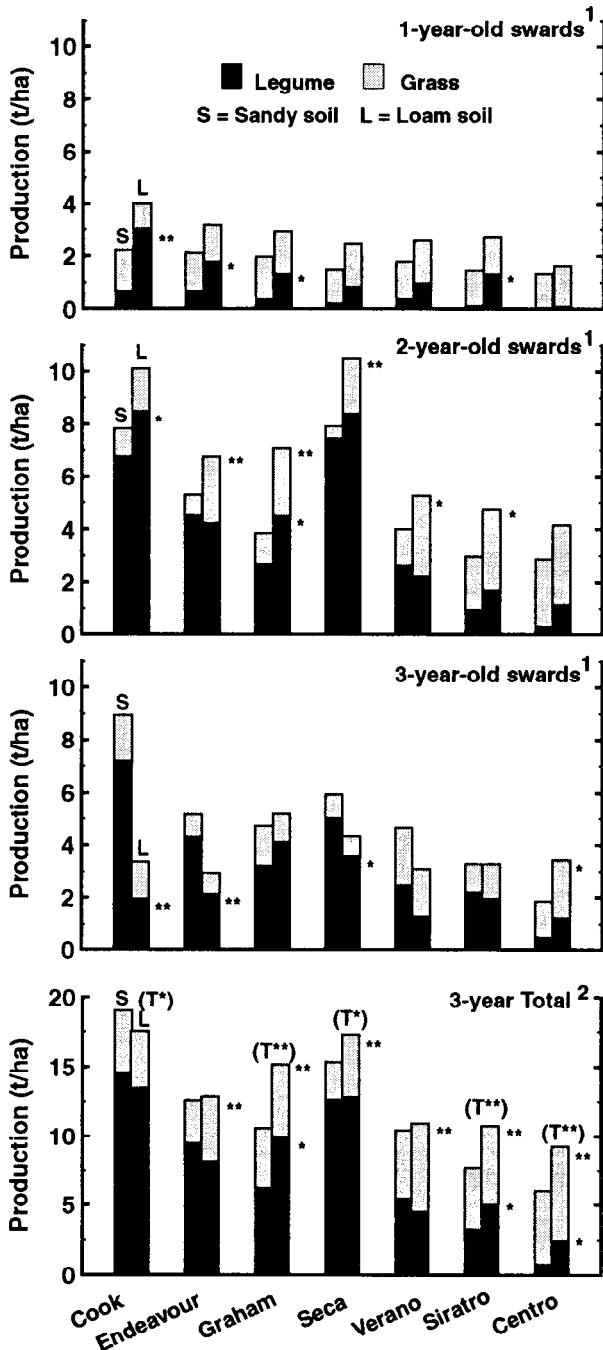


Table 6. Significant main effects for yield of 1-, 2-, and 3-year-old pastures sown on sand and loam soil at Gaopoling Farm (1981-83).

		Parameter	
		Legume	Grass
Year	One-year-old	0.84	1.45b
	Two-year old	3.99a	1.96a
	Three-year old	2.94b	1.37b
Sown legume	Cook	4.68a	1.42cde
	Endeavour	2.94b	1.31de
	Graham	2.70b	1.59bcd
	Seca	4.25a	1.2e
	Verano	1.66c	1.91ab
	Siratro	1.37c	1.71abc
	Centro	0.54d	2.01a

Main effect means within parameters followed by the same letter are not significantly different at $P < 0.05$.

sward regeneration of these legumes depended on the level of seed set at the end of the previous wet season.

Glycine did not survive the dry season (Table 4) and failed to produce sufficient seed for regeneration. On sandy soil, centro also suffered high plant mortality during the dry season (Table 4), but the small nucleus of surviving plants together with annual seedling recruitment resulted in a 0.5-t/ha contribution of centro in 3-year-old pastures (Fig. 3). The higher water-holding capacity of loam soil benefited centro, with 66% of first-year plants surviving into the second year (Table 4).

Grass and Legume Production

Cook and Seca stylos were the most productive legumes (Fig. 3; Table 6). Verano stylo and siratro yielded less than the other stylos but out-performed centro (Fig. 3; Table 6). Age of pasture affected ($P < 0.05$) stylo production with yield for 2- and 3-year-old swards exceeding 1-year-old pastures by up to 7.5 t/ha/year, depending on species and soil type (Fig. 3). Although production was higher for 1-year-old swards on loam soil, soil type had no overall effect on yield except for Graham stylo, which performed better on loam soil (Fig. 3).

The full effect of soil type on legume performance was masked by a wildfire which burned the 1981 loam site in late August, 1983, and significantly reduced yield of 3-year-old legume swards (Fig. 3). Production loss due to fire, predicted from logarithmic equations fitted to production data for 1-year-old and 2-year-old swards on loam soil, ranged from 1.3 t/ha for Graham stylo to 7 t/ha for Cook stylo. Better post-fire recovery was observed with Graham and Seca stylos, which produced higher ($P < 0.05$) yields as 3 year-old swards than other legumes on loam soil (Fig. 3). Production of centro and siratro was least affected by pasture age and fire (Fig. 3).

On sandy soil, production patterns of time for stylos were logarithmic ($\text{Year } 1 < \text{Year } 2 = \text{Year } 3$), except for *S. scabra* which produced significantly more dry matter in 2- than 3-year-old pastures. Centro yield was low and unaffected by time, but siratro yield increased ($P < 0.05$) with time and produced yield equivalent to Verano stylo as 3-year-old sward (Fig. 3).

There were differences ($P < 0.05$) in companion grass production associated with interactions between age of pasture, sown legume, and soil type. While there was no difference in companion grass yield between sandy and loam soils in 1- and 3-year-old legume swards, grass production on loam soil in 2-year-old stands was double that of sandy soil (2.5 vs 1.3 t/ha—Fig. 3). This was due to superior performance in 2-year-old plots on loam soil of brownseed grass (1.8 t/ha) sown with legumes in 1982.

On both soil types, Verano stylo and centro were least competitive with companion grass production exceeding 2 t/ha in 3-year-old legume swards, whereas Endeavour and Seca stylos reduced

¹One-year-old production mean of sequential sowings in 1981, 1982, and 1983. Two-year-old production mean of 1981 sowing cut in 1982 and 1982 sowing cut in 1983, and Three-year-old production is 1981 sowing cut in 1983.²Total yield = Total sown legume yield + total native & sown grass; * and ** indicates significant differences in legume or grass yield due to soil type at $P < 0.05$ and $P < 0.01$; (T*) and (T**) indicates significant differences in total yield due to soil type.

Fig. 3. Yield and composition of 1-, 2-, and 3-year-old legume pastures sown on sand and loam soils at Gaopoling Farm (1981-83).

soil types (Fig. 2).

B. Second, Third, and Total Production Legume Persistence

Legume density measured at the end of the first dry season for the 1981 and 1982 sowings showed that phasey bean and Townsville stylo did not survive the 7-month dry season (Table 4) and that

grass yield to <0.9 t/ha by the third production year (Fig. 3).

Total Sward Production

Total production was highest in Cook and Seca swards and lowest in siratro and centro plots on both soil types (Fig. 3). Due to superior yield of legumes in establishment year, accumulated production on loam soil for 1- and 2-year-old stands exceeded accumulated production on sand soil by 34% to 70%, depending on legume sown, but overall there was no difference between soil types in total pasture yield accumulated over 3 production years (11.7 vs 13.4 t/ha/3-yr) due to the effects of the wildfire on loam soil in 1983.

On sandy soil, total production of perennial stylo-based pasture exceeded 4.0 t/ha in 2- and 3-year-old swards, which is about 4 times the production expected from unimproved sandy rangeland. The tall growing stylos (1–2 m) cultivars, Cook, Endeavour, and Seca accounted for 75% or more of total production, whereas the shorter stylos (<1m), Graham and Verano, made up less than 70% of total production. Total production of siratro and centro were lower ($P<0.05$) than that of the stylos due to the small contribution of these trailing legumes to production in 1- and 2-year-old swards (Fig. 3).

For loam soil, yield of 2-year-old pastures exceeded unimproved rangeland by at least 2 t/ha and as much as 8 t/ha for swards of Cook and Seca stylo. Although the effects of the wildfire preclude comparisons for 3-year-old swards, prediction equations based on sand soil response pattern to age of pasture suggest that total production of perennial stylo-based pasture for 3-year-old swards on loam soil should exceed 8 t/ha and 5 t/ha for siratro-based pastures.

Discussion and Management Implications

Stylosanthes performed better than other genera on the 2 soil types, indicating the value of this genus for range improvement in south China. Of the stylos tested, the common stylo cultivars Cook, Endeavour, and Graham established better than Caribbean (Verano) and shrubby (Seca) stylos. The common stylos and siratro more than doubled the annual forage production expected from fertilized unimproved rangelands on both soil types (Michalk and Fu 1988).

Cook, a mid-season flowering type, was the highest yielding legume on both soil types even though the 1,001-mm annual rainfall in Dong Fang County is marginal for this cultivar (Cameron 1985). However, observations made on commercial pastures in Australia and China indicate that the performance of Cook stylo under grazing declines markedly with time and many disappear after several years. McIvor et al. (1979) found this decline to be most pronounced in 3-year-old swards after good growth in previous years. In contrast, Graham is more persistent under conditions of drought and heavy grazing, and is the common stylo recommended for range improvement on moderately fertile loam soils in the lower rainfall regions of south China in combination with siratro.

Low phosphorus requirements of Verano and Seca (McIvor 1984) enabled mixtures of these stylo cultivars to dominate swards on low P sandy soils, even without application of superphosphate (Michalk and Fu 1988). While carrying capacity may increase due to extra dry matter produced, livestock production may be limited by the low level of phosphorus in unfertilized Seca and Verano forage. Both species respond significantly to superphosphate applied to sandy soil (Michalk and Fu 1988, D.L. Michalk, unpublished data).

Mixtures of Verano and Seca are recommended for improvement of Hainan's sandy soil rangeland because Seca is relatively low yielding in its establishment year due to slower radicle elonga-

tion and seedling growth rate (Gardener 1978) and maintains a small seed pool with little seed surviving in the soil for more than 2 years (Mott 1982), whereas Verano establishes quickly and flowers continually throughout its vegetative growth phase to produce large seed reserves. This enables Verano to persist for long periods of time even when managerial extremes and grazing abuse prevent an annual seed increment (Gardener 1981).

When sown together, Verano is initially the dominant legume, but is overtaken by Seca after 2 or 3 years. However, Verano still maintains its well-disturbed seed pool from which it colonizes any site in the community left vacant by other plants (Gardener 1981). This provides a buffer against the need to change management policy such as a reduction in grazing pressure that would otherwise be required to aid re-establishment of Seca in a situation where large numbers of mature plants were lost through fire or disease (Mott 1982).

Townsville stylo, an annual which persists in dry climates by seed survival rather than plant survival, did not persist or produce acceptable yield in this evaluation. This may have been due to its intolerance of shading, and failure to keep companion grasses in check did not enable Townsville stylo to compete for light particularly in the seedling stage. Wet season grazing may improve establishment and production of Townsville stylo, but as an anthracnose-susceptible annual it is not likely to be used in preference to anthracnose-tolerant perennial stylos for range improvement in south China.

Siratro was the only nonstylo to produce moderate (2 t/ha) yield and show relative stability with sward age, especially on the more fertile loam soil. Superior drought tolerance enabled siratro plants to pass through the dry season without significant loss. With regular fertilization and controlled grazing, large area sowings on this soil type at Gaopoling Farm are still highly productive after 8 years with siratro still contributing 40% dry matter in siratro-*Setaria sphacelata* (Schum) Stapf ex Massey swards (Zhu Chiming, unpublished data). However, siratro has not persisted in other sowings in south China due to heavy wet season grazing (or cutting), and failure to fertilize regularly with superphosphate.

Siratro can re-populate regularly from soil seed reserves (Jones and Jones 1977) provided pastures are initially stocked lightly to allow seed reserves to accumulate. At Gaopoling Farm, large paddocks of siratro remain vigorous and productive because cattle were excluded from newly June/July sown siratro-based pastures until October and then grazed at 0.6 to 1 AU/ha until December to utilize 50% or less of available forage (Michalk and Dunn 1984).

Although not as productive as siratro, centro persisted on both soil types, and further testing is warranted on more drought hardy species. These include *C. acutifolium* Benth., a Colombian selection, which is sown with gama grass (*Andropogon gayanus* Kunth.) on infertile sandy soils in South America (CIAT 1987), and *C. brasilianum* Benth., which persists under grazing in dry tropical Australia (Anning 1982b).

Archer axillaris failed to establish on either soil type at Gaopoling Farm. However, it has performed well in wetter locations (annual rainfall 1,200 mm) in south China, and was one of the most successful legumes tested at the Qian Jiang Model Farm in Guangxi Province (Liu Ke-Wen, pers. comms.). In northern Australia, axillaris has shown long-term persistence and vigour under grazing on fertile soils but does not persist or effectively nodulate on sandy sites (Anning 1982b).

In addition to yield, grass-legume compatibility is an important aspect of legume evaluation. Legume content and animal performance are closely related with liveweight gains in cattle decreasing when legume content falls below 40% (Bryan and Evans 1973). Contribution of all perennial stylos and siratro in 3-year-old swards with volunteer companion grasses exceeded this threshold

on both soil types at Gaoping Farm in evaluation plots and in commercial sowings. When sown with brownsseed grass, Verano was the only stylo unable to compete with this aggressive grass and legume content declined to 22% on sandy soil and 11% on loam soil in 2-year-old swards. Compatibility of stylos and siratro with other grasses tested in western Hainan is reported by Michalk et al. 1993.

The wildfire which occurred on loam soil in 1983 confirmed the fire-resistance/drought-tolerance relationship reported by Gardener (1980) for stylos. As expected, Cook and Endeavour stylos, which are better adapted to wetter areas than Dong Fang County showed less resistance to fire in terms of post-fire dry matter production than the more drought-tolerant stylos. Fire resistance of Seca and Graham stylos is an important attribute as it allows rangelands oversown with these legumes to remain ungrazed with greater safety until required by cattle late in the dry season.

Fire resistance could also provide a useful management tool for pastures sown with Seca stylo as burning appears to be the easiest and cheapest method of removing aged woody growth and providing rejuvenated herbage of higher quality (Gardener 1980); however, a reduction in stocking rate may be needed to ensure regeneration of a productive sward (Mott 1982), especially when shrubby stylo is sown with Caribbean stylo as a companion. As is the case in northern Australia, fire could also play an important part in renovating Verano-based pastures which have a dense stand of native grass suppressing stylo germination (Mott 1982).

No incidence of anthracnose was observed in this legume study, but the fungus has attacked stylos swards at the Tropical Plant Research Institute in Danxian County (Hainan), and was reported in Guangxi Province in 1983 (Hong 1985). These attacks coupled with the known occurrence of more virulent races of *Colletotrichum* spp. highlights the need to import more germplasm of anthracnose-resistant stylos and other successful legume genera for testing in China.

Other genera which warrant testing include *Alysicarpus*, *Atylosia*, *Clitoria*, *Desmodium*, *Macrotyloma*, *Rhynchosia* and *Vigna* (Anning 1982b; Williams and Clements 1985). Some of these genera are endemic to southern China (Groff et al. 1923, 1924, 1925; Merrill 1927; Merrill 1928, 1930, 1932, 1934) and collections made in 1980 (Hwang et al. 1986) and 1984 (Schultze-Kraft et al. 1984) identified 14 potential forage legumes from which *Alsicarpus vaginalis* (L.) DC var. *diversifolius* Wall., *Desmodium heterocarpum* (L.) DC, and *Dendrolobium lanceolatum* (Dunn) Schindler (ex. *Desmodium dunii*) were selected for further evaluation by the Animal Husbandry Research Institute of Guangdong (Hwang et al. 1986).

Although further introduction and evaluation is needed to select forage legumes for other regions (e.g., rangelands with acid infertile soil) and to minimize disease incidence in stylos, assessment of fertilizer requirements, formulation of grazing strategies, development of seed production systems, and improvement of technical extension services are also needed to ensure long-term stability and profitability of legume-improved rangelands in south China. However, there is a dearth of trained personnel in these research areas and exchanges with advanced countries and training of Chinese scientists and technicians are also urgently needed (Hong 1985).

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Improvement of dry tropical rangelands in Hainan Island, China: 2. Evaluation of pasture grasses

DAVID L. MICHALK, FU NAN-PING, AND ZHU CHIN-MING

Authors are former director, former pasture technician, and production manager of Gaopoling Model Cattle Farm, Ba Suo, Dong Fang County, Hainan Island, People's Republic of China.

Abstract

During 1981-83, we studied 19 grasses for potential improvement of dry tropical (1,001 mm annual rainfall) rangelands in Hainan Island, China. The productivity and persistence of the grasses were tested on sandy (<5 mg/kg available P) and loam soils (12-25 mg/kg) under cutting in a randomized block design with plots split for sequential sowings in 1981, 1982, and 1983. Grass response to legume-fixed and nitrogen fertilizer was also assessed. Thirteen of the 19 grasses tested under cutting established satisfactorily (density >5 plants/m²), but only 6 cultivars produced yields >1.5 metric tonne (t)/ha. *Melinis minutiflora* Beauv., *Brachiaria decumbens* Stapf. and *Chloris gayana* Kunth. yielded more than 1.5 t/ha in 3-year-old swards on both soils, whereas *Panicum maximum* Jacq. and *Setaria sphacelata* (Schum.) Stapf. ex Massey only performed well on fertile loam soil. Grass establishment was superior on sandy soil, but plant density did not correlate well with production which was higher on red loam soil due to better water-

holding capacity and nutrient status. Compatibility of these successful grasses with companion legumes was low with legumes contributing <0.4 t/ha to total yield of 3-year-old *M. minutiflora*, *B. decumbens* and *P. maximum* swards, and having minimal effect on soil nitrogen. Nitrogen fertilizer (50 kg N/ha/yr) more than doubled grass production, but was profitable only where grass response exceeded grass/legume swards >4 t/ha. *S. sphacelata* was the only grass to form a stable mixture with companion legumes. [*Macroptilium atropurpurem* (D.C.) Urban and *Stylosanthes guianensis* (Aubl.) Sw.], which yielded more than 1.1 t/ha in 3-year-old swards on loam soil. This combination was recommended for improvement of loam soil rangelands. It is concluded from this study that range improvement with perennial grasses is confined to fertile soils, while direct broadcast of *Stylosanthes* legumes only into grazed native pastures is the practice recommended for improvement of infertile sandy soil until persistent low P tolerant grasses are found for the dry tropics.

Key Words: China, dry tropical, low phosphorus soil, *Setaria sphacelata*, N response, legume

Known as "wastelands", the rangelands of dry tropical Hainan Island, China, are dominated by low-producing grasses (<2.2 DM/ha/hr) of poor quality (Michalk and Fu 1988). Recent studies have identified suitable legumes for improvement of major soil types in western Hainan which significantly increase carrying capacity and beef output (Michalk et al. 1985, Michalk and Fu

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1988, Michalk et al. 1993). There is concern regarding the long-term stability of native pastures oversown with introduced legumes. Experience in the dry tropics of Australia indicates that increased grazing capacity of legume-improved rangeland may lead to pasture instability (Andrew 1988) caused by a sudden decline in the native perennial grass component (Winks et al. 1974) and invasion by annual species (Gillard and Fisher 1978). Perennial grasses are desirable components of range vegetation because they provide production stability, prevent ingress of woody weeds, and commence growth on less precipitation than do annual legumes and grasses (Norman 1967).

Like northern Australia, dominant native grasses of dry tropical Hainan are either of poor quality or readily damaged by heavy grazing. Heavy grazing has caused retrogression of rangelands in Hainan from bunchgrass-dominant swards through secondary transitional communities to prostrate, low-producing, grazing-tolerant grasses such as *Chrysopogon aciculatus* Trin. and *Axonopus compressus* (Swartz) Beauv. While domesticated local grasses such as *Miscanthus floridulus* Warb. ex K. Schum & Lauterb., *Digitaria sanguinalis* (L.) Scop., *Sorghum propingnum* (Kunth.) Hitchcock, *Hemarthria compressa* R. Br., and *Pennisetum polystachyon* Schult. have been cultivated and utilized for many years in the southern provinces (Hong 1985, Hwang et al. 1986), Chinese scientists and state farm managers realized that the introduction of grasses and legumes offers a faster and more efficient means of range improvement in south China (Hong 1985).

Planned introduction of pasture grasses and legumes began in the early 1950's, and under the supervision of the Chinese Academy of Agricultural Science, universities, and provincial agricultural departments, imported species have been tested and popularized to varying degrees in the tropical areas of China. Test plots of some Australian cultivars established in 1974 at the Livestock Research Institute of Guangxi Province first highlighted the potential of pasture species used commercially in northern Australia for improvement of the tropical and subtropical zone of China (Hong 1985). While many of the introduced grasses (e.g., *Panicum maximum* Jacq., *Pennisetum purpureum* Schum. and forage sorghums) have performed well in the wet tropical zone, little is known about the productivity and persistence of introduced grasses in the dry tropical regions of south China.

In this second paper focusing on improvement of dry tropical

rangelands in China, we report results of a 3-year (1981-1983) experimental program undertaken to evaluate grasses on 2 soil types at Gaopoling Model Cattle Farm (Dong Fang County) in western Hainan Island. Aims of the study were: (1) to assess the growth potential of some Australian grasses in dry tropical China; and (2) to determine grass response to legume-fixed and fertilizer nitrogen.

The results reported here were used in conjunction with legume evaluations also undertaken at Gaopoling Farm (Michalk et al. 1993) to formulate grass-legume mixtures for use under grazing in western Hainan.

Material and Methods

Site

The location, climate, soil types, and range vegetation of Gaopoling Model Cattle Farm (19°09'N; 108°68'W) are described in detail by Michalk et al. (1993). These conditions are representative of the 162,000 ha set aside in dry tropical Hainan Island for improvement for range-based cattle production.

Plot Design and Culture

To select grasses to improve range forage, an experiment was conducted on replicated (3) plots (3 m X 21 m) of 19 tropical grasses (Table 1) arranged in a randomized block design split in time for sequential sowings on sandy and red loam soils. Grasses were sown by hand at recommended seeding rates (Table 1) and lightly raked into weed-free, cultivated seedbeds in 1981 (4 August), 1982 (12 June), and 1983 (14 July).

The loam site for the 1981 sowing was newly cleared of soft-wood scrub, stick-raked, and ploughed between April and planting. Loam sites for the 1982 and 1983 sowings and all sandy sites were scrub-free, open grassland. Germination tests conducted prior to sowing showed seed of all grasses to be of good quality (Table 1).

Treatments

To test compatibility with legumes and contribution of legume-fixed nitrogen to grass production, plots were split for the 1981 sowing to include: (1) grass only; (2) grass + a mixture of *Macroptilium atropurpureum* (DC) Urban cv Siratro, *Stylosanthes hamata* (L.) Taub. cv Verano, and *S. scabra* Vog. cv Seca sown at 6 kg/ha on sandy soil, and siratro and *S. guianensis* (Aubl.) Sw. cv Cook at the same rate on loam soil, and (3) grass + fertilizer nitrogen (50 kg

Table 1. Name, sowing rate, germination percentage, and first-year establishment of tropical grasses tested at Gaopoling Farm, 1981-1983.

Botanical name	Common name & cultivar	Sowing rate	Germination	Establishment ¹	
				Sand	Loam
<i>Melinis minutiflora</i> Beauv.	Molasses grass	4	56	46a	23a *
<i>Setaria sphacelata</i> (Schum.) Stapf ex Massey	Setaria cv Kazungula	5	53	18bc	6cd *
<i>Brachiaria decumbens</i> Stapf.	Signal grass cv Basilisk	6	40	9def	7cd *
<i>B. mutica</i> (Forsk) Stapf	Para grass	6	31	12de	9cd
<i>Chloris gayana</i> Kunth.	Rhodes grass cv Samford	6	48	22b	8bcd*
<i>C. gayana</i>	Rhodes grass cv Callide	6	33	8ef	9bcd
<i>Panicum maximum</i> Jacq.	Guinea grass cv Hamil	6	37	18bd	13b *
<i>P. maximum</i> Jacq. var. <i>trichoglume</i> Eyles	Green panic cv Petrie	6	23	8ef	4d *
<i>Cenchrus ciliaris</i> L.	Buffel grass cv Gayndah	4	53	6f	8bcd
<i>C. ciliaris</i>	Buffel grass cv Biloela	4	28	18bc	11bc *
<i>Paspalum plicatulum</i> Michx.	Brownseed grass cv Bryan	6	32	7ef	4d *
<i>P. plicatulum</i>	Brownseed grass cv Rodd's Bay	6	68	16cd	5d *
<i>Urochloa mosambicensis</i> (Hack.) Dandy	Sabi grass cv Nixon	6	29	4f	7cd *
<i>Pennisetum clandestinum</i> Hochst. ex Chiov.	Kikuyu cv Whittet	2	48	F	F
<i>Paspalum dilatatum</i> Poir.	Dallis grass	10	63	F	F
<i>P. notatum</i> Flugge	Bahia grass	4	80	F	F
<i>Axonopus affinis</i> A.	Carpet grass	3	98	F	F
<i>Sorghum almum</i> Parodi	Columbus grass	3	55	F	F
<i>Cenchrus setigerus</i> Vahl.	Birdwood grass	4	36	F	F

Grass density means within soil type followed by the same letter are not significantly different at $P < 0.05$; * indicates a significant difference ($P < 0.05$) in grass density due to soil type; ¹ Establishment for grass/legume plots (Treatment 2) averaged over 3 sowings (1981, 1982, 1983). F = failed to establish.

N/ha/yr). Treatments 1 and 3 were sown in the 1981, but only grass/legume mixtures (Treatment 2) were sown in 1982 and 1983.

All plots were fertilized with local Grade 4 superphosphate (28 kg P/ha) at sowing and top-dressed each year (14 kg P/ha). Legume seed was inoculated and pelleted prior to sowing.

Sampling

In November of each establishment year, grass and legume establishment were estimated by counting plants in two 0.5-m² quadrats/plot. Dry matter yield was assessed by harvesting with hand shears the entire plot (3 m × 21 m) or subplot (3 m × 7 m) at the end of the wet (December) and dry (May) seasons each year. Harvested material was weighed in the field, and subsamples taken to determine dry matter content and botanical composition. Only "wet season" data for grass/legume plots (Treatment 2) were used to assess grass performance as "dry season" growth was negligible. All yields are expressed in metric tonnes (t)/ha.

Statistical Analyses and Experimental Design

Analyses of variance split in time were set up in the Genstat program (Payne et al. 1988) to analyze density and production data from the randomized block design for establishment year performance of sown grasses and companion legumes in the 3 sequential sowings with soil types (2), establishment years (3), and species (13) as main effects. Least significant differences based on error terms from the appropriate stratum of the analyses of variance were used to differentiate between significant and nonsignificant means.

Similar analyses were used to test significance of grass and legume yield in 1- (sequential sowings in 1981, 1982, and 1983); 2-(1981 sowing cut in 1982, and 1982 sowing cut in 1983); and 3-(1981 sowing cut in 1983) year-old pasture swards. A linear regression model with fitted terms for year, soil type, pasture age, species, and all significant ($P < 0.05$) second and third order interactions was used to predict yield of sward components and verify analyses of variance. The high degree of variability in grass ($R^2 = 0.94$), legume ($R^2 = 0.95$) and total ($R^2 = 0.95$) yields explained by these models indicated that there was no confounding between sites and years within soil types due to pooling data in the analysis of variance. Linear and nonlinear regressions were also used to examine relationships between species performance, rainfall, plant density, and age of pasture.

Analyses of responses of selected sown grasses to legume- and fertilizer-nitrogen were undertaken on both soils. This analysis included soil type (2), species (6), and nitrogen treatments (3) as main effects (Fig. 3).

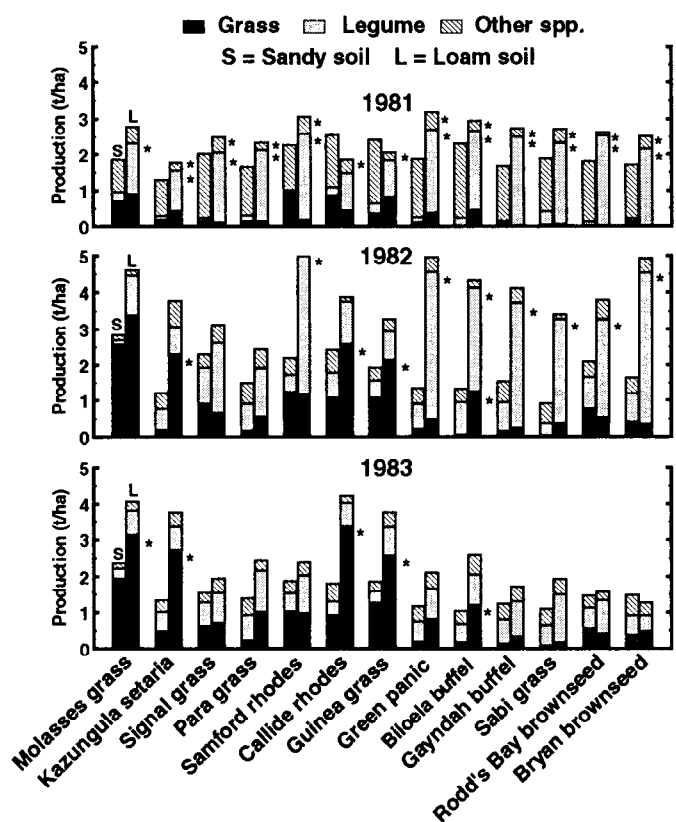
Results

A. Establishment Year

Plant Density

Thirteen grasses established successfully with average density > 5 plants/m² (Table 1). Soil type affected ($P < 0.05$) grass density with 60% more plants measured at the end of the first wet season in 1-year-old swards on sandy soil compared with red loam soil (Table 1) in all 3 sowings.

Molasses grass (see Table 1 for botanical names) established best on both soil types, producing dense, vigorous stands. After molasses grass, setaria, rhodes grass, guinea grass, and buffel grass established well on sandy soil with similar density (18 to 22 plant/m²), but on loam soil the number of guinea and Biloela buffel seedlings was higher than the other grasses (Table 1). Despite differences in length of growing season and rainfall (Table 2), there was no significant effect of year of sowing on establishment



* and ** indicates significant differences in legume or grass yield due to soil type at $P < 0.05$ and $P < 0.01$

Fig. 1. Establishment year production (t DM/ha) of grass/legume mixtures sown on sand and loam soils at Gaopoling Farm (1981-83).

density. Some grasses (e.g., green panic, Gayndahl buffel, columbus grass, and sabi grass) were present only as weak plants, many of which failed to survive the first dry season. Grasses which failed to establish in 1981 also failed at subsequent sowings.

Legume density and stylo:siratro ratio differed ($P < 0.05$) with soil type and year of sowing. Legume density was 36% higher with a greater proportion of siratro on loam soil (5:7 stylo: siratro; 11.5 plants/m²) whereas stylos established better on sandy soils (7:2 stylo:siratro; 8.5 plants/m²). Companion legumes did not affect grass establishment or vice versa. There was no correlation between grass and legume density ($R^2 = 0.13$).

Production in Establishment Year

Molasses grass produced highest establishment year yield followed by rhodes grass, guinea grass, and setaria, which all produced mean yields > 0.9 t/ha (Fig. 1), except for setaria grown on sandy soil (0.3 t/ha). Grass production in 1-year-old stands was affected by year of establishment with lower yield ($P < 0.01$) recorded in 1981 (Fig. 1). This was due to lower than average rainfall and the short growing season caused by late sowing (4 August). Grasses did not respond uniformly to more favourable growth conditions experienced in 1982 and 1983 (Fig. 1). Production of grasses which yielded < 0.5 t/ha at the first sowing was similar at subsequent sowing, where grasses with mean yield > 0.5 t/ha in 1981 produced between 0.6 and 1.9 t/ha more dry matter in the 1982 and 1983 sowings (Fig. 1).

Soil type did not affect establishment year yield of grasses with mean yield < 1 t/ha, except for Gayndahl buffel which produced more dry matter ($P < 0.05$) on loam soil (Fig. 1). Grasses with mean

production >1 t/ha (molasses, setaria, guinea grass, and Callide rhodes) were consistently more productive when grown on loam soil (Fig. 1). Correlation between grass yield (Fig. 1) and rainfall received during the sowing to harvest period accounted for most of the variation in production between establishment years on loam soil (R^2 0.98), but explained less variation on sandy soil (R^2 0.85) where nutrient deficiencies were more pronounced (Michalk et al. 1993).

For grass species which are more suited to regions with annual rainfall <1,000 mm (e.g., setaria and rhodes grass), fertility limited growth most on sandy sites as rainfall explained <25% of year-to-year variation in first-year production. In contrast, rainfall accounted for 90% of yield variation on sandy soil of grasses which perform best in >1,300 mm rainfall zones (e.g., guinea grass and green panic). For all species, first-year grass yield correlated poorly with plant density. Despite higher establishment density on sandy soil (Table 1), production of sown grasses was similar or superior on loam soil, depending on growth conditions and length of growing season (Table 2). Grass yield was not affected by legume density in establishment year.

Table 2. Significant main effects for establishment year production (t DM/ha) of grass/legume mixtures sown on and loam soils at Gaopoling Farm (1981-1983).

Main Effect	Comparison	Parameter		
		Grass	Legume	Other spp.
Soil type	Sand	0.54a	0.45b	0.76a
	Loam	0.98a	1.74a	0.35b
Year	1981	0.31b	1.04b	0.90a
	1982	0.96a	1.55a	0.40b
	1983	1.01a	0.69b	0.37b
Sown grass	Molasses grass	2.11a	0.64b	0.34b
	Signal grass	0.53def	1.09ab	0.62a
	Setaria	1.06bcd	0.63b	0.52ab
	Para grass	0.38f	1.20a	0.57a
	Callide rhodes	1.55b	0.70b	0.55ab
	Samford rhodes	0.94cde	1.44a	0.51ab
	Guinea grass	1.37bc	0.62b	0.56a
	Biloela buffel	0.37f	1.44a	0.64a
	Gayndah buffel	0.53def	1.26a	0.64a
	Green panic	0.16f	1.41a	0.60a
	Sabi grass	0.13f	1.29a	0.57a
	Rodd's Bay brownseed	0.42f	1.29a	0.51ab
	Bryan brownseed	0.30f	1.37a	0.60a

Main effect means within parameters followed by the same letter are not significantly different at $P<0.05$.

	Sowing to harvest		
	1981	1982	1983
Growth period (days)	130	172	159
Rainfall (mm)	458	879	1022

Unlike sown grasses, soil type affected ($P<0.05$) first year legume production with sandy soil producing only 9% to 60% of yield measured on loam soil, depending on year of establishment and companion grass (Fig. 1; Table 2). Highest first year legume yield was measured in the 1982 sowing on both soil types and lowest in 1981 on sandy soil and in 1983 on loam soil (Fig. 1). A higher ($P<0.01$) proportion of native grass measured in the 1981 sowing may explain poor legume growth on sandy soil, but there is no apparent reason for the 50% reduction of legume yield on loam soil for the 1983 sowing (Fig. 1). Aggressive grasses (e.g. setaria, guinea, molasses, and Callide rhodes) also affected legume performance by reducing yield by 1 t/ha, particularly on loam soil (Fig. 1) where grass growth was not limited by soil fertility.

B. Total Production

Molasses grass was the most productive grass tested (Fig. 2, Table 3) with yield averaged over soil types and production years exceeding that of signal grass, guinea grass, Callide rhodes grass, and setaria by at least 0.9 t/ha/yr. Overall, grass performance was affected ($P<0.05$) by soil type (Fig. 2) with loam soil producing 45% more dry matter than sandy soil (Table 3). However, grass

Table 3. Significant main effects for establishment year production (t DM/ha) and composition of 1-, 2-, and 3-year-old grass/legume mixtures sown in sand and loam soils at Gaopoling Farm (1981-1983).

Main Effect	Comparison	Parameter		
		Grass	Legume	Other spp.
Soil type	Sand	1.04b	0.77b	0.55b
	Loam	1.50a	1.49a	0.65a
Year	1-year-old	0.76c	1.08b	0.56b
	2-year-old	1.73a	1.60a	0.77a
	3-year-old	1.31b	0.73c	0.47c
Sown grass	Molasses grass	2.95a	0.81ef	0.20e
	Signal grass	2.05b	0.90def	0.53cd
	Setaria	1.65c	0.99cdef	0.59cd
	Para grass	0.95d	1.00cde	0.38d
	Callide rhodes	1.91bc	1.01cde	0.61bc
	Samford rhodes	1.67c	1.13cd	0.63bc
	Guinea grass	1.93bc	0.72f	0.47cd
	Biloela buffel	0.54efg	1.58ab	0.88a
	Gayndah buffel	0.39g	1.45ab	0.93a
	Green panic	0.46fg	1.45ab	0.63bc
	Sabi grass	0.33g	1.21bc	0.78ab
	Rodd's Bay brownseed	0.83de	1.26c	0.44d
	Bryan brownseed	0.82def	1.22bc	0.85a

Main effect means within parameters followed by the same letter are not significantly different at $P<0.05$.

response was not uniform: production of 6 grasses was affected significantly by soil type whereas 7 species (Samford rhodes, Callide rhodes, signal, Gayndah buffel, green panic, Bryan brownseed, and sabi) produced similar yields on both soil types. Where there was a significant difference in production due to soil type, yield of grasses was superior on loam soil, except for Rodd's Bay brownseed which produced 0.85 t/ha/yr more dry matter on sand soil (Fig. 2).

Grass yield for 1-year-old pastures on both soil types was generally less than half production of 2-year-old stands (Fig. 2), but the production pattern over the whole measurement period differed with species and soil type. For sandy soil, there was no difference between grass production in 2- and 3-year-old stands, except for molasses grass and signal grass where 3-year-old swards yielded less ($P<0.05$) than 2-year-old swards.

For loam soil, 5 of the 6 best grasses yielded less ($P<0.05$) as 3-year-old than as 2-year-old pastures (Fig. 2) due mainly to a wildfire which burnt the 1981 sown site in late August 1983. Guinea grass, signal grass, and setaria recovered best with yield still exceeding 2.4 t/ha (Fig. 2) in 3-year-old swards. The production pattern over time for grasses with yield >0.5 t/ha/yr was either parabolic (Year 1 < Year 2 > Year 3) or logarithmic (Year 1 < Year 2 = Year 3). There was no consistent relationship between age and yield of grasses on loam soil with mean 3-year yield <0.5 t/ha/yr.

For both soil types, grass and legume yields in 2- and 3-year old pastures were poorly related to plant density measured in either the current or previous season. Despite higher density at establishment and in subsequent years, production of sown grass on sandy soil was only 50% that of loam soil in 2-year-old stands (1.2 vs 2.2 t/ha).

Dominated by siratro, loam soil legume production (1.5 t/ha/yr) was twice that of the stylo-dominate legume component of sandy soil (Fig. 2). Despite difference in overall production levels, a

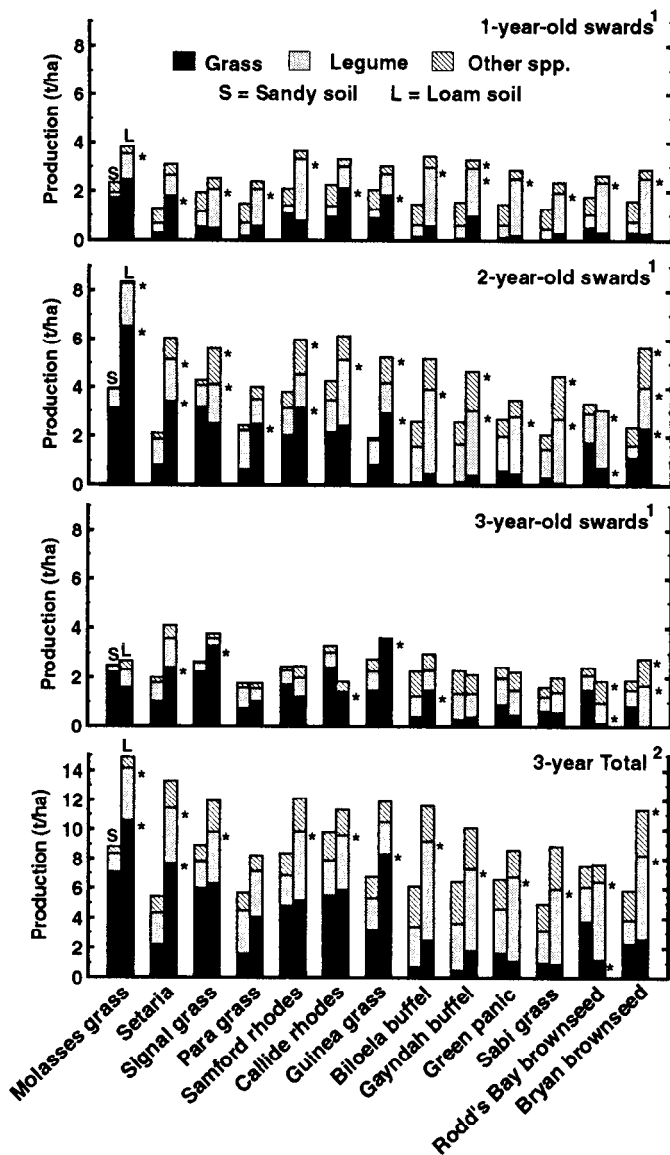


Fig. 2. Yield and composition of 1-, 2-, and 3-year-old grass pastures sown on sand and loam soils at Gaopoling Farm (1981-83).

similar parabolic pattern of legume production was evident on both soil types with more legume present in 2-year-old grass/legume mixtures. However, for loam soil this may be due to the 1983 wildfire which reduced legume to the same level as sandy soil.

Legume growth was suppressed ($P < 0.05$) by grasses such as molasses grass, signal grass, and setaria, but legume production on loam still exceeded sandy soil legume yield for each grass treatment by 0.5 to 1.3 t/ha/yr (Fig. 2), except for guinea grass, which responded vigorously to nutrients released by the 1983 wildfire and reduced legume yield to zero on loam soil. The proportion of legume present accounted for more than 25% of the total sward production over 3 years, except for grass species with total 3-year grass yield > 8 t/ha on loam and > 5.5 t/ha on sandy soil (Fig. 2).

Native bunch grasses on loam soil were more productive than stoloniferous species on sandy soil, but they did not compete as vigorously with sown grasses and legumes. In general, yield of sown grasses and legumes correlated inversely with yield of volunteer species on sandy soil (R^2 0.46), but were not related on loam soil (R^2 0.24). On sandy soil, competition was most intense in establishing pasture where native grasses accounted for 44% of total production, but declined in 2- and 3-year-old pastures

($< 18\%$) when the more erect sown grasses and legumes effectively shaded the prostrate natives. On loam soil, the contribution of native bunch grasses was highest (1.1 t/ha averaged over all grass/legume mixtures) in 2-year-old pastures.

Molasses grass most effectively controlled growth of native grasses, reducing their contribution to < 0.1 t/ha on both soil types by the second year of production. Signal grass and guinea grass were the next most competitive grasses which reduced native grass contribution to < 0.2 t/ha by the third year of production.

In general, total production followed a parabolic pattern with 2-year-old pastures producing significantly more dry matter than 1- or 3-year-old swards. Due to superior performance of sown grasses and legumes, total production on loam soil was higher ($P < 0.05$) than sandy soil in most treatments (Fig. 2). The largest species \times soil type interaction occurred with setaria where loam soil plots produced an additional 7.8 t/ha/3-yr above sandy soil production (Fig. 2).

Response to Nitrogen

Response of selected 2-year-old grass swards (1981 sowing) to legume- and fertilizer-nitrogen are shown in Figure 3 for both soil types. Nitrogen had little impact on establishment year yield, and results for 3-year-old swards were skewed by the 1983 wildfire on loam soil.

Overall, urea (50 kg N/ha) applied at the start of the wet season improved grass production by 68% on sand soil and doubled yield on red loam compared with grasses grown without companion legumes and nitrogen fertilizer (Fig. 3, Table 4). However, species showed differential responses to nitrogen and soil type. On loam soil, all grasses yielded more ($P < 0.05$) when fertilized with urea (Treatment 3), whereas on the sandy site, only molasses grass and signal grass responded significantly (Fig. 3). This indicated that other factors such as soil moisture and other soil nutrients limited grass response on sandy soil.

There was no difference in grass yield between grass only (Treatment 1) and grass/legume plots (Treatment 2) to indicate active transfer of legume-fixed nitrogen to sown or indigenous companion grasses on either soil type (Table 4) even in treatments where legume yield exceeded 2 t/ha.

Volunteer native grasses failed to respond to nitrogen applied to sandy soil (0.7, 0.6, and 0.8 t/ha for Treatments 1, 2, and 3, respectively), but increased yield by 0.5 to 1.3 t/ha on loam soil in

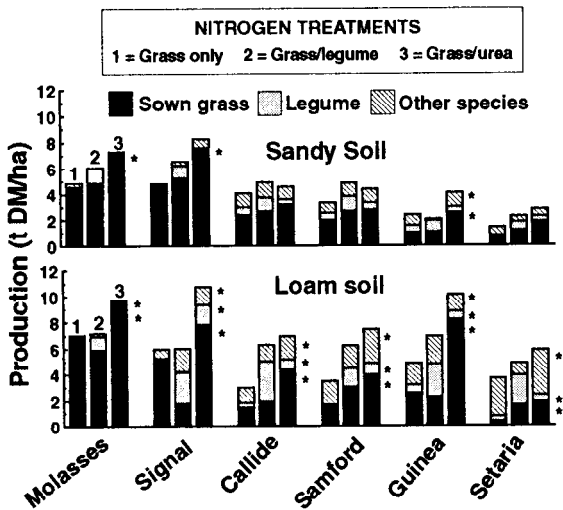


Fig. 3. Response of selected 2-year-old grass swards to legume- and fertilizer-nitrogen when grown on sand and loam soils at Gaopoling Farm.

Table 4. Significant main effects for response of selected grasses to legume and fertilizer nitrogen.

Main Effect	Comparison	Parameter		
		Grass	Legume	Other spp.
Soil type	Sand	2.92a	0.56b	0.70b
	Loam	3.59a	1.16a	1.48a
N-treatment	Grass only	2.48b	0.37b	1.01b
	Grass/legume	2.59b	1.61a	0.97b
	Grass/urea	4.69a	0.59b	1.29a
Sown grass	Molasses grass	6.54a	0.41b	0.09d
	Signal grass	5.29b	0.91a	0.85c
	Callide rhodes	2.68c	0.79a	1.52a
	Samford rhodes	2.69c	1.04a	1.25b
	Guinea grass	2.94c	0.74a	1.50a
	Setaria	1.26d	0.96a	1.19b

Main effect means within parameters followed by the same letter are not significantly different at $P < 0.05$.

all sown grass plots except guinea grass and molasses grass, which suppressed native grass growth (Fig. 3).

Discussion and Management Implications

The initial evaluation criteria for grasses introduced to dry tropical environments include: (1) ability to establish and produce under variable rainfall regimes; (2) ability to survive a protracted dry season; and, (3) compatibility with companion legumes (Edye 1975). Only 6 grasses fulfilled these requirements by producing mean yields > 1.5 t/ha. Soil type was an important determinant of grass adaptation and yield. Molasses grass, signal grass, and guinea grass yield exceeded 1.5 t/ha as 3-year-old swards on both soil types, but only the latter 2 responded significantly to the higher soil fertility and produced superior yield on loam soil. Setaria failed on sandy soil, but produced 2.4 t/ha in 3-year-old stands on loam soil whereas Callide rhodes and Rodd's Bay performed better on sandy soil.

These evaluation results were used to formulate grass/legume mixtures for improvement of sandy and red loam rangelands in western Hainan. For pasture development on red loam soil, a mixture of Graham stylo and Siratro (Michalk et al. 1993) combined with guinea grass, signal grass or setaria is recommended for drilling into prepared seedbeds. Adaptation to lower rainfall and cooler temperature regimes enabled setaria to make significant growth on "unseasonable rainfall" during the cooler dry season, and make it the preferred grass for red loam even though it yielded less than either signal grass or guinea grass in this experiment.

Subsequent development of 515 ha of setaria-based pasture at Gaopoling Farm (Michalk and Dunn 1984) demonstrated that setaria can be successfully grown on red loam soil using low fertilizer inputs (28 kg P/ha/3-years; no nitrogen). These pastures have remained highly productive with siratro still contributing 40% of the dry matter after 8 years of grazing (Zhu Chin-Ming, unpublished data). Setaria has also proved to be a valuable grass for improvement of acid soil areas below 1,000 m altitude in subtropical Guangdong (Michalk and Ryan 1989), Fujian (Wu et al. 1986), Guangxi (Michalk 1988), and Yunnan (Bruce-Smith et al. 1990) provinces.

A mixture of stylos (Seca, Verano, and/or Graham), either broadcast directly into native rangeland or combined with rhodes grass or signal grass on rough disked seedbeds are recommended improvement procedures for sandy soil. However, there are indications that these sown grasses may lack persistence, particularly if grazing management is poor. For example, while rhodes grass performed well on both soil types in this study, subsequent observations in commercial sowings indicate that the commonly reported

pattern of rapid early colonization but lack of long-term persistence (Anning 1982) is also true for the 2 cultivars tested at Gaopoling Farm. Similarly, signal grass is unlikely to survive years in which the onset of the wet season is delayed (probability of 1 in 7 years).

Failure of buffel grass and sabi grass in this dry tropical zone of Hainan indicates their intolerance of low soil fertility and poor competitiveness with native grass and companion legumes, a result also noted by Anning (1982) in northern Queensland. While the superphosphate rate (28 kg P/ha) used in the present study has proved to be sufficient to maintain legume-based pastures on sandy soil for at least 3 years (Michalk et al. 1985, Michalk and Fu 1988), higher P inputs may be required to establish and improve performance of grasses from these genera.

Other studies at Gaopoling Farm indicate that a doubling of the superphosphate rate will increase buffel grass to 1 t/ha in the establishment year on sandy soil (D.L. Michalk, unpublished data). This has also been observed in verano stylo-sabi grass pastures in northern Australia where sabi grass only becomes dominant with high superphosphate applications (McIlvor 1984). Additional studies are needed to specify initial and maintenance phosphorus requirements of sown grasses in south China, particularly for phosphorus infertile sands.

As a "pioneer" species to provide quick cover in establishment year, molasses grass may be sown with these mixtures on either soil type. With time, however, more strongly perennating, grazing-resistant, and fire-tolerant grasses take over to form a stable pasture which is more acceptable to cattle. Molasses grass may also be used in scrub control to provide rapid fuel build-up prior to burning and ensure a hot fire to exact maximum damage to shrubs (Humphreys 1978). Scrub encroachment is a major problem for range improvement on red loam soil (Colman and Wolfe 1987).

Brownseed grass was initially recommended for sandy soils in Hainan (Michalk et al. 1985), but commercial experiences in Queensland (Anning 1977) and more recently in China (Colman and Wolfe 1987) indicate that this grass should not be shown because it is often too competitive even for the perennial stylos and has low acceptability to cattle (Whiteman et al. 1985) unless heavily fertilized with nitrogen (Yet 1980). However, even when abundant forage is available, beef output on brownseed grass pastures is very low (Whiteman et al. 1985). Further, in the present study, brownseed grass did not recover from the 1983 wildfire.

Poor compatibility with companion legumes is a major concern with some of the successful grasses, and careful grazing management may be required to maintain legume component above 40%, the proportion desired for high cattle production (Bryan and Evans 1973). With legume content < 0.4 t/ha in 3-year-old swards of molasses grass, signal grass, and guinea grass (loam soil only), contribution of companion legume to soil nitrogen was minimal. Further, the parabolic production pattern of molasses grass and signal grass with time on sandy soil is indicative of productivity losses described by Hutton (1979) as grass dominant pastures become progressively nitrogen deficient.

In contrast, setaria formed a stable mixture on loam soil with siratro/stylo yield exceeding 1.1 t/ha by the third season of production. Slower establishment of setaria appears to favour the associated legumes, particularly siratro, but the long-term stability of setaria/legume association depends on the legume chosen, grazing management, and fertilizer policy (Hacker and Jones 1969).

The inadequacy of legumes to provide sufficient nitrogen for companion grass growth was highlighted by the comparison of grass-legume swards with grasses fertilized with nitrogen, particularly on loam soil where moisture was less restrictive than on sandy soil. Molasses grass, signal grass, and guinea grass produced between 3.7 and 6 t/ha when fertilized with nitrogen. Assuming a value for pasture dry matter of Yuan 0.05/kg DM (\$US 1 = Yuan

5.5) and nitrogen fertilizer cost of Y3.27/kg N plus Y16/ha for application (D.L. Michalk, unpublished data), the use of 50 kg N/ha/yr in the present study would be profitable only where grass response exceeded 4 t/ha/yr.

Lack of grass response to sown legumes was probably due to a low level of available legume-fixed nitrogen caused by poor Year 1 legume growth (0.4 t/ha sand; 1.2 t/ha loam) and not to a failure of legumes to nodulate. The lack of response of legumes to applied nitrogen supports this conclusion. Based on Henzell's (1968) finding that legume-fixed nitrogen (LFN) available to companion grass can be estimated by the equation: $LFN = 0.8 \times 1.5 \text{ legume DM} \times 2.5\% \text{ N}$, only 12 (sand) to 36 (loam) kg/ha of LFN was available to grasses at the start of the second wet season. This is similar to estimates reported by Wetselaar (1967) for first year Townsville stylo (*S. humilis* H.B.K.) pastures in dry monsoonal Australia. In subsequent years, however, Townsville stylo fixed more than 80 kg N/ha/year (Wetselaar 1967). Other studies at Gaopoling Farm have also demonstrated the value of sown legume on companion grass production in established swards (Fu and Michalk, unpublished data).

Fire can also have a significant effect on grass-legume balance, with fire generally favouring perennial grasses. Some introduced grasses such as guinea grass tolerate burning, whereas others like molasses grass are destroyed by fire. Recovery of molasses grass after burning in this study suggests that the wildfire on loam soil was not a hot fire. However, the legume component was reduced significantly by fire due mainly to poor post-fire recovery of Cook stylo, a result also reported by Michalk et al. (1993).

The results of this evaluation study indicate that the use of introduced grasses such as setaria will be mainly confined to red loam soils where existing vegetation (including scrub) can be removed by cultivation, and where acceptable grass production is possible with minimal phosphorus inputs. However, range improvement on sandy soil is confined to low-cost introduction of legumes, especially stylos, into burnt native pasture until more persistent, low phosphorus-tolerant grasses are found.

Grasses not included in the present studies which warrant testing in Hainan Island include *Andropogon gayanus* Kunth. (gamba grass); *Bothriochloa insculpta* (Rendle) Schweick (creeping blue grass); and *Brachiaria humidicola* (Hochst. ex A. Rich.) A. Camus, which have both shown compatibility with recommended legumes, disease resistance, and adaption to a wide range of soil types in northern Australia (Anning 1982) and South America (Hutton 1979).

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Effects of mechanical treatments and climatic factors on the productivity of Northern Great Plains rangelands

MARSHALL R. HAFERKAMP, JERRY D. VOLESKY, MICHAEL M. BORMAN, RODNEY K. HEITSCHMIDT, AND PAT O. CURRIE

Authors are range scientist USDA-ARS, Fort Keogh Livestock and Range Research Laboratory, Miles City, Mont. 59301; research animal scientist USDA-ARS, Forage and Livestock Research Laboratory, El Reno, Okla. 73036; range ecologist USDI-BLM, Oregon State University, Corvallis, Ore. 97331; range scientist and research leader, and range scientist (retired) USDA-ARS, Fort Keogh Livestock and Range Research Laboratory, Miles City, Mont. 59301.

Abstract

Impacts of 7 range treatments and climate on late spring herbage standing crops (SC) were measured in rangelands near Miles City, Mont., from 1983 to 1990. Treatments, established in 8 pastures at 2 sites, were: (1) untreated control + season long grazing (SL); (2) soil tillage (ST) + SL; (3) ST + drill seeding legumes (DS) + SL; (4) brush control (BC) + ST + DS + switchback grazing (utilizing 2 pastures); (5) BC + ST + DS + SL; (6) ST + nitrogen fertilization + SL; and (7) contour furrowing (CF) + aerial seeding legumes + SL. Data were analyzed using years as a repeated measure. Treatments increased ($p \leq 0.05$) total SC 320 kg/ha over controls, but did not affect species/species group composition. Treated pastures produced similar ($p \geq 0.10$) SC of 881 kg/ha. Total SC averaged 490 kg/ha more ($p \leq 0.05$) in 1983, 1986, 1987, 1989, and 1990 than in 1984, 1985, and 1988. Perennial cool-season grass SC was greatest in 1986 (651 kg/ha). Peak annual grass SC (337–506 kg/ha) occurred in 1983 and 1984, the 2 years following ST or CF, and 1989 and 1990, the 2 years following severe drought. Although regression analyses showed fall, winter, and spring precipitation and temperature were closely related to spring SC, less than 50% of the variation in SC was accounted for when precipitation and temperature were summed on a 1-month, 2-month, or 3-month basis. Above-average fall and spring precipitation (September and April) resulted in the greatest total SC. Species composition varied temporally with changing weather conditions and management strategies.

Key Words: climate, temperature, precipitation, western wheatgrass, Japanese brome, drought, standing crop, annual grass competition

The magnitude of secondary productivity in grazed ecosystems is largely dependent upon primary production. To successfully increase livestock production in most grazed ecosystems often requires an increase in forage production. The broad objective of this study was to quantify the integrated impacts of soil tilling, legume interseeding, brush removal, nitrogen fertilization, and climate on herbage production of Northern Great Plains rangelands. This objective was founded on the results of previous

research conducted at various locations in the Northern Great Plains which has shown precipitation and ambient air temperatures are the principal factors affecting plant growth and development (Sims and Singh 1978, White 1985, Sala et al. 1988, Frank 1988), and that dynamic shifts in herbage production occur with addition of nitrogen (Goetz et al. 1978, Wight 1976, Wight and Black 1979), removal of woody plants (Vallentine 1980), and mechanical disturbance of soil (Lacey et al. 1985, White et al. 1981, Wight et al. 1978, Kartchner et al. 1983). Moreover, the relative impacts of these treatments have been shown to vary temporally in concert with climatic variations, soil type, slope, and post treatment management tactics (White et al. 1981, Gartner 1988). This study was designed to examine the integrated effects of these factors on herbage production at a single location over several years.

Study Areas and Methods

Study Areas

Research was conducted at 2 sites on the Fort Keogh Livestock and Range Research Laboratory (46°22'N 105°5'W) near Miles City, Mont. Regional topography ranges from rolling hills to broken badlands with small intersecting ephemeral streams flowing into large rivers located in broad, nearly level valleys. Indigenous vegetation on the 22,500-ha research station is a grama-needlegrass-wheatgrass (*Bouteloua-Stipa-Agropyron*) mix (Küchler 1964). Long-term annual precipitation averages 338 mm with about 60% received during the April through August growing season (NOAA 1982–90). Total annual precipitation during the 8-year study was below average in 6 of the 8 years (Fig. 1). Temperatures often exceed 38° C during summer and decrease to –40° C or less during winter. The average frost-free period is 150 days.

The 2 study sites were located about 6 km apart. Topography of both sites ranged from gently sloping (<2%) to nearly level. Soils at site 1 were primarily a composite of Absher and Gerdrum series (heavy clay and claypan soils) (Borollic Natrargids). Soils at site 2 were silty clay loams and loams of the Ethridge and Pinelli series (Borollic Camborthids). Vegetation at both sites was indicative of a low seral stage when the study was begun. Dominant perennial grasses were: western wheatgrass [*Agropyron smithii* Rydb.; = *Pascopyrum smithii* Rydb. (Love)]; bluegrama [*Bouteloua gracilis* (H.B.K.) Lag. ex Griffiths]; Sandberg bluegrass (*Poa secunda* Presl.); needle-and-thread (*Stipa comata* Trin. & Rupr.); june grass [*Koeleria pyramidata* (Lam.) Beauv.], and tumblegrass [*Schedonnardus paniculatus* (Nutt.) Trelease]. Threadleaf sedge (*Carex filifolia* Nutt.) was the dominant grass-like species and

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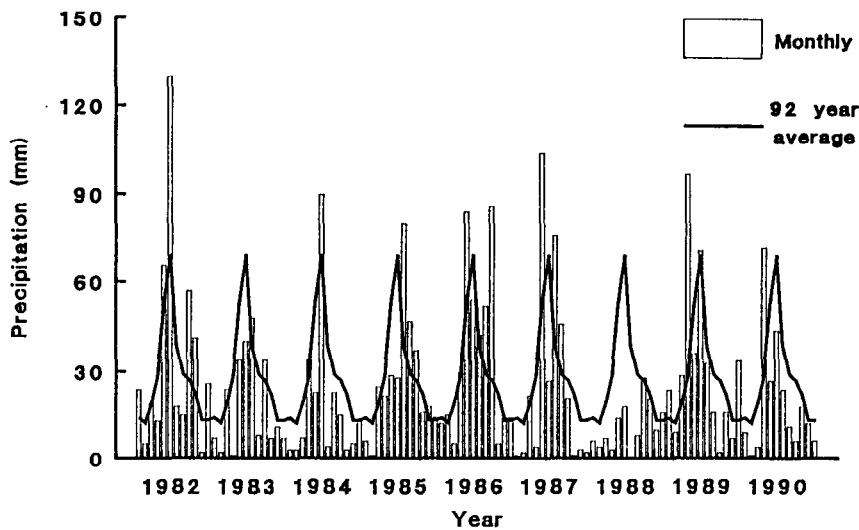


Fig. 1. Actual (Jan.-Dec., 1982-1990) and long-term (92 year) average precipitation for Miles City, Mont.

downy (*Bromus tectorum* L.) and Japanese brome (*B. japonicus* Thunb.) were the dominant annual grasses. Wyoming big sagebrush (*Artemisia tridentata* Pursh. subsp. *wyomingensis* Beetle and Young) was the dominant shrub.

Treatments

Seven treatments were established in eight 12-ha pastures at both sites in 1982. Treatments were: (1) untreated control + SL; (2) ST + SL; (3) ST + DS + SL; (4) BC + ST + DS + SB; (5) BC + ST + DS + SL; (6) ST + NF + SL; and (7) CF + AS + SL, where

BC = brush control

SL = season long grazing

SB = 2 pasture, 1 herd switchback SL grazing (treatment 4)

ST = soil tilling with Range Improvement Machine (RIM) (Currie et al. 1989)

CF = contour furrowing (Kartchner et al. 1983)

DS = drill seeding with RIM

AS = aerial seeding, and

NF = nitrogen fertilization.

Interseeded legumes were alfalfa 'Spreador II' (*Medicago falcata* L.) and cicer milkvetch (*Astragalus cicer* L.). Both were seeded at a rate of 2.2 kg/ha with the RIM (DS) or 4.4 kg/ha aurally (AS). Brush was controlled (BC) at Site 1 by mechanical chopping during the winter of 1982 whereas at Site 2 control was achieved by ground spraying with 2,4-D [(2,4-dichlorophenoxy) acetic acid] at a rate of 2.8 kg/ha before legumes emerged. Level of

control at both sites was near 100%. Nitrogen fertilizer (NF) was applied with the RIM, as a single application of 56 kg N/ha of ammonium nitrate in 1982. All treatments, with the exception of BC at Site 1, were applied in spring.

All treatments were grazed during summer beginning in 1983. Grazing intensity was moderate with 3 to 5 yearling steers (avg. initial wt. = 360 kg) allotted to each SL pasture. Generally an equal number of steers grazed each pasture except for the SB treatment. Usually 10 steers grazed the 2 SB pastures (treatment 4). In this treatment, steers grazed the initial pasture until near the midpoint of the grazing season, and then they were switched to the second pasture. The pasture grazed first was alternated each year. A put-and-take stocking strategy was implemented in 1987 and 1988 in an attempt to maintain similar levels of grazing pressure among treatments. Initial stocking rates were based on standing crop estimates made before the start of grazing, and adjustments were based on standing crop estimates made during the grazing season. Dates grazing was initiated varied among years (15 May to 10 June) depending upon the spring growing conditions. Length of grazing seasons varied among years depending upon annual growing conditions, ranging from 30 days in 1988 to 90 days in 1983, 1984, 1986, and 1987.

Field sampling

Herbage standing crops were estimated annually in all pastures just before the beginning of the grazing season by hand harvesting

Table 1. Degrees of freedom (df), mean squares (MS), and F values for AOV models used to statistically analyze spring (adjusted to 5 June) standing crops for 2 sites, 7 treatments, and 5 species/species groups across 8 years (1983-1990).

Model	Species/Species Group			Total		
	df	MS	F	df	MS	F
Site (Blocks)	1	171380.9		1	856904.6	
Treatment (Trt.)	6	53847.9	4.7*	6	269239.7	4.7*
Error a	6	11536.2		6	57681.0	
Species (Sp.)	4	2739769.8	116.0**			
Trt. × Sp.	24	21008.8	0.8 NS			
Error b	28	23613.0				
Year (Yr.)	7	212219.5	13.9**	7	1061097.3	13.1**
Yr. × Trt.	42	5762.4	0.4 NS	42	28811.9	0.4 NS
Yr. × Sp.	28	134105.2	8.8**			
Yr. × Trt. × Sp.	168	6709.9	0.5 NS			
Error c	245	15304.3		49	80861.4	

*significant differences $p \leq 0.05$

**significant differences $p \leq 0.01$

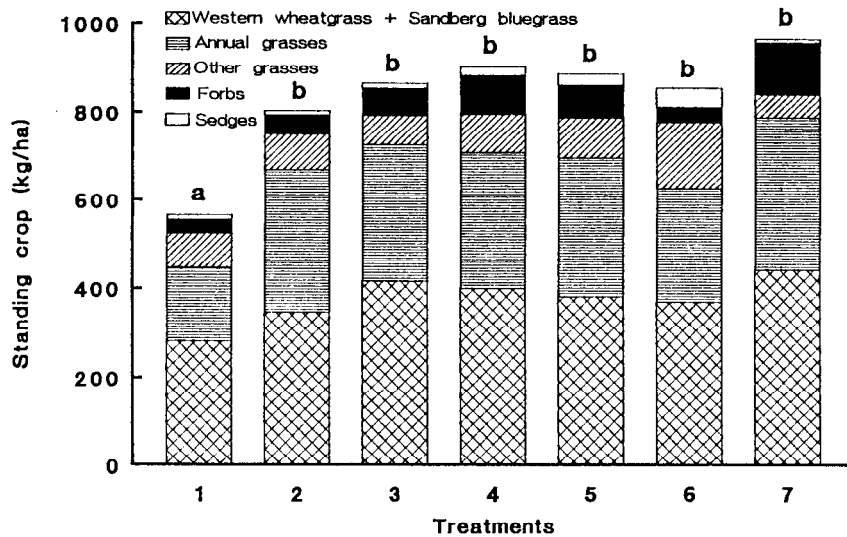


Fig. 2. Least square mean herbage standing crops by treatment (see methods for treatment definitions) averaged across 2 sites and 8 years ($LSD_{0.05} = 199$ kg/ha). Means between columns, followed by the same letter, are not significantly different at ($p \geq 0.05$).

all current year's herbage above a 25-mm stubble height in fifteen 30 by 60-cm plots per pasture. Herbage was separated by species, oven dried in a forced draft oven at $100^{\circ}C$, and weighed.

Data Analyses

Experimental design was a randomized, complete block design (site = blocks). Because clipping dates varied among years all data were adjusted to day 156 (5 June) using regression. Total, individual species, and species groups (western wheatgrass + Sandberg bluegrass, annual grasses, other grasses, sedges, and forbs) standing crops were analyzed using year as a repeated measure factor (Table 1). Means were separated where appropriate using Fisher's Least Significant Difference ($p \leq 0.05$).

Regression subset analyses were used to quantify relationships between precipitation and temperature occurring during September through May, and total, western wheatgrass + Sandberg bluegrass, and annual grass standing crops. Precipitation (mm) and temperatures ($^{\circ}C$) were entered as independent variables on a 1-month, 2-month, or 3-month basis.

Results

Treatments

Treatments increased spring total standing crops an average of 320 kg/ha (Fig. 2). Differences among treatments in total standing crop were not significant and the absence (Table 1) of significant 2 and 3-way treatment interaction effects confirmed species/species group composition did not vary among treatments during the 8-year study period. The largest components of the standing crops at both sites were western wheatgrass + Sandberg bluegrass and annual grasses (Fig. 2).

Years

Total standing crops were significantly (Table 1) greater in 1983, 1986, 1987, 1989, and 1990 than in 1984, 1985, and 1988 (Table 2). Western wheatgrass + Sandberg bluegrass standing crop was greatest (651 kg/ha) in 1986 and least (<300 kg/ha) in 1983, 1984, 1985, and 1988 (Table 2). Standing crops of western wheatgrass averaged 526 and 438 kg/ha in 1986 and 1987 and 310 and 459 kg/ha in 1989 and 1990. Sandberg bluegrass standing crops were 18 and 29% of the perennial cool-season component in 1986 and 1989, respectively, averaging 123 kg/ha.

Annual grasses contributed 37 and 52% of the standing crops produced in 1983 and 1984. During the 2 years following the severe

Table 2. Annual least square mean standing crops on 5 June by species/species groups averaged across 7 treatments and 2 range sites near Miles City, Mont.

Year	Species Groups					Total
	Grasses			Sedges	Forbs	
	W. wheatgrass	Annual	Other			
	S. bluegrass	Annual	Other	Sedges	Forbs	
	kg/ha					
1983	268d ¹	384b	235a	28	116	1032ab
1984	190d	337bc	67b	18	30	642c
1985	219d	190d	58b	12	58	537cd
1986	651a	205d	83b	24	100	1064ab
1987	486c	264cd	66b	20	77	914b
1988	275d	26e	59b	7	40	408d
1989	428c	418ab	57b	12	64	920b
1990	524b	506a	67b	30	57	1184a
	----- $LSD_{0.05} = 87$ -----					$LSD_{0.05} = 206$

¹Means within a column followed by same letters are not significantly different at ($p \geq 0.05$).

drought of 1988 annual grasses contributed 43%. Annuals, however, contributed only 6 to 29% of the standing crop in 1986 through 1988. Japanese brome and downy brome contributed 60 to 96% of the annual grass standing crop from 1984 to 1990. Other annual grass species included little barley (*Hordeum pusillum* Nutt.) and 6-weeks fescue [*Vulpia octoflora* (Walter) Rydb.]. Brome species were not separated in 1983, so percentages were not determined. From 1984 to 1990, species composition of the annual grass component ranged from 28 to 72% Japanese brome and from 20 to 60% downy brome. Japanese brome averaged >50% of the annual grass standing crop in 1984, 1985, 1988, 1989, and 1990, whereas downy brome averaged >50% in 1986 and 1987.

The remaining components of the herbage (other grasses, sedges, and forbs) were only minor components of standing crops during the study (Table 2). These categories did not vary significantly among years except for the decline in other grasses after 1983 (Table 2). The decline in other grasses may have been related to the stimulatory effect of mechanical range treatments on western wheatgrass + Sandberg bluegrass (Wight et al. 1978, White et al. 1981, Gartner 1988).

Climate

Since there was no significant interaction between treatments,

species/species groups, and years, the standing crops data were pooled to examine the effect of precipitation and temperature on the total standing crop and those of the 2 dominant (see Fig. 2 and Table 2) species groups; perennial cool-season (western wheatgrass + Sandberg bluegrass) and annual grasses (Table 3). Monthly precipitation in October and November accounted for 44% of the variation in total standing crop the following spring. Two-month precipitation totals for September + October and November + December precipitation accounted for 44% of the variation, and 3-month totals of precipitation and average temperature for December–February accounted for 40% of the variation.

Table 3. Regression equations and coefficients of determination that best describe the relationship between monthly precipitation and average monthly temperature during September through May and total, western wheatgrass + Sandberg bluegrass, and annual grass standing crops.

Total species	
1-month	R ²
y = 714.139 + 15.227 J ¹	0.06
y = 310.065 + 15.711 O + 32.153 N	0.44
2-month	
y = 408.852 + 17.940 ND	0.34
y = 204.064 + 4.028 SO + 18.341 ND	0.44
3-month	
y = 614.385 + 0.228 (DJF) ²	0.27
y = 865.354 + 0.242 (DJF) ² + 47.850 TDJF	0.40
y = 619.866 + 10.590 DJF + 2.245 MAM + 50.010 TDJF	0.43
Western wheatgrass + Sandberg bluegrass	
1-month	R ²
y = 226.28 + 1.158 (N) ²	0.40
y = 292.583 + 1.104 (N) ² - 0.739 (TD) ²	0.50
2-month	
y = 294.847 + 0.114 (ND) ²	0.15
3-month	
y = 151.34 + 2.467 MAM	0.23
y = -205.101 + 0.185 (DJF) ² + 5.443 (TMAM) ²	0.42
y = -170.866 - 27.748 DJF + 0.663 (DJF) ² + 72.217 TMAM	0.49
Annual grasses	
1-month	R ²
y = 140.383 + 10.570 D	0.22
y = -191.476 + 10.911 D + 4.259 (TO) ²	0.34
y = 171.310 + 8.765 O - 21.878 J + 5.798 A	0.38
2-month	
y = 76.797 + 8.824 ND	0.24
y = 223.500 + 4.313 MA + 30.680 TJF	0.36
3-month	
y = 579.817 - 3.948 (TMAM) ²	0.14
y = 430.707 + 1.302 MAM - 3.559 (TMAM) ²	0.20
y = 212.186 + 9.236 MAM - 0.042 (MAM) ² - 4.577 (TMAM) ²	0.30
y = -265.437 + 11.726 MAM + 37.050 TS0N - 0.053 (MAM) ² - 3.517 (TMAM) ²	0.36

¹S-Sept., O-Oct., N-Nov., D-Dec., J-Jan., F-Feb., M-March and May, A-April, T-temperature

At least 49% of the variation in standing crops of western wheatgrass + Sandberg bluegrass was explained by monthly precipitation in November and average temperature in December, and 3-month precipitation totals in December–February and average temperature in March–May. Monthly precipitation in October, January, and April; 2-month precipitation totals in March + April and average temperature in January + February; and 3-month precipitation totals in March–May and average temperatures in March–May and September–October were the most important factors affecting annual grass production.

Discussion

We conclude from the results of this 8-year study that the

mechanical disturbance of the soil surfaces was the dominant component of the 6 established treatments associated with the observed increases in herbage standing crops, and that annual variations in climatic conditions tended to have a greater impact on standing crops than did the treatments. Maximum year-to-year effect in our study was about 1.6 the treatment effect. Results suggest the increase in forage production was not attributed to major shifts in species composition over time. This finding is in contrast to the results from most studies which have shown that mechanical furrowing increased yield of perennial (Wight et al. 1978, White et al. 1981, Griffith et al. 1985, Gartner 1988) or annual (Gartner 1988, Klemmedson and Smith 1964) cool-season grasses. We assume the pretreatment dominance of western wheatgrass and annual grasses in our study areas limited species response to treatments.

Definitive trends in species response to annual variation in climatic conditions were apparent. Forage production of Sandberg bluegrass tended to increase following drought, and both Sandberg bluegrass and western wheatgrass increased when fall and spring precipitation were above average. Several authors have reported increases in Sandberg bluegrass following drought (Hurt 1951, Reed and Peterson 1961, Whitman et al. 1943) and a positive relationship between production of perennial and annual cool-season grasses and amounts of fall and spring precipitation (Sneva 1982, Smoliak 1986, White 1985, Whisenant 1990).

Standing crops of annual grasses were greatest the 2 years immediately following mechanical disturbance of the soil and the 2 years immediately following the severe drought of 1988. Annual grasses have been shown previously to increase with soil disturbance in the Great Basin (Klemmedson and Smith 1964) and South Dakota (Gartner et al. 1986) similar to that resulting from the establishment of contour furrows. Japanese brome often invades in South Dakota without disturbance (Whisenant 1990, Whisenant and Uresk 1990), with its invasion enhanced by wet falls or the presence of a dense cover of ground litter when fall precipitation is average or less.

The permanency of the increase in annual grasses, particularly Japanese brome, that occurred following the severe drought in 1988 is unknown. It seems reasonable to assume, however, that annual grasses will continue to increase in stature throughout the northern mixed prairie particularly on areas where fire and/or intensity of grazing by large herbivores has been greatly reduced (Whisenant 1990). We suspect also that because the range in climatic condition during this 8-year study was broad (e.g., severe drought in 1988) and because contour furrowing has been shown to dampen year-to-year variation in forage production (Wight et al. 1978, White et al. 1981), the relationships revealed in the analyses may not reflect longterm trends. For example, the significant correlations during these years between September and March ($r=0.37$), September and May ($r=0.74$), October and March ($r=0.31$), November and April ($r=0.43$), and November and May ($r=0.74$) precipitation may have unduly impacted vegetation response and/or the statistical analyses thereof. Thus, the low R^2 s relating precipitation and temperature to June standing crops were not totally unexpected.

The dynamic nature of the relationship between environment and vegetation in the Northern Great Plains continually poses a challenge for land managers. Maintenance of a viable livestock industry requires special management skills especially in a region characterized by large and rapid changes in forage production, resulting from periods of above- and below-average precipitation. Predictive equations or models (Wight et al. 1984) are needed that can be used by livestock producers early in the growing season to predict or determine the potential forage production for that year.

This should permit more efficient management of livestock and enhance management of rangeland in the region.

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Long-term effects of root plowing on vegetation in the eastern south Texas plains.

DONALD C. RUTHVEN III, TIMOTHY E. FULBRIGHT, SAMUEL L. BEASOM, AND ERIC C. HELLGREN

Authors are graduate research assistant, Caesar Kleberg Wildlife Research Institute, Texas A&I University, Kingsville 78363; professor and chair, Department of Agronomy and Resource Sciences, Texas A&I University, Kingsville 78363; and director and associate professor, Caesar Kleberg Wildlife Research Institute, Texas A&I University, Kingsville 78363.

Abstract

The long-term effects of root plowing in plant communities in south Texas are not clearly understood. Our objective was to compare plant species composition and diversity on root-plowed rangelands and untreated rangelands. Two rangeland sites that were root plowed during 1973-74 and 2 sites of native, untreated brush were selected on the Santa Gertrudis Division of the King Ranch, Kleberg and Jim Wells counties, Texas. Woody plant canopy cover was estimated with the line intercept method, and density was estimated with 20-x 1-m plots during 1990. Herbaceous canopy cover was estimated with 20 x 50-cm quadrats. Percent grass, litter, and bare ground coverage were similar on root-plowed and untreated rangelands. Woody plant species and diversity averaged 19 ± 2 species/ treatment ($\bar{x} \pm SE$) and 2.56 ± 0.15 on untreated areas compared to 7 ± 1 species/treatment and 1.18 ± 0.01 on root-plowed areas. Forb canopy coverage on root-plowed sites was about twice that of untreated sites. Huisache (*Acacia smallii* Ilsey) canopy cover and density were both more than 7-fold greater on root-plowed sites than on untreated sites. Browse species preferred by white-tailed deer (*Odocoileus virginianus* Raf.), such as colima [*Zanthoxylum fagara* (L.) Sarg.] and guajillo (*Acacia berlandieri* Benth.), were absent on root-plowed sites.

Key Words: browse, brush, brush management, range improvement, wildlife habitat

Mechanical brush management became prevalent following World War II with development of heavy equipment such as the root plow in 1949 (Fisher et al. 1973), which has been used throughout the southwestern United States to manipulate woody vegetation (Allison and Rechenthin 1956, Carlton et al. 1973). Woody plants reestablish within 2 to 20 years following mechanical brush management, depending upon the type of treatment, woody plant species, and environmental conditions following treatment. In the thornscrub woodland of the western South Texas Plains, herbaceous plant diversity increased during the first 2 years following mechanical brush management (Bozzo et al. 1992). Woody plant diversity of similar communities was lower than that of the original communities 25 to 32 years following root plowing and roller chopping (Fulbright and Beasom 1987) and 7 years following repeated shredding (Fulbright 1987). Root plowing reduced the abundance of highly preferred white-tailed deer browse plants in the western South Texas Plains (Fulbright and Beasom 1987). Long-term reductions in shrub species diversity following root plowing have also been reported in the more mesic

Texas coastal prairies (Mutz et al. 1978).

There is concern among conservation and environmental groups that range management practices decrease diversity (Lewis et al. 1988). A priority for range research relevant to concerns of biological diversity is a determination of the role of human perturbations on changes in species composition of vegetation communities (McMinn 1991). Long-term changes in woody or herbaceous plant composition may be detrimental to certain wildlife species. Our objective was to determine the long-term effects of root plowing on the composition of herbaceous and woody plant communities in the eastern South Texas Plains.

Materials and Methods

The study area was on the King Ranch (27° 35' N, 98° 0' W) in the eastern South Texas Plains (Gould 1975, Scifres 1980, Hatch et al. 1990). Climate is characterized by hot summers and mild winters with an average daily minimum winter (January) temperature of 8° C and an average daily maximum summer (July) temperature of 36° C, and a growing season of about 290 days (Minzenmayer 1979, D. Largo, NAS Kingsville, pers. commun., 1992). Precipitation peaks occur in late spring (May-June) and early fall (September-October). The 30-year (1962-1991) and 10-year (1982-1991) annual precipitation averaged across the 4 study sites were 68 cm and 61 cm, respectively (P. Lieck, King Ranch Inc., pers. commun. 1992). Annual precipitation during the past 10 years averaged 4 cm greater in the root-plowed sites.

Two separate sites, one 1,282 ha in size and one 870 ha, were root plowed during 1973-1974 (R.H. Thompson, King Ranch Inc., pers. commun., 1992). Untreated sites, one 1,140 ha and one 679 ha, consisted of undisturbed brush with small areas that were chained during 1976. Chaining in south Texas brushlands reportedly does not significantly reduce woody plant diversity (Scifres et al. 1976).

Root-plowed and untreated sites were within a 5.8-km radius of each other and were on the Czar-Delfina-Orelia soil association (State Soil Survey Staff 1977). Soils of the Czar-Delfina-Orelia association consist of loamy sands, fine sandy loams, and sandy clay loams. The study area was not mapped by soil series and the composition of each site relative to soil series was unknown (State Soil Survey Staff 1977). The Czar series are fine-loamy, mixed, hyperthermic Pachic Argiustolls; the Delfina series are fine-loamy, mixed, hyperthermic Aquic Paleustalfs; and the Orelia series are fine-loamy, mixed, hyperthermic Cumulic Haplustolls. Topography was nearly level to gently sloping and elevation ranged between 30 and 50 m (R.W. Schmidt, SCS, pers. commun., 1992).

Plant communities belonged to the Mesquite (*Prosopis glandulosa* L.)-Granjeno (*Celtis pallida* Torr.) association (McLendon 1991). Within this association were 2 primary communities, the

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Mesquite-Colima [*Zanthoxylum fagara* (L.) Sarg.]/ Granjeno community, in which colima and bluewood brasil (*Condalia hookeri* M.C. Johnst.) are the subdominants, and the Mesquite-Granjeno/Hog-plum [*Colubrina texana* (T. & G.) Gray] community, in which hog-plum is the subdominant. Prominent herbaceous species included multi-flowered false rhodesgrass [*Chloris pluriflora* (Fourn.) Clayton], hooded windmillgrass (*Chloris cucullata* Bisch.), Texas virginsbower (*Clematis drummondii* T. & G.), orange zexmenia (*Wedelia hispida* Jacq.) and bundle flower (*Desmanthus* sp. Willd.).

The study area has been grazed by domestic livestock since the 18th century (Lea 1957, Lehmann 1969). Cattle were the major form of livestock since about 1870, whereas sheep were grazed from about 1750–1870. Recent grazing by cattle was yearlong and stocking rates, averaging 7.4 ha/AU, were similar for all 4 study sites during 1990 and 1991 (T.J. Haegelin, King Ranch, Inc., pers. commun. 1992).

Twenty-five transects ranging from 72 to 351 m long were randomly located within each study site, and four 20-m lines were randomly placed along and perpendicular to each transect (100/site). Woody plant canopy coverage was estimated during late summer and early fall 1990 by the line-intercept method (Canfield 1941). Woody plant density and frequency were estimated by counting individual plants in 100 20-x 1.5-m plots in each site. Woody species diversity was quantified with Shannon's Index (Pielou 1975). Woody plant density and frequency were used to calculate the index. Herbaceous canopy cover was visually estimated during early fall 1990 (September–October) and early spring 1991 (March–April) in 20-x 50-cm quadrats placed at 2-m intervals along a randomly placed line on each transect (250/site) (Daubenmire and Daubenmire 1968). Species frequency data were used to calculate Shannon's Index. Sample sizes were determined by the Stein 2-staged sample test (Steel and Torrie 1980). Similarity indices were calculated with plant frequency data for both woody and herbaceous species by Motyka's version of Sorensen's similarity index (Chambers and Brown 1983). Scientific and common names of all plants are from Hatch et al. (1990).

Woody plant parameters were analyzed by a 1-way analysis of variance with treatment as the main effect (SAS Institute, Inc. 1987). Herbaceous canopy cover estimates were compared with a 2-way analysis of variance, with treatment and season as the main effects and a treatment by season interaction.

Results

Woody species, diversity, and evenness were greater on untreated areas (19 ± 2 species/treatment [$\bar{x} \pm SE$], $P = 0.051$; 2.56 ± 0.15 , $P = 0.085$; 0.78 ± 0.02 , $P = 0.061$, respectively) than on root-plowed areas (7 ± 1 species/treatment, 1.18 ± 0.01 , 0.61 ± 0.04) (Table 1). Important deer browse species absent on root-plowed areas included guajillo, blackbrush (*Acacia rigidula* Benth.), colima, coma (*Bumelia celastrina* Kunth in *H.B.K. LA*), desert yaupon (*Schaefferia cuneifolia* Gray), palo verde [*Parkinsonia texana* (Gray) S. Wats.], and guayacan (*Guaiacum angustifolia* Engelm.). Huisache comprised $10 \pm 3\%$ of the woody plant canopy on untreated areas, compared to $72 \pm 1\%$ of the woody canopy coverage on root-plowed areas. Mesquite ($P = 0.046$), granjeno ($P = 0.038$), and Texas persimmon ($P = 0.057$) canopy cover were greater on untreated areas. Huisache density was 740% greater ($P = 0.048$) on root-plowed areas than on untreated areas (Table 2). Lotebush [*Ziziphus obtusifolia* (T. & G.) Gray] density was greater ($P = 0.079$) on untreated areas than on root-plowed areas. Similarity indices between root-plowed sites were $IS_{mo} = 0.90$, between untreated sites $IS_{mo} = 0.65$, and between treatments $IS_{mo} = 0.49$.

Overall herbaceous plant canopy coverage estimates averaged $49 \pm 6\%$ on untreated areas and $81 \pm 0\%$ on root-plowed areas

Table 1. Woody plant canopy cover (%) of root-plowed ($n = 2$) and untreated ($n = 2$) areas on the Santa Gertrudis Division of the King Ranch, Kleberg and Jim Wells Counties, Texas, 1990.

Species	Untreated		Root plowed	
	\bar{x}	Range	\bar{x}	Range
	----	(%)	----	(%)
Honey mesquite	59	52–67	23	20–26
Huisache	10	7–13	72	71–73
Granjeno	7	7–7	2	1–3
Hog-plum	2	1–3	3	2–3
Texas persimmon	4	3–5	Tr	
Colima	4	4–4		
Whitebrush	3	<1–5		
Bluewood brasil	2	1–4	<1	
Blackbrush	2	<1–3		
Guajillo	1	0–3		
Lotebush	1	1–2	Tr	
Desert yaupon	1	1–1		
Paloverde	1	<1–1		
Shrubby blue sage	1	<1–1		
Coma	<1	<0–1		
Wolfberry	<1		Tr	
Catclaw acacia	<1			
Twisted acacia	<1			
Coyotillo	<1			
Goatbush	<1			
Guayacan	<1			
Cedar elm	<1			
Texas ebony	<1			
Hackberry	<1			
Total canopy coverage	38	38–38	32	28–35

Table 2. Woody plant density (plants ha⁻¹) on root-plowed ($n = 2$) and untreated ($n = 2$) areas on the Santa Gertrudis Division of the King Ranch, Kleberg and Jim Wells Counties, Texas, 1990.

Species	Untreated		Root plowed	
	\bar{x}	Range	\bar{x}	Range
	--	(plants/ha)	--	(plants/ha)
Honey mesquite	285	250–320	184	170–197
Huisache	82	43–120	607	493–720
Granjeno	258	173–343	100	83–117
Hog-plum	154	60–247	112	76–147
Texas persimmon	50	33–67	3	0–5
Colima	244	157–330		
Whitebrush	100	3–197		
Bluewood brasil	45	13–77	9	7–10
Blackbrush	79	17–140		
Guajillo	10	0–20		
Lotebush	42	30–53	3	3–3
Desert yaupon	23	13–33		
Paloverde	2	0–3		
Shrubby blue sage	67	53–80		
Coma	2	0–3		
Wolfberry	7	7–7	4	0–7
Catclaw acacia	22	<1–43		
Twisted acacia	2	0–3		
Coyotillo	4	0–7		
Goatbush	2	0–3		
Guayacan	8	3–13		
Cedar elm	1	0–2		
Texas ebony	<1			
Hackberry	1	0–2		
Total density	1,204	1,346–1,630	1,025	862–1,176

(Table 3). Forb cover was significantly ($P = 0.048$) greater on root-plowed areas ($39 \pm 1\%$) than on untreated areas ($20 \pm 4\%$). Herbaceous plant richness was similar between treatments in both

Table 3. Visual estimates of foliar cover (%) of forbs, grass, litter, and bare ground at the Santa Gertrudis Division of the King Ranch, Kleberg and Jim Wells Counties, Texas (Fall 1990, Spring 1991), as affected by root plowing and season, ($n = 2$ /treatment/season).

	Forb	Grass	Litter	Bare ground
	----- (%) -----			
Fall 1990				
Root plowed	38	43	43	40
Untreated	16	27	38	53
Spring 1991				
Root plowed	40	41	38	37
Untreated	24	31	38	45
ANOVA P-value				
Treatment	0.0478	0.0888	0.6324	0.2267
Season	0.4991	0.8717	0.5617	0.5340
TRT*Season	0.7294	0.6328	0.6324	0.7511

fall and spring, with 139 and 155 species on root-plowed sites and 115 and 147 species on untreated sites. Species diversity was also similar between treatments, measuring 3.82 and 4.01 on root-plowed sites and 3.93 and 4.13 on untreated sites in spring and fall. Similarity between root-plowed sites was $IS_{mo} = 0.60$ in Fall 1990 and $IS_{mo} = 0.55$ in Spring 1991. Similarities between untreated sites were $IS_{mo} = 0.41$ (Fall 1990) and $IS_{mo} = 0.52$ (Spring 1991), and between treatment indices were $IS_{mo} = 0.42$ (Fall 1990) and $IS_{mo} = 0.41$ (Spring 1991).

Averaged across sampling dates, grass canopy cover was 45% greater on root-plowed areas (Table 3). Dominant grasses that were more frequent ($P < 0.05$) on root-plowed areas included Kleberg bluestem [*Diachanthium annulatum* (Forssk.) Staph.], bermudagrass [*Cynodon dactylon* (L.) Rich.], sandbur (*Cenchrus incertus* L.), threeawn (*Aristida* spp. L.), fall witchgrass (*Digitaria cognata* Fabr.), and panicum (*Panicum* spp.). Although not dominant, buffelgrass (*Cenchrus ciliaris* L.), which is highly rated as a pasture grass, was more frequent ($P \leq 0.0001$) on root-plowed ($9 \pm 0\%$) than on untreated ($4 \pm 0\%$) areas. Hooded windmillgrass was common on both treatments.

Dominant forbs that were more frequent on root-plowed areas include croton (*Croton* sp.), palafoxia (*Palafoxia* sp.), slender verbena (*Verbena officinale* L.), and anemone (*Anemone* sp.) (Table 5). Broomweed (*Xanthocephalum* sp.) percent frequency was greater on untreated areas than on root-plowed areas. Forbs that were frequent in spring on both treatments included lazy daisy (*Aphanostephus riddellii* L.), pepperweed (*Lepidium* sp.), and woodsorrel (*Oxalis* sp.). Frequency of snoutbean (*Rhynchosia*

Table 4. Frequency (%) of dominant (frequency $\geq 10\%$) grasses on root-plowed ($n = 4$) and untreated ($n = 4$) areas at the Santa Gertrudis Division of the King Ranch, Kleberg and Jim Wells Counties, Texas (September–October 1990, March–April 1991).

	Root plowed		Untreated		P-value
	\bar{x}	SE	\bar{x}	SE	
	----- (%) -----				
Threeawn	13	1	4	2	0.0081
Sandbur	12	2	2	1	0.0010
Hooded windmillgrass	11	3	15	2	0.4263
False rhodesgrass	5	2	30	14	0.1344
Bermudagrass	19	3	4	2	0.0067
Kleberg bluestem	47	4	12	3	0.0004
Fall witchgrass	16	3	5	1	0.0108
Lovegrass	14	6	5	2	0.1935
Panicgrass ¹	12	2	1	0	0.0472

¹Spring only ($n = 2$)

Table 5. Frequency (%) of dominant (frequency $\geq 10\%$) forbs on root-plowed ($n = 4$) and untreated ($n = 4$) areas at the Santa Gertrudis Division of the King Ranch, Kleberg and Jim Wells Counties, Texas (September–October 1990, March–April 1991).

	Root plowed		Untreated		P-value
	\bar{x}	SE	\bar{x}	SE	
	----- (%) -----				
Ragweed ¹	22	13	3	0	0.2830
Anemone ¹	11	1	0	0	0.0082
Lazy daisy ¹	13	11	13	1	0.9753
Croton	28	2	2	0	≤ 0.0001
Tropic croton ²	9	4	11	9	0.8254
Silky evolvulus	8	3	12	2	0.3592
Pepperweed ¹	43	8	20	1	0.1109
Woodsorrel ¹	31	3	21	7	0.3273
Palafoxia	15	1	3	2	0.0007
Plantain ¹	25	6	4	0	0.0688
Ruellia	11	5	12	3	0.8085
Slender verbena	21	4	7	3	0.0319
Broomweed	2	1	12	1	0.0007

¹Spring only ($n = 2$)

²Fall only ($n = 2$)

spp.), preferred by white-tailed deer, was also greater ($P = 0.001$) on root-plowed ($7 \pm 1\%$) than on untreated (0%) areas.

Discussion and Conclusions

Huisache occurs primarily in the Texas coastal prairie and eastern South Texas Plains (Scifres et al. 1982). Based on our results and those of Mutz et al. (1978), we conclude that root plowing in these regions may result in development of a depauperate woody plant community dominated by huisache on rangeland that formerly supported a species-rich community dominated by mesquite. Twisted acacia (*Acacia schaffneri* S. Wats.) increases in abundance westward into the South Texas Plains with a concomitant decrease in huisache (Mutz et al. 1978, Scifres et al. 1982). In the more arid western South Texas Plains, twisted acacia and mesquite dominate root-plowed areas (Fulbright and Beasom 1987). The long-term reductions of preferred deer browse species such as guajillo, blackbrush, colima, bluewood brasil, guayacan, coma, and desert yaupon in the eastern South Texas Plains were consistent with reports in other regions (Mutz et al. 1978, Fulbright and Beasom 1987). The changes in the woody plant community following root plowing were also similar to short-term observations in the Texas coastal prairie (Box 1964) and South Texas Plains (Davis and Winkler 1968).

The abundance of Kleberg bluestem on the root-plowed areas can be attributed to reseeding following treatment. The dominance of sandbur on the root-plowed areas may have resulted from its adaptability to invade cleared, reseeded ranges (Gould 1978). The increase of bermudagrass on the root-plowed areas relative to the untreated areas may have also resulted from its proclivity to invade disturbed areas (Gould 1975). The apparent decrease in broomweed on the root-plowed areas could be due to increased competition with grasses and other forbs. Greater canopy cover of herbaceous vegetation 16 to 18 years after root plowing was similar to the short-term observations of Drawe (1977) on the Texas coastal prairies. Double chaining and raking in south Texas (Scifres et al. 1976) and double chaining in central Texas (Rollins and Bryant 1986) also resulted in increased herbaceous coverage.

Short-term impacts of root plowing rangeland are well documented (Powell 1968, Davis and Winkler 1968, Urness 1974, Guthery et al. 1979); however, the long-term impacts of the shift from diverse thornscrub to a less diverse (woody) community on ecosystem productivity and wildlife populations are unknown and need

further investigation. Lower browse diversity on root-plowed sites was apparently not detrimental to white-tailed deer in the eastern South Texas Plains, presumably because of great forb abundance and utilization by white-tailed deer (Ruthven 1992). However, during dry, hot summers in the western South Texas Plains, deer diets are primarily browse (Varner and Blankenship 1987). Thus, further research on the long-term effects of root plowing on white-tailed deer are needed in more xeric environments such as the western South Texas Plains where lower annual precipitation may result in low forb availability. The effects of root plowing on the diversity of the vertebrate and invertebrate communities also need to be addressed.

Appendix Table 1. Scientific names of brush, forb, and grass species.

Scientific name	Common name
Browse	
<i>Acacia greggii</i> Gray	Catclaw acacia
<i>Aloysia gratissima</i> (Gill & Hook) Troncoso	Whitebrush
<i>Diospyros texana</i> L.	Texas persimmon
<i>Castela texana</i> Turpin	Goatbush
<i>Celtis laevigata</i> Willd.	Hackberry
<i>Karwinskia humboldtiana</i> (Schult.) Zucc.	Coyotillo
<i>Lycium carolinianum</i> Walt.	Wolfberry
<i>Pithecellobium flexicaule</i> (Benth.) Coult.	Texas ebony
<i>Salvia ballotiflora</i> Benth.	Shrubby blue sage
<i>Ulmus crassifolia</i> L.	Cedar elm
Forbs	
<i>Ambrosia</i> sp. L.	Ragweed
<i>Aphanostephus riddellii</i> T. & G.	Lazy daisy
<i>Croton glandulosa</i> L.	Tropic croton
<i>Evolvulus sericeus</i> Sw.	Slender evolvulus
<i>Lepidium</i> sp. L.	Pepperweed
<i>Oxalis</i> sp. L.	Woodsorrel
<i>Plantago</i> sp. L.	Plantain
<i>Ruellia</i> spp. L.	Ruellia
<i>Xanthoxylum</i> sp.	Broomweed
Grasses	
<i>Eragrostis</i> spp. Wolf	Lovegrass

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Broom snakeweed responses to drought: I. Photosynthesis, conductance, and water-use efficiency

CHANGGUI WAN, RONALD E. SOSEBEE, AND BOBBY L. MCMICHAEL

Authors are postdoctoral research associate and professor, Department of Range and Wildlife Management, Texas Tech University, Lubbock 79409, and plant physiologist, USDA-ARS, Cropping Systems Research Laboratory, Lubbock, Texas. Contribution No. T-9-629 of the College of Agricultural Sciences, Texas Tech University. The senior author is visiting scientist of Gansu Grassland Ecological Research Institute, Lanzhou, China.

Abstract

The effects of water deficit on photosynthesis, transpiration, stomatal conductance, canopy development, and water-use efficiency of broom snakeweed (*Gutierrezia sarothrae* (Pursh) Britt and Rusby) were studied during the spring-summer growing season in pot-grown plants subjected to 5 soil water regimes. Stomatal conductance was proportionately more reduced by a mild water stress (soil water potential = -0.2 MPa) than were canopy development and photosynthesis. However canopy development was most affected by moderate to severe soil water deficit (<-1.1 MPa), followed by photosynthesis; transpiration and leaf conductance were least affected. When subjected to severe water stress, broom snakeweed controlled its water loss mainly through reduced canopy development rather than stomatal closure. Photosynthesis was more limited by mesophyll conductance than by stomatal conductance. Water-use efficiency was not affected by mild water stress. As soil water deficit developed, water-use efficiency declined, which was a response to nonstomatal limitation to photosynthesis and less sensitive stomata to severe water deficit. Broom snakeweed maintained positive net photosynthesis at soil water potential as low as -3.4 MPa and leaf water potential of -8.19 MPa. Water-spending behavior (low water-use efficiency) and high degree of drought tolerance were the main physiological characteristics of broom snakeweed subjected to water stress.

Key Words: rangeland xerophytes, water relations, gas exchange, drought tolerance, canopy development

Broom snakeweed (*Gutierrezia sarothrae* (Pursh) Britt and Rusby) is a widespread suffrutescent shrub in large areas of the semiarid rangelands of the western U.S. and southern Canada. Its population fluctuates according to climatic conditions (Pieper and McDaniel 1989). However, when it reaches densities common to many southwestern rangelands, it seems no longer cyclical, but rather predominates year after year (Sosebee 1988). The growth habits of snakeweed preclude grasses from growing in the same community. If soil water is adequate in the fall and winter, snakeweed will remain evergreen and use much of the available soil water during the period when warm-season grasses are dormant. In the early spring when grasses start growing, snakeweed has a distinct competitive advantage over grasses because of its above- and below-ground biomass.

Growth habit alone cannot fully explain the predominance of

broom snakeweed in the natural plant community. For example, in summer drought when most grasses become quiescent, snakeweed remains green and turgid. This may indicate that broom snakeweed can make better use of available soil water under soil water deficit than the grasses. In the Great Basin, the shallow-rooted snakeweed had a lower plant water potential than the deep-rooted drought resistant shrub big sagebrush (*Artemisia tridentata* spp. *tridentata* Nutt.), yet its stomatal conductance and photosynthesis were much higher than that of big sagebrush (DePuit and Caldwell 1975).

Chemical control of snakeweed has been successful in recent years. The cost of control, however, can significantly reduce the profit margin of the ranching operation. Since snakeweed infestations are cyclical, the question often arises as to whether the rancher should control snakeweed by spraying or wait for the possibility of the plants dying anyway because of limited soil moisture. Since snakeweed populations are influenced by weather patterns, it is incumbent on the scientific community to provide input to the rancher on the conditions and the probabilities that snakeweed will continue to remain evergreen, die-back to the perennial stems, or die out completely. This information is crucial for planning management strategies or evaluating the economics of investing in a control program. This information should include understanding of responses of various physiological parameters of broom snakeweed to soil water deficit.

DeLucia and Heckathorn (1989) suggested that ability of big sagebrush to compete with other species rests on its profligate use of water (low WUE) and high degree of drought tolerance. We hypothesize that the above physiological traits also exist in broom snakeweed when subjected to water stress, which allows this species to become a successful competitor on semiarid rangelands. Specific objectives of this research were to evaluate the impact of soil water deficit on the basic physiological processes of photosynthesis, transpiration, leaf conductance, water-use efficiency and canopy development.

Materials and Methods

Six hundred broom snakeweed seedlings were transplanted into 19-l plastic pots (30 cm high and 29 cm in diameter) from a rangeland plant community in west Texas in the fall of 1990 and grown in an outdoor nursery on the Texas Tech University campus. The pots were filled with Amarillo fine sandy loam (fine-loamy, mixed, thermic Aridic Paleustalfs), a typical soil on which broom snakeweed grows on the southern High Plains of Texas. The plants had become well established before the experiment began in April, 1991. The 600 plants were separated into 5 treatments of 120 plants each. Plant size was stratified across treatments

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so that each treatment had 24 similar-sized plants (about 10 cm high) when the study began. The 10-cm high plants were placed on benches 10-cm from each other. The initial soil water content was kept at field capacity (-0.03 MPa). Treatment 1 was irrigated twice a week (420 g of water per day per plant) to replace transpirational water loss (300 to 400 g per day per plant) and hence maintain soil moisture at field capacity. The plants in Treatments 2 through 4 received 50%, 25%, and 12.5% of the irrigation quota of Treatment 1. The plants in Treatment 5 were irrigated in mid April, and were not further irrigated during the experiment except at the end of the vegetative stage in late June. Treatments 1 through 5 were denoted as well watered (WW), slightly stressed (SS), moderately stressed (MS), severely stressed (SVS), and extremely stressed (ES), respectively. Plants subjected to the different soil water regimes were covered with a temporary "rain-out" shelter to protect them from natural precipitation events during experimentation. Measurements of the various physiological parameters were begun approximately 14 days after the experiment had begun and the treatments established.

Soil water content was monitored every month using time domain reflectometry (TDR) equipment (Topp et al. 1980, 1982, Ledieu et al. 1986, Dalton and Poss 1990). Stainless steel rods 0.32 cm in diameter were cut into 26 cm lengths and inserted permanently in 5 pots per treatment as TDR probes. Pairs of the rods were inserted horizontally into the soil at a parallel distance of 5 cm at 3 depths (10, 18, and 26 cm) within each pot. Soil electromagnetic capacitance and reflectance patterns were measured with a Tektronix 1502C cable tester (Textronix, Beaverton, Ore.) connected to the soil probes. The cable tester readings of electromagnetic wave length were converted to a dielectric constant (K), and soil volumetric water content (Φ_p , $\text{cm}^3 \text{cm}^{-3}$) was calculated from K using the following empirical equation:

$$\Phi_p = -5.3 \cdot 10^{-2} + 2.92 \cdot 10^{-2} \cdot K - 5.5 \cdot 10^{-4} \cdot K^2 + 4.3 \cdot 10^{-6} \cdot K^3 \quad (\text{Topp et al. 1980}) \quad (1)$$

Volumetric water content (Φ_p) obtained with the TDR technique was calibrated with water content (Φ_v) determined gravimetrically. The average volumetric water content (Φ_v) along a pair of rods was used to regress against the corresponding Φ_p , and the following equation was derived:

$$\Phi_v = -0.0313 + 1.14 \cdot \Phi_p \quad (p < 0.0001, r^2 = 0.95, n = 27) \quad (2)$$

The slope of the line was not significantly different from 1 and the intercept was not significantly different from 0, suggesting a 1:1 relationship.

Soil water retention curve was developed from thermocouple psychrometry, allowing soil water potential to be predicted from soil water content. The equation for the water retention curve was:

$$\text{Log}(\text{WC}) = 1.0925 - 0.3272 \cdot \text{Log}(\text{WP}) \quad (r^2 = 0.89, n = 18) \quad (3)$$

Where, WC is gravimetric water content (%) and WP is soil water potential ($10 \cdot \text{MPa}$).

Photosynthesis (A), stomatal conductance (g), transpiration rate (E), and leaf and air temperatures were measured with a LI-6200 portable photosynthesis system (Licor Inc., Lincoln, Nebr.). The uppermost foliated twigs were used in the measurements. The measurements were taken at 10:00 a.m. on sunny days on 3 plants in each of the 5 treatments 3 times a month from late April until mid August (11 sampling days). Air temperatures were $30 \pm 2^\circ \text{C}$, and photon flux density was $> 1,200 \mu\text{mol m}^{-2} \text{s}^{-1}$ PAR during the time when measurements were taken. Water-use efficiency (WUE) was determined as $\text{WUE} = \text{A}/\text{E}$ ($\text{mmol CO}_2/\text{mol H}_2\text{O}$) (Larcher 1982). Intercellular CO_2 concentration (C_i , $\mu\text{L L}^{-1}$) was calculated by the software for the LI-6200 photosynthesis system. Mesophyll conductance to CO_2 (g_m) was calculated as $g_m = \text{A}/\text{C}_i$ ($\text{mmol m}^{-2} \text{s}^{-1}$) (Fites and Teskey 1988). Midday plant

water potential was measured with a Scholander-type pressure bomb once every month using 3 replicates. The very low plant water potentials in the severely stressed and extremely stressed treatments often caused equipment failure, thus only the data collected in June were presented.

The total canopy area was assumed to be proportional to the leaf area of an individual twig (Comstock et al. 1988). Therefore, canopy development was estimated from twig development. Twig development was determined as leaf area on individual twigs during the vegetative stage. Five twigs were harvested from 5 different plants in each treatment on each sampling date at time interval of 10 days. The leaf area was determined with a LI-3100 area meter (Licor inc., Lincoln, Nebr.). At the end of the vegetative stage (30 June), total canopy area (1 side) was measured.

The experimental design was completely randomized. Since measurements of photosynthesis, transpiration, and leaf conductance were made on the same individual plants of each treatment over the sampling dates, the results were analyzed by repeated measures analysis of variance (ANOVA). The treatment means were separated with Fisher's least significant difference at $p < 0.05$.

Results and Discussion

Soil water potential declined from -0.023 MPa in the well-watered treatment to -3.4 MPa in the extremely stressed treatment, while the midday plant water potential declined from -2.85 to -8.19 MPa (Table 1). Plant water potential and relative water content both declined in response to soil drying.

As soil water decreased, average stomatal conductance and transpiration rate declined linearly (Fig. 1a, 1b). Plants in the well-watered treatment had the highest conductance and transpiration, followed in order by slightly, moderately, extremely, and severely stressed treatments. However, the differences in conductance and transpiration between slightly and moderately, moderately and severely, or severely and extremely stressed treatments were not significant ($p > 0.05$, Fig. 1a, 1b). In severely and extremely stressed treatments, respectively, transpiration was 58% and 59%, and conductance was 37% and 39% of those in well-watered treatment. These declines were relatively small when compared to another major shrub species mesquite (*Prosopis glandu-*

Table 1. Average soil water content (Φ_p , $\text{cm}^3 \text{cm}^{-3}$), soil water potential (MPa) predicted by water retention curves developed from thermocouple psychrometry and midday water potential and relative water content (RWC) of broom snakeweed in June, 1991.

	Treatment				
	WW ¹	SS	MS	SVS	ES
Soil water content ² ($\text{cm}^3 \text{cm}^{-3}$)	0.221	0.124	0.080	0.067	0.056
SEM (n=5)	0.009	0.012	0.007	0.003	0.003
Soil water potential (MPa)	-0.023	-0.199	-1.10	-1.98	-3.40
SEM (n=5)	0.000	0.007	0.10	0.09	0.17
Plant water potential (MPa)	-2.85	-3.48	-3.93	-5.94	-8.19
SEM (n=3)	0.25	0.31	0.50	0.81	1.20
Plant RWC	0.88	0.74	0.59	0.55	0.51
SEM (n=6)	0.02	0.02	0.02	0.04	0.01

¹WW-well watered; SS-slightly stressed; MS-moderately stressed; SVS-severely stressed; ES-extremely stressed.

²Soil water content is the average of 5 sets of observations made once every month during April through August. Each set of observations produce 5 treatment means of Φ_p ; each mean is based on 9 TDR readings on 3 pots of each treatment.

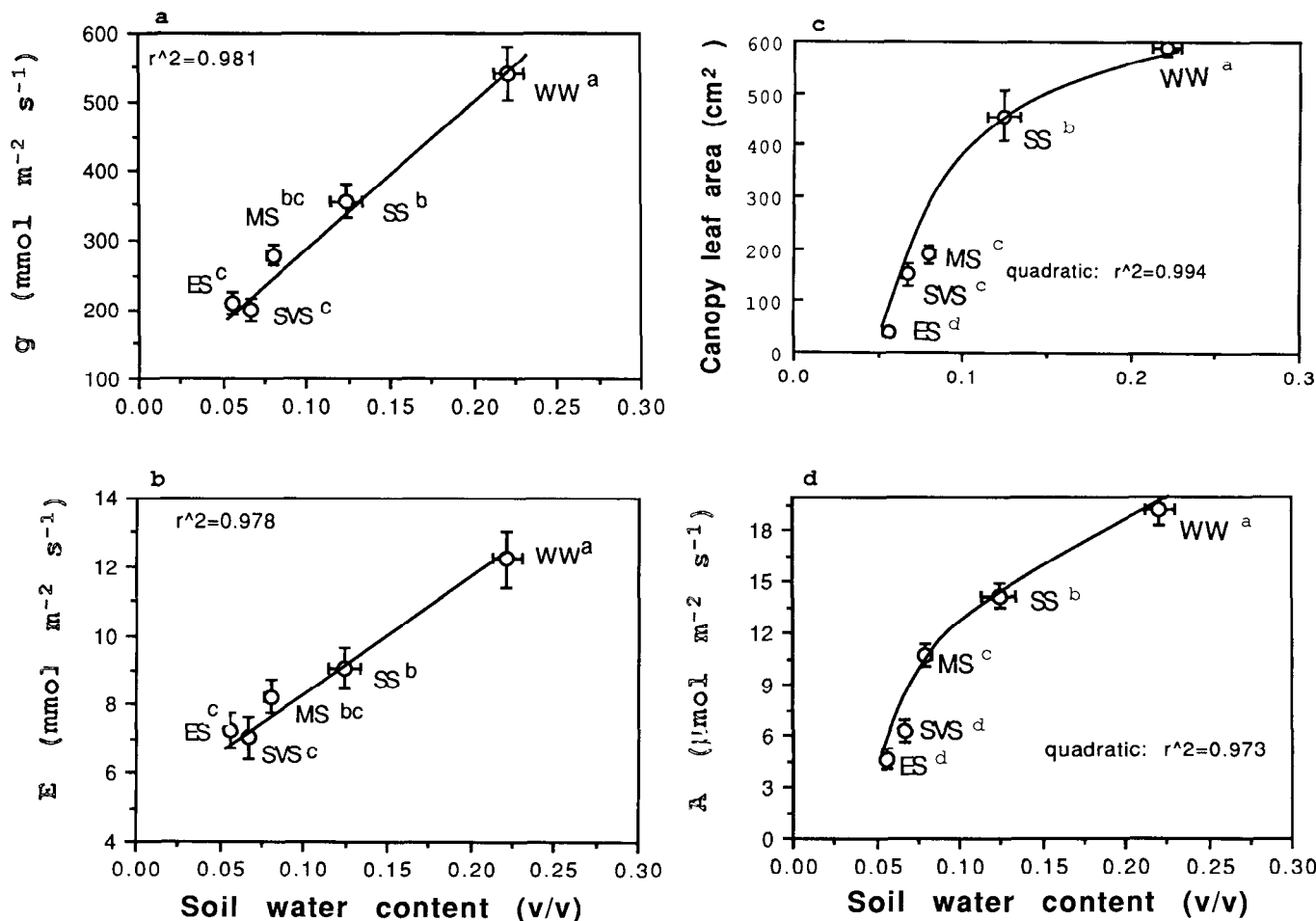


Fig. 1. a. Stomatal conductance, b. transpiration rate, c. canopy area development, and d. photosynthesis rate as influenced by soil water content in the well-watered (WW), slightly stressed (SS), moderately stressed (MS), severely stressed (SVS), and extremely stressed (ES) treatments. The vertical and horizontal bars represent ± 1 standard error. Means followed by the same letter are not different at $p < 0.05$.

losa Torr.) in which transpiration and conductance decreased 3.5- and 6-fold, respectively, from a wet June to a drought in July (Wan and Sosebee 1991). DePuit and Caldwell (1975) suggested that when subjected to summer drought, diurnal stomatal control over water loss was less pronounced in broom snakeweed than in other semidesert species.

Canopy leaf area and photosynthesis responded curvilinearly to water stress (Fig. 1c, 1d). Under slightly stressed treatment, leaf area and photosynthesis declined only 23–26%. Then a break point was reached at which leaf area declined 68% in the moderately stressed treatment (-1.1 MPa); photosynthesis declined 67% in the severely stressed treatment (-2 MPa), indicating leaf area was more sensitive than photosynthesis to moderate soil water deficit.

Stomatal conductance was 34% less ($p < 0.05$) in the slightly stressed than in the well-watered treatment (Fig. 1a); the magnitude of the reduction in conductance was greater than the reduction in leaf area (23%, $p < 0.05$, Fig. 1). There was significant reduction in leaf area ($p < 0.05$) but not in conductance ($p > 0.05$) in plants grown in the moderately stressed treatment as compared to those grown in the slightly stressed treatment. Canopy area in plants within the extremely stressed treatment decreased to only 25% of that in the severely stressed treatment ($p < 0.05$, while conductance did not differ between extremely and severely stressed treatment. Under low soil water availability as in the extremely stressed treatment, canopy size became very low (Fig. 1c). Other studies have shown that for a given hydraulic conductivity of a stem, leaf specific conductivity increases with a decline in stem leaf

area (Zimmerman 1983). This may explain why a slightly higher g was maintained in the extremely rather than in the severely stressed treatment.

According to Bradford and Hsiao (1982), canopy development is generally more sensitive to water stress than stomatal conductance for many species. Our data have shown somewhat different results; stomata of broom snakeweed seem to respond more sensitively to a mild water stress than canopy development does. As water stress increases, canopy development is more affected. These alternate modifications in leaf area and conductance in response to different levels of water stress suggest that leaf growth and stomatal conductance are attuned to regulate total water consumption in accordance with water supply.

Stomata were less responsive to water stress when soil water potential dropped to < -1.1 MPa, i.e., in the moderately, severely, and extremely stressed treatments. In summer drought, water potential in the topsoil is often reduced to < -1.5 MPa (Wan and Sosebee 1991) and broom snakeweed usually sheds leaves during the summer (DePuit and Caldwell 1975). With a smaller canopy size, conductance often remains relatively high. Meinzer and Grantz (1990) found that sugarcane stomata adjusted to the ratio of total hydraulic conductance to total transpiring leaf area.

Leaf expansion in individual twigs produced distinct patterns of growth in the 5 treatments (Fig. 2). Plants in the well-watered treatment had the greatest leaf expansion rate followed by plants in the slightly stressed treatment. Plants in the extremely stressed treatment had a negative leaf growth. The mean leaf area in each

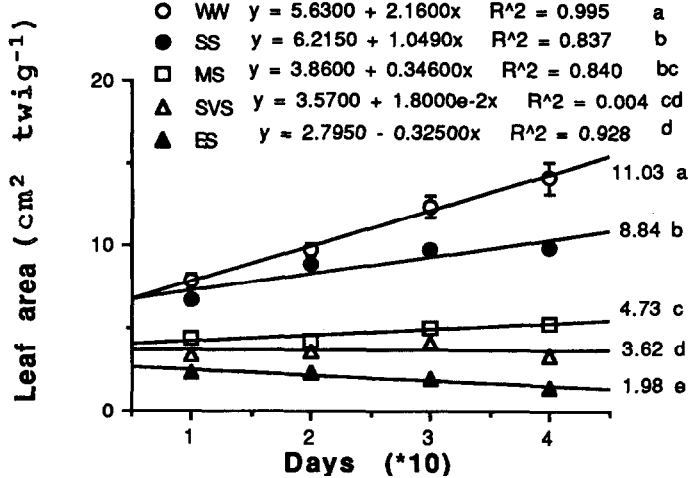


Fig. 2. Leaf area per twig during 21 May through 21 June. Slopes of the equations followed by the same letter are not different ($p < 0.05$). The numbers on the right of each line are the means of leaf area per twig, and they are different from each other ($p < 0.05$).

twig during May through June was also different ($P < 0.05$) between any 2 treatments. Slow leaf growth was observed in the moderately stressed treatment; leaf shedding was a prominent phenomenon in the severely and extremely stressed treatments. When soil water deficit reached -1.1 MPa, leaf growth was severely inhibited. At soil water potential < -2 MPa, the stress became sufficient that the plants shed leaves in order to keep balance with the soil water supply.

It is generally assumed that stomatal closure is a reversible response to drought. By using stomata to control water loss, plants can maintain higher productivity under a mild water stress (-0.2 MPa) and avoid leaf senescence, which is an irreversible process and represents a loss of carbon. Leaf senescence occurs only when stress threatens plant survival (Bradford and Hsiao 1982).

Similarly, conductance was more reduced than photosynthesis (26%) in plants grown in the slightly stressed treatment, while conductance was less affected than photosynthesis in plants in the moderately, severely and extremely stressed treatments (Fig. 1). Because of a greater degree of stomatal closure in plants grown in the slightly stressed treatment, broom snakeweed maintained intercellular CO_2 concentration ($259 \mu\text{L L}^{-1}$, data not shown) comparable to that in the well-watered treatment ($263 \mu\text{L L}^{-1}$), thus optimizing carbon gain with respect to water loss (Cowan 1982) and resulting in higher productivity. Intercellular CO_2 concentration in snakeweed plants in severely and extremely stressed treatments became higher (283 and $290 \mu\text{L L}^{-1}$, respectively, $p < 0.05$) than in those grown in the well-watered and slightly stressed treatments, reflecting a reduced photosynthetic capacity in the severely stressed plants (Farquhar and Sharkey 1982). Photosynthesis was more highly correlated with mesophyll conductance to CO_2 (g_m) ($r^2 = 0.955$, $p < 0.0001$, $n = 165$, Fig. 3) than with stomatal conductance ($r^2 = 0.50$, $p < 0.0001$, $n = 165$). Mesophyll conductance includes diffusion of CO_2 in the liquid pathway across cell wall, membranes, and the cytosol to carboxylation sites in the chloroplast, and carboxylation capacity and photochemistry in the chloroplasts (Bradford and Hsiao 1982). Mesophyll conductance can be affected by any changes in the above processes, some of which are related to mesophyll water status (Bradford and Hsiao 1982). The close correlation between photosynthesis and mesophyll conductance suggests the significance of nonstomatal control of photosynthesis in broom snakeweed and supports the research of Teskey et al. (1986) and Dang et al. (1991), who found that in woody plants

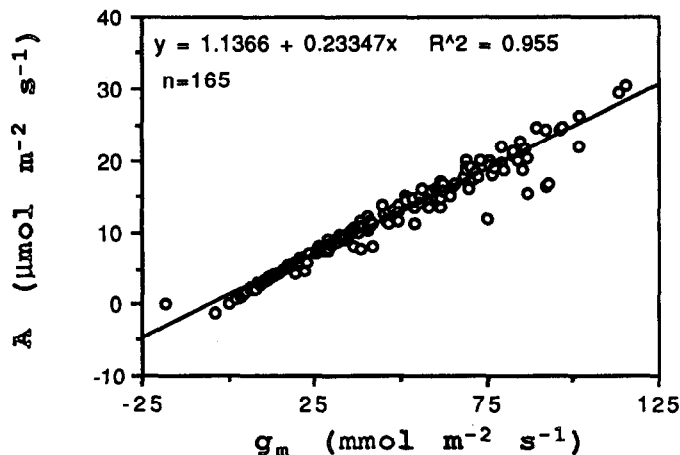


Fig. 3. Relationship between mesophyll conductance (g_m , $\text{mmol m}^{-2} \text{s}^{-1}$) and photosynthesis (A , $\mu\text{mol m}^{-2} \text{s}^{-1}$). Each data point represents 1 observation.

photosynthesis is more limited by mesophyll conductance than by stomatal conductance. But, we have to interpret this with caution because an uncontrolled error may occur in the calculation of mesophyll conductance in which chloroplast CO_2 concentration is usually assumed to be zero.

Water-use efficiency (WUE) at the single twig level remained the same for the well-watered and slightly stressed treatments, but declined dramatically in severely and extremely stressed treatments (Fig. 4). A moderate decline (17% from the maximum value)

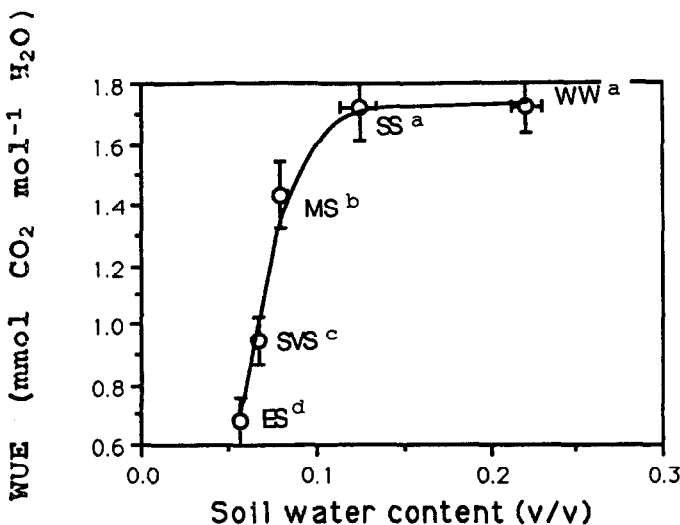


Fig. 4. Relationship between water-use efficiency (WUE, A/E $\text{mmol CO}_2/\text{mol water}$) and soil water regime. The vertical and horizontal bars represent ± 1 standard error.

occurred in moderately stressed treatment. Stanhill (1986) stated that water-use efficiency increased when plants were subjected to drought conditions because stomatal closure caused a proportionately greater reduction in transpiration than photosynthesis. DeLucia and Heckathorn (1989) found that water-use efficiency in both big sagebrush and ponderosa pine (*Pinus ponderosa* Laws) increased as soil drought increased. The opposite behavior exhibited by broom snakeweed is probably due to the predominance of nonstomatal limitation to photosynthesis and stomata less sensitive to severe water deficit. When photosynthetic capacity was greatly reduced under severe water stress, stomata remained par-

tially open, which favored transpirational water loss over carbon fixation (Stanhill 1986).

The photosynthetic apparatus of broom snakeweed can tolerate extremely low soil water potential. The average total soil water potential in the extremely stressed treatment was -3.4 MPa but plant water potential was about -8.1 MPa (Table 1). However, broom snakeweed was able to maintain a positive average gas exchange at all sampling dates. This supports the field research of DePuit and Caldwell (1975), who found that when big sagebrush often had negative CO_2 exchange rates in the droughty summer afternoons, photosynthesis in broom snakeweed remained positive. Since photosynthesis is significantly correlated with stomatal conductance ($r^2=0.50$, $p<0.0001$, $n=165$), we attribute the positive photosynthesis, to some extent, to the relatively higher stomatal conductance in the severely stressed plants.

Recovery of photosynthesis from water stress upon rewetting the soil is very fast in broom snakeweed. After all plants were irrigated at the end of the vegetative stage, photosynthesis in the extremely stressed treatment ($17.1 \mu\text{mol m}^{-2} \text{s}^{-1}$, data not shown) approached that in the well-watered treatment ($19.2 \mu\text{mol m}^{-2} \text{s}^{-1}$) within 2 days. This may be indicative of fast water uptake when soil is rewet.

Broom snakeweed has sensitive stomatal behavior under mild stress conditions (soil water potential = -0.2 MPa). This is a trade-off for maintaining a large canopy and hence a high productivity. However, native plant species are often exposed to a much drier soil environment (Caldwell 1985). Although most species close their stomata with increasing stress, stomata of broom snakeweed do not respond sensitively from moderate to extreme stress, which results in low water-use efficiency. Broom snakeweed has a shallow root system that gives it access to water at the same soil depth as most perennial grasses (Pieper and McDaniel 1989). A conservative strategy in water use (stomata sensitive to stress) might place this half-shrub at a disadvantage to its competitors whose root systems can take up water rather rapidly from the upper soil layers (Cohen 1970, Richards 1986). Therefore, an alternative strategy must be used in water consumption by broom snakeweed. In contrast, deep rooted species such as mesquite are largely free of competition for deep water reserves with the associated range species. The relatively conservative stomatal behavior observed in mesquite (Wan and Sosebee 1991) may help the plant to survive a prolonged drought. Because stomata of broom snakeweed remain partially open under water deficit, the plant tolerates a low internal water status as observed in this study.

In conclusion, stomatal conductance and transpiration in broom snakeweed were more sensitive to mild soil water deficit than photosynthesis and canopy development. In contrast, canopy development and photosynthesis were more sensitive to severe soil water deficit than stomatal conductance and transpiration, which results in low water-use efficiency. Broom snakeweed exhibits positive photosynthesis under very low internal water status. Therefore, we do not reject our hypothesis that the combination of low water-use efficiency and high degree of drought tolerance are the basic physiological traits in broom snakeweed that enable it to compete effectively for the limited water resource in the semiarid rangelands.

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Broom snakeweed responses to drought: II. Root growth, carbon allocation, and mortality

CHANGGUI WAN, RONALD E. SOSEBEE, AND BOBBY L. MCMICHAEL

Authors are postdoctoral research associate and professor, Department of Range and Wildlife Management, Texas Tech University, Lubbock 79409; and plant physiologist, USDA-ARS, Cropping Systems Research Laboratory, Lubbock, Texas.

Abstract

The effects of soil water deficit on root growth, carbon allocation, and plant mortality of broom snakeweed (*Gutierrezia sarothrae* (Pursh) Britt and Rusby) were studied during the spring-summer growing season in plants subjected to different soil water regimes. As soil water deficit developed, root length density decreased, indicating that water deficit reduced root proliferation. Root/shoot ratio remained unchanged ($p > 0.05$) as soil water potential decreased from -0.023 MPa to -2 MPa; but it became higher ($p < 0.05$) in extremely stressed plants (-3.4 MPa), indicating that root growth was favored over shoot growth. Root length density was more closely correlated with green tissue dry weight/stem dry weight ratio ($r = 0.82$, $p < 0.0001$) than with root/shoot ratio ($r = 0.52$, $p < 0.05$). This suggests that (1) expansion of photosynthetic area was more sensitive than stem growth to water deficit and (2) carbon allocation within the shoot was more sensitive to water deficit than allocation between root and shoot. Plants died when gravimetric soil water decreased to around 0.03 g g^{-1} (equivalent to a soil water potential of -7.5 MPa). The leaf relative water content just before death was about 0.50. Soil water content in the top 20 or 30 cm of the profile is the single most important factor determining mortality of the snakeweed plant and can be used in making decisions in snakeweed control programs.

Key Words: rangeland xerophytes, water relations, root/shoot ratio, root length density, drought damage

Plant adaptation in arid and semiarid area is often associated with changes in root growth relative to shoot growth (Fernandez and Caldwell 1975, Sharp and Davies 1979, Morgan 1984). Morgan (1984) stated that in the absence of osmoregulation, a well-observed adaptational response is a reduction in shoot growth relative to root growth. Wan et al. (1993a) have found osmotic adjustment in field-grown broom snakeweed (*Gutierrezia sarothrae* (Pursh) Britt and Rusby) subject to drought, but not in the greenhouse-grown plants which adapted to drought through increased apoplastic water fraction. We do not know if increased root/shoot ratio contributes to drought adaptive mechanisms in broom snakeweed. Osman and Pieper (1988) indicates that root/shoot ratio in broom snakeweed seedlings grown in the field was nearly constant in early summer and decreased slightly in late summer. A fairly constant root/shoot ratio in broom snakeweed seedlings suggests that the plant can maintain a proper balance in

carbon investment between water acquisition and consumption under increasing drought. But since soil moisture was not monitored in this study, the effect of soil drying on root growth was not elucidated. It may also be possible that the modification in carbon allocation within shoots plays a significant role in the endurance of the stressed plants (Tyree and Sperry 1989).

The objectives of this research were to test: (1) the effects of various water deficit levels on root length and biomass of snake-weed; (2) the effects of various water deficit levels on carbon allocation pattern; and (3) the threshold water deficit level at which quiescence occurs and perennial stems die.

Materials and Methods

The experiment layout and methods for soil and plant water potential measurements were similar to those of Wan et al. (1993b). A total of 120 broom snakeweed plants were subject to 5 irrigation (irr.) treatments: well-watered (WW, 100% irr.), slightly stressed (SS, 50% irr.), moderately stressed (MS, 25% irr.), severely stressed (SVS, 12.5% irr.), and extremely stressed (ES, no irr.). Soil volumetric water content in the field was measured with the TDR technique (Wan et al. 1993b). Stainless steel rods 0.64 cm in diameter were cut into 20-, 40-, and 60-cm lengths and pairs of rods were inserted vertically into the soil at a parallel distance of 5 cm. Four replications were installed at the study site. Mortality of broom snakeweed plants was monitored during the experiment and was related to soil water availability. Field observation of plant mortality was also made to verify the results from the pot study.

Above- and below-ground biomass, green tissue (green leaf plus green stem) area, and total root length were measured at the end of the vegetative stage (30 June). Green tissue area was measured with a Li-3100 area meter. The root system was sorted as white roots and brown-colored suberized roots. Biomass of various plant parts was measured as oven-dry weight (70°C for 24 hours), and root length was measured with a Comair optical scanner (Hawker Dehavilland Inc., Australia). Root length density (RLD) was calculated as root length per unit soil volume ($\text{cm root cm}^{-3} \text{ soil}$).

The experiment consisted of a complete randomized design with 5 treatments. Three plants per treatment were harvested to obtain the above- and belowground biomass means. The treatment means were separated with Fisher's least significant difference at $p < 0.05$. Correlations were made between various parameters using the Pearson correlation procedure.

Results and Discussion

Root length density was highest in the well-watered treatment (-0.02 MPa), followed by the slightly (-0.2 MPa) and moderately stressed (-1.1 MPa) treatments, and lowest in the severely (-2

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Table 1. Root length, root dry weight, root length density (RLD), and root/shoot ratio in broom snakeweed subject to 5 treatments (Trt) sampled at the end of the vegetative stage in late June.

Trt	Root length		Root weight		RLD	Root/shoot
	White root	Suberized root	White root	Suberized root		
	----- (m) -----		----- (g) -----		- (cm cm ⁻³) -	
WW ¹	330.5 a	2.57 ab	3.31 a	2.67 ab	1.75 a	0.23 a
SD	54.1	2.18	1.12	0.27	0.29	0.03
SS	172.6 b	3.05 a	2.08 b	3.20 a	0.91 b	0.25 a
SD	8.8	1.36	0.25	0.50	0.05	0.03
MS	170.2 b	0.54 ab	1.46 bc	2.49 ab	0.91 b	0.36 a
SD	11.4	0.17	0.16	0.23	0.06	0.02
SVS	82.0 c	0.48 ab	1.03 bc	1.82 bc	0.43 c	0.29 a
SD	33.1	0.25	0.17	0.44	0.18	0.04
ES	42.9 c	0.39 b	0.56 c	1.24 c	0.23 c	0.56 b
SD	25.6	0.07	0.19	0.59	0.14	0.17

¹WW-well watered, SS-slightly stressed, MS-moderately stressed, SVS-severely stressed, ES-extremely stressed, SD-standard deviation, n=3 for each treatment. Means followed by the same letter are not different at $p < 0.05$ level.

and extremely stressed (-3.4 MPa) treatments (Table 1 and Wan et al. 1993b). Sharp and Davies (1979) found absolute root growth increased in maize seedlings subjected to an intermediate degree of water deficit. In the present study, white root length was lower under increased water stress. The root/shoot ratio in the extremely stressed treatment was significantly greater than in any other treatment ($p < 0.05$, Table 1); no difference ($P > 0.05$) was found among the other 4 treatments. Because the extremely stressed treatment did not receive any irrigation during mid April to late June, the plants exploited the soil by proportionately more root growth. The root/shoot ratio was significantly correlated with suberized root/white root ratio ($r = 0.67$, $p < 0.01$) (Table 2), indicating an increased proportion of suberized root biomass under soil water deficit. Increased root suberization can prevent water

Table 2. Correlation coefficients between the parameters.

GTA ¹	GTDW	SDW	GTDW:SDW	WRL	SRL	WRW	SRW	S/W	RLD	R/S	
1.0	.999	-.21	.837	.867	.668	.864	.69	-.51	.867	-.65	GTA
0.0	.001	.448	.000	.000	.006	.000	.004	.052	.000	.009	
	1.0	-.21	.843	.881	.659	.879	.699	-.51	.880	-.64	GTDW
	0.0	.443	.000	.000	.007	.000	.004	.052	.000	.010	
		1.0	-.52	-.31	-.12	-.30	.134	.123	-.29	-.34	SDW
		0.0	.046	.263	.668	.272	.633	.662	.289	.213	
			1.0	.825	.337	.879	.385	-.49	.822	-.44	GTDW
			0.0	.000	.219	.000	.157	.006	.000	.102	:SDW
				1.0	.535	.918	.531	-.65	.989	-.53	WRL
				0.0	.039	.000	.042	.009	.000	.044	
					1.0	.511	.507	-.30	.542	-.35	SRL
					0.0	.051	.054	.269	.037	.194	
						1.0	.480	-.64	.909	-.51	WRW
						0.0	.069	.01	.000	.050	
							1.0	.007	.562	-.38	SRW
							0.0	.979	.029	.155	
								1.0	-.60	.667	S/W
								0.0	.017	.006	
									1.0	-.52	RLD
									0.0	.049	

¹GTA-green tissue area, GTDW-green tissue dry weight, SDW-stem dry weight, WRL-white root length, SRL-suberized root length, WRW-white root weight, SRW-suberized root weight, S/W-suberized root weight/white root weight, RLD-root length density, R/S-root/shoot ratio. (The second number in each cell is the p value).

Table 3. Green tissue area (GTA), Green tissue dry weight (GTDW), stem dry weight (SDW), GTDW/SDW, Green tissue area/biomass (GTA/DW) in broom snakeweed subject to 5 treatments (Trt) sampled at the end of the vegetative stage in late June, 1991.

Trt	GTA	GTDW	SDW	GTDW/SDW	GTA/DW
	(cm ²)	(g)	(g)		(cm ² /g)
WW	590.2 a	24.05 a	1.42 a	18.42 a	23.21 a
SD	17.7	1.29	0.41	5.53	0.79
SS	456.8 b	18.40 b	2.71 abc	7.21 b	21.69 b
SD	48.4	1.77	0.77	1.62	1.01
MS	188.9 c	8.11 c	2.89 ab	3.13 bc	17.29 b
SD	17.4	0.73	0.96	1.08	2.25
SVS	150.9 c	6.10 c	3.85 bc	1.58 bc	15.11 c
SD	22.5	0.98	0.29	0.17	0.48
ES	37.9 d	1.68 d	1.54 ab	1.18 c	11.88 c
SD	1.0	0.13	0.43	0.35	1.42

n=3 for each treatment, SD-standard deviation. Means followed by the same letter are not different ($p > 0.05$).

movement from the root to the very dry soil (Nobel and Sanderson 1984).

Green tissue area/unit of biomass was ordered according to WW=SS>MS>SVS>ES ($p < 0.05$) (Table 3). The green tissue/woody stem ratio declined linearly with increasing soil water deficit ($r^2 = 0.99$, Fig. 1). In the severely and extremely stressed treatments as compared to other treatments, this ratio dropped to less than 1.6, suggesting that a greater proportion of exported carbon was invested in stems and a smaller proportion was partitioned into expansion of photosynthetic area. It could also mean a loss of leaves as shown by Wan et al. (1993b). But, stem dry weight was over 2-fold greater ($p < 0.05$, Table 3) in the severely stressed treatment than in the well-watered treatment, indicating more carbon was invested in the stems under severe stress. DePuit and Caldwell (1975) found that green leaf/green stem ratio of snakeweed in the cold desert declined from spring to summer. Apparently, the car-

bon allocation pattern in the shoot was more sensitive to drought than the root/shoot ratio.

Sperry and Tyree (1990) indicated that xylem embolism occurs daily in droughted plants at threshold plant water potentials ranging from -2.0 MPa in balsam fir (*Abies balsamea* (L.) Mill.) to -3.5 MPa in eastern redcedar (*Juniperus virginiana* L.). In the present study, plant water potentials in the moderately, severely, and extremely stressed treatments were lower (Wan et al. 1993b) than the threshold values for the conifers species including the drought tolerant eastern redcedar, which is least vulnerable to cavitation (Tyree and Ewers 1991). Less stomatal control over water loss and low soil water potentials in these treatments (Wan et al. 1993b) also could cause runaway embolism (Tyree and Ewers 1991). Individual branches of the droughted broom snakeweed plants often showed signs of stress damage (losing green color), while other branches were not affected. This dead-branch leaf loss is consistent with, and perhaps caused by, some loss of xylem elements (Tyree and Sperry 1989). This characteristic may be advantageous to the plant survival because it reduces whole plant transpiration and prevents the main branch from cavitation (Zimmerman 1983). Jones and Sutherland (1991) pointed out that the stressed plant could invest additional carbohydrate to build excess conducting tissue as a buffer against some loss of xylem vessels. This may explain the increased carbon investment in stems in the stressed broom snake-weed plant.

Root length density, an index of water uptake capacity, is more closely correlated with the green tissue/stem ratio ($r=0.82$, $p<0.0001$, $n=15$, Table 2) than with the root/shoot ratio ($r=-0.52$, $p<0.049$, $n=15$). This seems to indicate that expansion of photosynthetic area is more sensitive to water deficit than stem growth and modification of carbon allocation within the shoot is more significant to the plant than changes in root/shoot ratio in response to soil drying. In the moderately, severely, and extremely stressed treatments when soil water availability is very low (<-1.1 MPa, Wan et al. 1993b), additional carbon investment in the roots does little to improve the plant water balance. Consequently, less carbon will be invested in construction of transpiring area, resulting in reduced water consumption. More carbon may be allocated to the conduits through more rapid primary (and secondary) wall growth, resulting in smaller pit-membrane pores which are less vulnerable to cavitation (Tyree and Sperry 1989). Snakeweed has photosynthetic stems that can account for up to 20% of the total carbon fixation during drought (DePuit and Caldwell 1975). Increased carbon allocation to the self-supportive stems reduces surface area/volume ratio; therefore, this can be a very important drought-adapted strategy.

From April until mid September, 80% of plants in the extremely stressed treatment and 8% of plants in the severely stressed treatment died ($n=24$). Before the plants died, we repeatedly measured volumetric soil water content of about $0.044 \text{ cm}^3 \text{ cm}^{-3}$, which is equivalent to a gravimetric water content of 0.03 g g^{-1} and water potential of -7.5 MPa. Similar observations were made by Courtney (1984), who found that a major "die-off" of broom snakeweed plants occurred when water content in a sandy loam soil dropped to 0.03 g g^{-3} under field conditions.

In the field, when water content in the top 20-cm of soil decreased to $0.065 \text{ cm}^3 \text{ cm}^{-3}$ (0.043 g g^{-1} , Fig. 2) in mid July and early August, death of some snakeweed plants was also noted. The water content of the topsoil in the field was similar to that in the severely stressed treatment ($0.067 \text{ cm}^3 \text{ cm}^{-3}$, -2 MPa) in which 8% of plants died. It appears that broom snakeweed is sensitive to changes in soil water content in the topsoil, where most of its root system is located (DePuit and Caldwell 1975). When exposed to a soil water potential of -2 MPa for some period of time, some mortality will occur. However, the major die-off will not take place

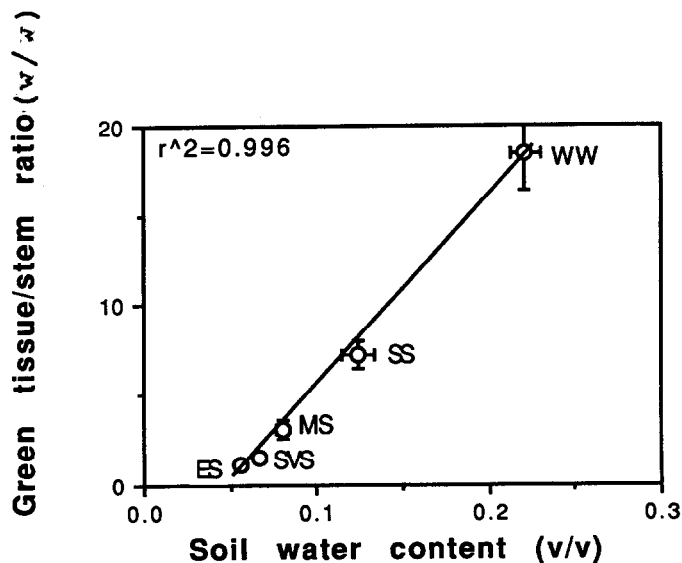


Fig. 1. Green tissue dry weight/stem dry weight ratio as influenced by soil water regimes for each treatment. Each data point is the average of 3 observations.

until soil water potential is further reduced to -7.5 MPa (or water content of 0.03 g g^{-1} in the fine sandy loam soil). Leaf relative water content (RWC) was often reduced to 50% ($\pm 2.8\%$ SE, $n=6$) before the plants showed signs of dying (leaves turn brown). This is comparable to the findings of Hinckley et al. (1983) that revealed that the relative water content at which irreversible cell damage occurred in 6 shrub species ranged from 45.7% to 62.7%. Plant water potential in the extremely stressed treatment was about -8 MPa, which may make the plant operate on the verge of catastrophic xylem dysfunction and may explain much of the plant death.

The soil volume occupied by the root system is different in the pot- versus field-grown plants, as is the total water availability in the rooting zone. It is also possible that soil temperature can vary from the pot to field conditions. Despite these differences, the

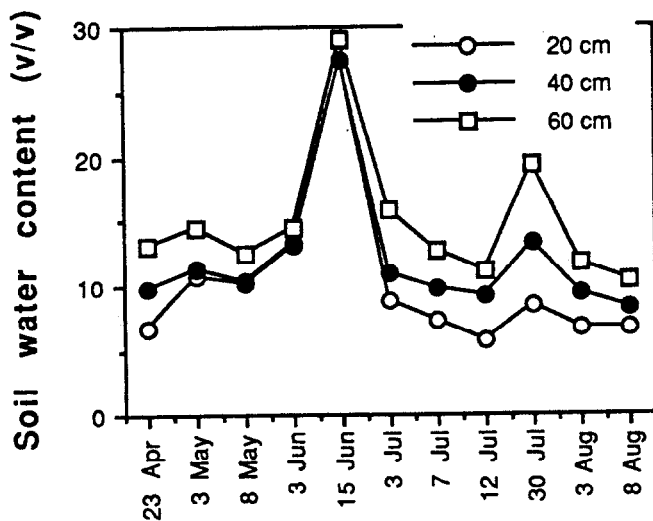


Fig. 2. Soil water content ($\text{cm}^3 \text{ cm}^{-3}$) at 3 soil depths measured with a TDR unit throughout the spring-summer growing season in the field. Each data point is an average of 4 replications. The standard errors of the mean are smaller than the symbols. Death of some broom snakeweed plants was noted during mid July when water content in the 20-cm profile decreased to $0.065 \text{ cm}^3 \text{ cm}^{-3}$.

threshold soil water content at which broom snakeweed dies was very similar for the pot study and field observations. This indicates that soil water content in the top 20 or 30 cm of the profile is the single most important factor determining mortality of the snake-weed plant and can be used in making decisions in snakeweed control programs.

In the severely and extremely stressed treatments, the plants were exposed to low soil water potentials for prolonged periods (late April to late June and mid July to September). There was some adjustment to the water deficit through reducing canopy development and decreasing stomatal conductance which (Wan et al. 1993b), therefore, could increase their endurance to some extent. In the field, however, plant death occurred in less than 10 days from a sudden moderate to severe stress (from 3 to 12 July, Fig. 2). Accelerated canopy development occurred in the wet month of June, and plants were not able to reduce the canopy area sufficiently in the subsequent drought period. In addition, because stomata were less responsive to severe soil drought (Wan et al. 1993b), transpirational water loss was relatively high, causing tissues dehydration and possible xylem embolism. Therefore, when the threshold water content is reached in the field the time frame for snakeweed die-off is fairly short (weeks instead of months) if the drought is not relieved by precipitation events.

In conclusion, soil water deficit significantly reduced root length and biomass of broom snakeweed. The root/shoot ratio remained relatively constant at soil water potential between -0.02 and -2 MPa, but increased significantly ($p < 0.05$) at -3.4 MPa. Carbon allocation within the shoot was more sensitive to soil water deficit than allocation between root and shoot. Broom snakeweed died at an average water content of 0.03 g g^{-1} in the top 20- to 30-cm of the soil profile on the sandy loam soil, which was equivalent to a soil water potential of -7.5 MPa.

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Cattle avoidance of leafy spurge: A case of conditioned aversion

SCOTT L. KRONBERG, RUSSELL B. MUNTIFERING, ELDON L. AYERS, AND CLAYTON B. MARLOW

Authors are former research associate, former associate professor, former research associate, and associate professor, respectively, Department of Animal and Range Sciences, Montana State University, Bozeman 59717.

S. L. Kronberg is currently with the USDA-ARS, U.S. Sheep Experiment Station, Dubois, Ida. 83423 and R. B. Muntifering is currently with the Alabama Agr. Exp. Sta., Auburn Univ., Alabama 36849-5403.

Abstract

Leafy spurge (*Euphorbia esula* L.) represents a serious threat to the productivity and profitability of many cattle ranches in the midwestern U.S. Sheep and goats will graze the weed, but cattle generally do not. We hypothesized that cattle avoid leafy spurge because it contains 1 or more chemicals that elicit a conditioned flavor aversion when consumed. First, we tested cattle to determine if they reduced their intake of a novel feed on subsequent days if we modestly increased rumen fill by introducing additional feed or additional feed plus an aversive agent (lithium chloride, LiCl) after they had consumed the novel feed. We observed that cattle became averted ($P = .0001$) to the novel feed only when LiCl was administered with additional feed. Simply increasing rumen fill by a small amount did not cause cattle to reduce their intake of the novel feed the following day. Secondly, we tested cattle to determine if they reduced their intake of a novel feed on subsequent days if we introduced leafy spurge into their rumina following consumption of the novel feed. We also tested cattle to determine if a spurge-induced aversion to a novel feed was preventable by inoculation with rumen microbes from sheep with spurge in their diets. We found that introducing spurge into cattle after their intake of novel feed reduced ($P < .01$) their intake of the novel feed on subsequent days. Cattle inoculated with rumen microbes from spurge-adapted sheep had similar ($P > .40$) aversions to a novel feed paired with spurge introductions. Apparently, cattle avoid leafy spurge partly or wholly because they develop a conditioned aversion after first ingesting some threshold amount of it.

Key Words: noxious weeds, ruminants, food aversion learning

Leafy spurge (*Euphorbia esula* L.), an aggressive perennial weed from Eurasia, is seriously threatening the productivity and profitability of many range-based cattle operations in the United States. While sheep or goats may ingest and consequently help control the spread of spurge, cattle generally consume little, if any (Lym et al. 1988). It is commonly believed that spurge is harmful to cattle (Lacey et al. 1985, Lym and Kirby 1987), yet sheep and goats can sustain high productivity with considerable daily intake of growing spurge (Landgraf et al. 1984, Bartz et al. 1985, Lym et al. 1988). Their high productivity is likely a response to high crude protein (15–28% of dry matter) and low acid detergent fiber (13–25% of dry matter) levels in spurge's vegetative and flowering stages (Fox et al. 1991).

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Small ruminant grazing can effectively check spurge expansion, but spurge abundance will increase if grazing is discontinued (Lacey et al. 1984). If cattle could be adapted to tolerate and graze spurge similarly to sheep or goats, then cattle, the predominant range livestock in the U.S., could be used to check the spread of this weed while utilizing it as forage. One obstacle in making this practice work is the potential of cattle forming aversions to spurge.

Burritt and Provenza (1989) demonstrated that sheep will develop conditioned aversions to novel feeds when these feeds are paired with negative post-ingestive consequences. We observed cattle consume small amounts (≤ 1 kg) of pre-senescent spurge on range and in confinement for 1 or 2 days, then stop consuming it. Consequently, we speculated that cattle avoid leafy spurge because they develop a conditioned aversion to spurge after they first consume it.

We hypothesized that 1 or more aversive compounds in leafy spurge elicit negative post-ingestive consequences in cattle, and further that the aversive compounds in spurge could be modified or degraded before eliciting negative post-ingestive malaise. Ruminant microbes can degrade some plant toxins (James et al. 1975, Carlson and Breeze 1984), hence we reasoned that sheep may harbor 1 or more ruminal microbial species capable of metabolically altering potentially aversive compounds in spurge, while cattle may lack this capacity and are consequently averted to spurge.

In this paper, we report on 2 experiments designed to investigate aspects of cattle feeding behavior with respect to leafy spurge. The first experiment was designed solely to test part of the methodology used in the second experiment. The objective of the first experiment was to determine whether cattle will avoid or reduce their intake of a novel feed, simply because the bulk fill in their rumina is modestly increased by the introduction of additional plant material (ruminal fill was increased by a similar amount in both experiments), or if the introduction of an aversive chemical (e.g., lithium chloride) is necessary to elicit reduction in novel feed intake. The objectives of our second experiment were to determine whether the introduction of leafy spurge into cattle rumina causes conditioned feed aversion, and if we might prevent a spurge-induced aversion by introducing ruminal digesta (with its complement of microbes) from spurge-consuming sheep into cattle.

Materials and Methods

Experiment 1

Fifteen rumen-fistulated Hereford calves (mean wt, 181 kg) were randomly divided into 3 treatment groups of 5 calves each. During the trial, Group-1 calves were dosed with alfalfa (*Medicago sativa* L.) pellets within 0.5 hour after consuming a novel feed (Vitality

Milk Plus Pellets¹). This feed is a highly palatable concentrate. Group-2 calves were dosed with alfalfa pellets plus lithium chloride (LiCl) (80 mg/kg body weight) within 0.5 hour after consuming the novel feed, while Group-3 calves did not receive post-consumption dosages after consuming the novel feed. Lithium chloride is an aversive agent which is quickly absorbed from the digestive tract (Harrison et al. 1963) and has been used in numerous studies to elicit conditioned taste aversions (Braveman and Bronstein 1985). Alfalfa pellets and LiCl were placed into calves' rumina through their fistulas.

For calves in Groups 1 and 2, the amount of alfalfa pellets placed in the rumen each trial day was equal to the weight of the novel feed they had consumed that day; LiCl was administered in the gelatin capsules. Each calf in Groups 1 and 2 was given alfalfa pellets or alfalfa pellets and LiCl on each trial day that it ingested any amount of the novel feed. Beginning on day 1 of the trial, 907 grams (2 pounds) of the novel feed were offered to each calf from 0800 to 0900 hours. The calves were tested for aversion to the novel feed on days 3, 5, 7, and 9 following their initial exposure to the novel feed on day 1. The amount of novel feed consumed by each calf was determined on each day.

In addition, all calves received a basal ration of alfalfa pellets sufficient to permit an average daily gain of 0.2 kg (NRC 1984). Calves were fed their basal ration in 2 equal feedings at 0900 and 1500 hours; this schedule was started 2 weeks prior to the initiation of the trials. Calves were allowed 1.5 hours to eat their basal ration, then were released into large pens with unlimited access to trace-mineral salt and water.

Experiment 2

Fifteen rumen-fistulated Hereford calves (mean wt, 172 kg) were randomly divided into 3 treatment groups of 5 calves each. Group-1 calves received pre-trial inoculations of ruminal microbes (in digesta) from 2 adult sheep that had about 1 kg/day of fresh-cut leafy spurge (seed-development growth stage) in their diets for 2 weeks before ruminal digesta was collected. On 3 alternate days of the week preceding the trial, each calf in Group 1 received 200 ml/day of ruminal digesta from the sheep. On the mornings of these 3 days, about 750 ml of ruminal contents were collected from each sheep. The 2 collections were pooled, mixed, and stored in an insulated container. Each calf received its portion within 0.5 hour after the digesta had been collected. Calves in Groups 2 and 3 did not receive pre-trial manipulations of their rumen environment. Calves in Groups 1 and 2 received spurge during the trial and Group-3 calves served as controls.

During the pre-trial period, calves received a basal ration of alfalfa pellets which were fed at a rate to permit an average daily gain of 0.2 kg (NRC 1984). Calves were fed their basal ration in 2 equal portions at 0800 and 1500 hours. The basal ration was fed for 2 weeks before the trial began. Calves were allowed 1.5 hours to eat their basal ration, then were released into large pens with unlimited access to trace-mineral salt and water.

During the trial, calves in Groups 1 and 2 had leafy spurge introduced into their rumina on each day that they consumed any amount of the novel feed (an alfalfa- and grain-based horse pellet). The novel feed was offered at 0800 hours in place of the basal ration. Calves were fed individually, and the amount of novel feed offered each calf equaled the weight of the basal ration they had been fed at 0800 hours during the pre-trial period. A quantity of fresh spurge, equal to the weight of novel feed consumed, was introduced into each calf's rumen within 2 hours after it consumed the novel feed. The dose of spurge was matched with the amount of

novel feed consumed to provide the calves with a realistic intake ratio of novel feed to spurge. One-half of the daily basal ration was fed at 1500 hours.

Leafy spurge, in seed-development stage, was cut about 6 cm above the ground from rangeland at the Red Bluff Research Ranch, 56 km west of Bozeman, Mont. Spurge was hand-chopped into about 1.5 cm² pieces before insertion into designated calves. The order in which the calves received chopped spurge was adjusted daily to control for potential change in chemical characteristics of spurge over the 2-hour period from harvest to treatment. Leafy spurge contains potentially inflammatory diterpenoid ingenols (Upadhyay et al. 1978; Seip and Hecker 1982) that may be the aversive agents for cattle. The chemical instability of ingenols is reported to be high in heat, light, oxygen, and alkaline or acidic conditions (Evans 1986); therefore we attempted to minimize the time between harvest and introduction of spurge into the cattle. The calves were tested for aversion to the novel feed on 5 consecutive days following their initial exposure to the novel feed on day 1.

For both experiments, data for novel feed intake on day 1 were analyzed with analysis of variance as a completely randomized design with the General Linear Models (GLM) procedure of SAS (1988). Data for novel feed intake on subsequent days were first analyzed by analysis of covariance with novel feed intakes on day 1 as the covariate. If the covariate was not significant ($P > 0.10$), it was excluded from the model used for analysis of variance. Data for novel feed intake on subsequent days were analyzed using a repeated measures design and the GLM procedure of SAS (1988). Individuals were nested within treatment groups and the calf (treatment) mean square was the error term for the F statistic for treatment. Data were balanced for both experiments. When appropriate, individual means were compared using the protected LSD procedure (SAS 1988).

Results and Discussion

Experiment 1

On the first day of the trial, novel feed intake was similar ($P = 0.28$) among calves in all 3 groups (Table 1). Novel feed intake on

Table 1. Mean daily intakes (g) of the novel feed (\pm SE) for treatment groups in Experiment 1.

Group	Day	Day 3 ^a	Day ^b	Day ^b	Day 9 ^b
			(g \pm SE)		
1 ^c	907 ^f \pm 0	907	907 ^f \pm 0	907 ^f \pm 0	907 ^f \pm 0
2 ^d	884 ^f \pm 23	0	84 ^g \pm 42	344 ^g \pm 212	135 ^g \pm 56
3 ^e	895 ^f \pm 12	907	907 ^f \pm 0	907 ^f \pm 0	907 ^f \pm 0

^aThere was no variation in intakes among individuals in the 3 groups on day 3; therefore, analysis of variance was not conducted on data for this day.

^bCalves in groups 1 and 3 ate all of the novel feed offered on these days.

^cGroup 1 calves received alfalfa pellets after they ate the novel feed.

^dGroup 2 calves received alfalfa pellets and LiCl after they ate the novel feed.

^eGroup 3 calves received neither alfalfa pellets nor LiCl after they ate the novel feed.

^{f,g}Means for the same day with different superscripts differ ($P < 0.01$).

day 1 was not a significant covariate ($P > 0.20$) in the models for novel feed intake on days 3, 5, 7, and 9. However, treatments had a strong effect ($P = 0.0001$) on novel feed intake on subsequent days of the trial. Individual days and the interaction of days with treatments were not important ($P > 0.20$) variables affecting novel feed intake. The group of calves that received LiCl (2) was the only group that was averted to the novel feed on the test days ($P < 0.01$). In contrast, calves in Groups 1 and 3 ate all of the novel feed offered on these days. Apparently, a small increase in rumen fill resulting from introduction of alfalfa pellets into Group-1 calves had no negative effect on their consumption of novel feed. Our results agree with those of Olson and Ralphs (1986), who averted cattle to alfalfa pellets by ruminal infusions of lithium chloride or an extract

¹Nutrena Feed Div., Cargill, Minneapolis, Minn. 55440. Use of this product does not constitute an endorsement by the Montana Agr. Exp. Sta.

from the poisonous plant tall larkspur (*Delphinium barbeyi* L. Huth) after cattle had eaten alfalfa pellets. Their heifers developed strong and persistent aversions to alfalfa pellets by the fifth feeding paired with either type of infusion.

Experiment 2

On the first day of the trial, calves in all groups had similar ($P = 0.70$) intake of novel feed (Fig. 1). Novel feed intake on day 1 was not a significant covariate ($P < 0.49$) in the models for novel feed

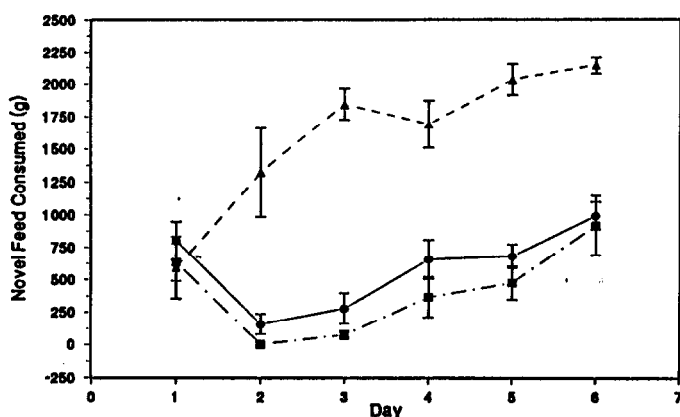


Fig. 1. Consumption of novel feed (g) during a 1-hour period by 3 treatment groups of cattle on each day of a 6-day trial. Group 1 calves (—●—) received pre-trial inoculations of ruminal microbes (in digesta) from sheep that had leafy spurge in their diets and the calves received spurge each day shortly after they ate the novel feed. Group 2 calves (---■---) did not receive a pre-trial treatment, but they received spurge each day shortly after they ate the novel feed. Group 3 calves (---△---) did not receive a pre-trial treatment and they did not receive spurge when they ate the novel feed. Bars represent \pm SE.

intakes on days 2 through 6. However, subsequent intakes varied ($P = 0.0001$) as functions of treatment and day; the day \times treatment interaction was not significant ($P = 0.41$). Both groups that had received chopped spurge after consuming the novel feed on day 1 ingested less ($P = 0.001$) of the novel feed on day 2 than Group-3 calves that had not received spurge. Calves in Group 1 that received ruminal digesta from sheep were as averted ($P > 0.17$) to the novel feed as calves that received spurge without a rumen pre-treatment (Group 2).

Transferring ruminal digesta from sheep with spurge-containing diets did not prevent cattle from developing a spurge-induced aversion. This finding suggests that if sheep harbor ruminal microbes that can alter or degrade aversive chemicals in spurge and if we successfully transferred them, they may not be able to exist (or exist in sufficient numbers) in cattle rumina. Alternatively, ruminal microbes in cattle may produce an aversive substance from spurge, whereas sheep ruminal microbes may not. If this possibility occurs, transferring ruminal microbes from sheep to cattle would not alter the aversive response of cattle to spurge.

Calves that did not receive spurge (Group 3) ate increasing amounts of novel feed during the trial. After day 2, the groups that received spurge ate gradually increasing amounts of the novel feed. Their responses are similar to those observed by Burritt and Provenza (1989) with lambs offered LiCl-treated or untreated corn, oats, or calf-manna, and to those of Provenza et al. (1990) with goats offered pellets of older-growth blackbrush (*Coleogyne ramosissima* Torr.) which had been coated with purified condensed tannins. There are several possible explanations for the increased intake of novel feed by calves which received spurge. First, calves may have developed a physiological tolerance to the aversive chemical(s) in spurge. Second, calves' ruminal microbes may have developed enhanced metabolic capacity to degrade aversive chemicals in spurge; consequently, calves may have absorbed lower levels of

the aversive chemicals and had reduced levels of negative feedback. Finally, previous exposure to spurge may have sequentially reduced the level of post-ingestive malaise that calves experienced with each additional exposure to aversive compounds in spurge; consequently, they experienced declining aversion to spurge. This preexposure effect has been discussed by Braveman (1977).

Summary

Aversions by calves to a novel feed were induced only when the aversive chemical LiCl was introduced following intake of the novel feed. Introduction of a small amount of additional forage into calves' rumina, with consequent increase in rumen bulk fill, did not reduce intake of the novel feed on subsequent days. The introduction of leafy spurge into cattle rumina elicited conditioned aversions to a novel feed they consumed. This finding suggests that cattle avoid spurge partly or wholly because they develop a conditioned aversion to it after initially ingesting some threshold amount. Introduction of ruminal digesta and microbes from sheep with spurge in their diets did not prevent cattle from developing a spurge-induced aversion.

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Livestock grazing impacts on infiltration rates in a temperate range of Pakistan

FAIZUL BARI, M. KARL WOOD, AND LEIGH MURRAY

Authors are former graduate student and professor, Dept. of Animal and Range Sciences; and associate professor, Dept. of Experimental Statistics, New Mexico State University, Las Cruces 88003.

Abstract

This study was conducted in a temperate range of northern Pakistan in 1987 and 1988. The main purpose of the experiment was to determine a suitable residual phytomass level for the moist temperate ranges of Pakistan. Data were collected for 2 consecutive growing seasons. A completely randomized design, with 4 treatments and 2 replications, was used. The treatments were 4 different residual phytomass levels. A rainfall simulator applied rainfall to 48 flexible circular plots (1 m²). Analysis of variance and the LSD multiple mean comparisons determined treatment differences, and stepwise multiple regression identified the important vegetation and soil variables affecting infiltration.

The control (no grazing) resulted in the highest infiltration while the treatment having the lowest residual phytomass had the lowest infiltration. Among the independent variables, standing phytomass was the most important variable affecting infiltration. Foliar and basal cover were also highly correlated to infiltration.

Key Words: infiltration rates, grazing phytomass, cover

The degree to which the grazing lands are being used by local and migratory livestock herds in Pakistan's temperate areas is of immediate concern to natural resource managers. The livestock use these ranges intensively in the growing season. As a result of heavy grazing and trampling, standing phytomass of the herbaceous and shrubby vegetation is consumed to a low level. This results in high runoff and unacceptable erosion.

Livestock grazing influences on water infiltration and runoff have long been studied. Most researchers have determined only effects of grazing use or intensity on these variables, mostly in parts of the United States. Grazing management on rangeland is based on controlling the timing, intensity, frequency, and selectivity of grazing animals (Stoddart et al. 1975). Generally, range managers recognize intensity as the most critical of these factors. Intensity determines how much vegetation remains to maintain the plant, soil, wildlife, and water components of range ecosystems. A U.S. rule of thumb with international extensions as been to take half and leave half (50% utilization) of the current year's growth.

Grazing influences infiltration, primarily through impacts on soil and vegetation. Heavy grazing generally decreases infiltration (Rhoades et al. 1964, Rauzi and Hanson 1966, Lusby 1970). Livestock grazing alters infiltration rates of rangeland soils by removing protective plant cover and by trampling. Vegetation and mulch cover protect the soil surface from raindrop impact and influence soil surface properties such as bulk density, organic matter content, and aggregation (Osborn 1954, Copeland 1963, Blackburn 1975, Meeuwig and Packer 1976, Blackburn et al. 1982).

Mismanagement of domestic livestock, especially with high stocking rates, has caused severe degradation in much of the

world's rangelands (Bentley 1898, Box 1967, Dregne 1978). Moderate stocking rates designed to use about half the current year's forage production are generally accepted as proper grazing management (Stoddart et al. 1975), but the take-half-and-leave-half practice has several problems, especially in areas with great variation in precipitation and subsequent forage production. It is not unusual for a range to produce a few hundred kilograms per hectare one year and several times that much another year. In such a situation, the take-half-and-leave-half concept might not be the best management decision.

Liacos (1962), working on California annual grasslands, found runoff depths of 3.3 cm, 9.7 cm, and 23.2 cm for ungrazed, lightly grazed and heavily grazed sites, respectively. The author attributed the increased runoff to an increase in bulk density. Sharp et al. (1964) obtained hydrologic data on Cottonwood, S.D., from small rangeland watersheds grazed lightly, moderately, and heavily. Relatively little difference in total runoff from the lightly, moderately, and heavily grazed watersheds occurred as a result of 4 runoff-producing storms. However, in 3 of the 4 storms, runoff increased markedly with increased grazing pressure. During these 3 storms, total runoff from the heavily grazed areas was about 1.5 times greater than that from moderately grazed watersheds. Runoff under light grazing was only 1/10th as great as that under heavy grazing.

Knoll and Hopkins (1959), working on blue grama (*Bouteloua gracilis* [Willd. ex. H.B.K.] Lang ex. Griffiths) and buffalograss (*Buchloe dactyloides* [Nutt.] Engelm.) range near Hays, Kans., observed infiltration rates of 6.6, 5.3, and 4.0 cm hour⁻¹ on ungrazed, moderately grazed, and heavily grazed pastures, respectively. Reed and Peterson (1961) found infiltration rates on sandy and clayey soils in the northern Great Plains decreased with increased grazing intensity. Infiltration was markedly slower on buffalograss than on western wheatgrass (*Elymus smithii* [Rydb.] Gould) types for the heaviest- and lightest-grazed ranges. Rhoades et al. (1964), working on loamy fine sand soil in the southern Great Plains of Oklahoma, with a dominant vegetation of sand sagebrush (*Artemisia filifolia* Torr.) and an average canopy cover of 38%, found infiltration rates were inversely proportional to the degree of continuous grazing pressure. The average stocking rates or grazing intensities were exclusion, 9 ha per animal unit (ha/AU), 7 ha/AU, and 5 ha/AU for nongrazed, lightly grazed, moderately grazed, and heavily grazed, respectively.

Rauzi (1963) conducted a study in North Dakota on an Elliott beard grass bluestem (*Andropogon elliotii* Chapm.), western wheatgrass, and needle-and-thread (*Stipa comata* Trin. & Rupr.) community, and found the infiltration rate decreased with increasing stocking rate. Investigation showed the loss of surface cover and heavy use of livestock decreased the rate of water intake. Total water intake on the moderately grazed pasture was 1.6 times greater than that on the heaviest grazed pasture. Water intake on the ungrazed area was 1.8 times greater than that of the moderately

grazed pasture. Dadkhah and Gifford (1980), working near Logan, Ut., found decreased infiltration rates with increased trampling percentage up to 40%. Above 40% trampling, infiltration rates were no longer affected.

McCalla et al. (1984) and Thurow et al. (1986) determined the effects of livestock grazing on infiltration rates on the Edwards Plateau of Texas. They found total vegetation cover and grass standing crop were among the variables which significantly influenced infiltration rates. Weltz and Wood (1986) evaluated the influence of short duration grazing, continuous grazing, and exclusion in New Mexico. Total water infiltration in the grazed short duration pasture was half that of a continuous grazed pasture. The decrease was attributed to reduced phytomass and increased bare ground.

The main objective of this study was to determine an appropriate residual phytomass level that would protect the watershed by minimizing the runoff. The residual phytomass is assumed to be more important than the percentage utilization of annual production because of fluctuations in production from year to year. It was hypothesized that various residual phytomass levels had significantly different levels of runoff and infiltration because of the relationship between phytomass and other independent variables such as foliar and basal cover. The second objective was to determine suitable predictive equations for terminal infiltration and cumulative infiltration.

Study Area

Location

The study was conducted at Lilawani Ranch near Alpuri in the subhumid zone in northwestern Pakistan. The area lies between 34° 31' and 35° 8' N latitude and 72° 35' and 73° 01' E longitude. It is bounded on the northeast by the upper Indus Kohistan district; on the north and northwest by Malakand Agency, Swat and Swat Kohistan; on the south and southwest by Bunir subdivision; and on the southeast and east by the Indus River. The entire area forms part of the Indus River catchment. The country's largest dam, the Tarbela, has been constructed on this river. The silt accumulation rate behind this dam is so high the original estimated life span of 120 years has been reduced to 60 years. Accelerated erosion has created this problem, which in turn is the outcome of the mismanagement practiced in the high hills of the catchment area. Along with many other factors, heavy grazing is a major problem. The specific study site has been used for grazing as well as grass cutting to make hay. The same practice is common in the surrounding areas and has been since the last century. The elevation varies from 450 to 4,500 meters, and land is used mostly for agriculture and grazing. Moderate to precipitous slopes are common area features; slopes less than 30% are not common. The surface configuration is generally rugged and uneven.

Rock and Soils

The study area falls in the mountainous region of the Swat Valley. Mountains occupy most of the study area. These mountains are residual and colluvial in nature. The exposed rocks are mostly plutonic and sedimentary.

Mountainous soils are dominantly loamy and contain a variable proportion of coarse rock fragments and are mostly underlain by bedrock within 1 m depth. Generally, the surface soils are well humified and dark colored, and sufficiently base rich, structured, and thick to qualify for the mollic epipedon. The epipedon is more pronounced in wetter and cooler locations. The organic matter content of the surface mineral horizons varies from about 1% to more than 9%, and virgin soils may contain more organic matter than their cultivated counterparts. Surface soils are weakly to moderately granular, whereas subsoils are dominantly subangular

blocky. Most of the soils would be classified as mollisols. The soils in the study area have been classified as Shangla series. Because they occur on sloping surfaces, these soils are subject to active water erosion, with erosion intensity depending on the vegetational cover and slope gradient.

Climate

The study area climate is sub-humid temperate. The average minimum temperature in January in Besham is 6.7° C, and average maximum temperature is 38.4° C in June. The mean minimum temperature during December and mean maximum temperature during June recorded at the Saidu Sharief Meteorological Station are 11.7° C and 37.7° C, respectively.

Precipitation occurs both as rain and snow. The average monthly rainfall is 80 mm. Snowfall generally starts by the end of November on the higher peaks and descends in December and January.

The flow of water in streams is at maximum during summer monsoon rains. The drainage rate is high and the entire area is drained by the tributaries of, or directly by, the Indus River. The most important among these tributaries is the Kana-Khuband Khuwar, which drains the Kana, Alpuri, and Lilawani valleys.

Vegetation

The study area falls in a pure blue pine (*Pinus wallichiana* Wall.) zone between 1,677–2,440-m elevation, which borders mixed silver fir (*Abies pindrow* Spash.) forests at higher elevation, while it borders pure chir pine (*Pinus roxburghii* Roxb.) forests on the lower side. The underwood consists of, in the lower parts, walnut (*Juglans regia* Linn.) bird cherry, (*Prunus padus* Linn.), Batangi (*Pyrus pashia* Ham.), amlook (*Diospyros lotus* Linn.), hill toon (*Cedrela serrata* Royle.), and horsechestnut (*Aesculus indica* Hiern.). The undergrowth consists of kori (*Berberis lycium* Royle.), gangali gulab (*Rosa moschata* Mill.), shadshad (*Buxus sempervirens* Linn.), ghoraje (*Indigofera pulchella* Roxb.), and chambali (*Jasminum humile* Linn.).

Grasses and forbs in the study area include lung (*Cymbopogon iwarancusa* Schult.), surmal (*Heteropogon contortus* Beauv.), pisholamae (*Cenchrus ciliaris* Linn.), changae (*Aristida depressa* Retz.), dadum (*Sorghum halepense* Pers.), and khabl (*Cynodon dactylon* Pers.).

Methods

The data were collected for 2 growing seasons, during the summers of 1987 and 1988. A hand-portable rainfall simulator described by Wilcox et al. (1986) was used to apply rainfall to 48 flexible circular plots (1 m²). A single stationary nozzle was placed 200 cm above the center of the plot, and the application rate was 12.7 cm hour⁻¹. The plots were constructed from galvanized steel sheets about 15 cm wide and 3.54 m long. A small, metal runoff tray was connected to the plot to collect runoff. The soil was of such a nature that metal strips could easily be tamped into the soil without bending. The lower inside and outer side borders were sealed to prevent leakage. The soil seal was covered with a mulch layer to protect it from raindrop impact and subsequent soil particle detachment. The area of each plot was determined by a grid constructed from 1.2 cm × 1.2-cm mesh. Simulated rainfall was applied to each plot at the existing or antecedent soil water level for 30 minutes, and runoff collected and weighed. Plots were then covered with clear plastic to prevent evaporation and ensure fairly uniform soil water conditions for the second rainfall application. The second rainfall application was applied when the soil was still at field capacity after a lapse of 20–24 hours. Water was applied for 30 minutes during this second application. Infiltration rate was determined by subtracting runoff rate from application rate for each plot.

Time was the cumulative period from the beginning of rainfall application. Runoff from each plot was collected at 5-minute intervals and weighed. Cumulative infiltration (cm) was the total amount of water that infiltrated during a given application period. Surface water storage, interception loss, and evaporated water were considered to be negligible, and were not accounted for in calculating infiltration.

Standing biomass (g m^{-2}) was determined for grasses and forbs by clipping to ground level on each plot. The litter was also hand collected. The phytomass material for each plot was placed in separate paper sacks, dried at 60–70°C for 48 hours, then weighed. Foliar and basal cover for each species within each plot were determined using a point sampling method (Pieper 1978). A total of 120 points were read per plot for both foliar and basal cover, using a 100-cm wide metal frame with 20 vertical pins. Foliar cover was determined before plots were clipped, and basal cover after clipping the plots.

Antecedent soil water was calculated for 0–5 and 5–10 cm depths by the gravimetric method. Samples were collected adjacent to the runoff plots before the initial rainfall application. Bulk density was also determined at 0–3 and 5–8 cm before the second rainfall application by the core method (Black 1965). After the wet run, soil samples were taken from 0- to 10-cm depths for particle size and organic carbon analysis. Particle size distribution was estimated using the hydrometer method (Bouyoucos 1962). Organic carbon percentage was estimated by the Walkley-Black method (Black 1965). A micro-relief meter was used to determine soil surface roughness within each plot. Six readings (20 points each) of the micro-relief meter were taken per plot. Three readings were taken on the fall line and 3 readings perpendicular to the fall line. Mean soil depth to bedrock was also measured.

A homogenous area was subdivided into 8 plots. Within each plot, 6 subplots of 1 m² were randomly located. Because treatments were randomly and independently allotted to the various plots, the experimental design was a completely randomized design with subsampling with 4 treatments, 2 plots per treatment and 6 subplots per plot. The treatments were 4 different residual phytomass levels. In year 1, treatments 1, 2, 3, and 4 had a residual phytomass of 2,667, 1,432, 1,020 and 627 kg ha⁻¹, while in year 2, the residual phytomass levels were 3,382, 1,443, 1,037, and 620 kg ha⁻¹ for treatment 1, 2, 3, and 4, respectively. Treatment 1 was not grazed and represented the potential phytomass each year. The remaining residual phytomass levels were achieved by allowing grazing in the plots until the desired levels were achieved. The treatments were not equally spaced and, therefore, were considered nonstructured.

The data for each year were analyzed separately. Overall differences among treatments were tested using analysis of variance by the General Linear Model procedure (SAS Institute 1985). If the analysis of variance F-test was significant, a protected Fisher's Least Significance Difference (LSD) was used to separate means at 0.01, 0.05, 0.01 and 0.20 significance levels. Stepwise multiple regression was used to select the highest correlated vegetation and soil variables influencing infiltration.

Results and Discussion

In the first year, natural rainfall was less than the long-term average, resulting in the low ungrazed phytomass production of 2,667 kg ha⁻¹ as compared to the second year of 3,382 kg ha⁻¹. The remaining residual levels were kept nearly the same in both years. Table 1 shows the potential phytomass of both years and the various residual phytomass levels achieved after grazing. Although the percentages of total phytomass are different, the residual levels are nearly the same in both years, except for the control. These levels were chosen because they generally represent moderate, heavy, and very heavy grazing.

Table 1. Percentage residual phytomass.

Treatment	Year 1		Year 2	
	Phytomass kg ha ⁻¹	Percentage of total	Phytomass kg ha ⁻¹	Percentage of total
1	2667 (7.79) ¹	100	3382 (18.27)	100
2	1432 (9.72)	54	1443 (5.57)	43
3	1020 (3.79)	38	1037 (3.18)	31
4	627 (4.52)	24	620 (3.47)	18

¹Standard error (SE) is given in the parenthesis for the phytomass.

Terminal Infiltration

Terminal infiltration rate is an important statistic in the infiltration process. At this level, the infiltration rate becomes almost constant and a fixed quantity of water enters through the soil surface. In the experiment, the constant terminal infiltration rate was obtained within 30 minutes of applying simulated rainfall. In year 1 at the antecedent soil water level, the F-value was 7.37 and the p-value was 0.0416, while with soil water near field capacity, these values were 3.62 and 0.1232, respectively. In year 2, the F-value and p-value were 32.18 and 0.0019 at the antecedent soil water level, while these values were 26.32 and 0.0043 for soil water near field capacity, respectively. In general, p-values are less than the 0.05 level of probability. Treatment comparisons are shown for terminal infiltration for both years in Tables 2 and 3.

Table 2. Treatment comparisons for terminal infiltration rates at the antecedent soil water level and near field capacity for year 1.

Treatment	Phyto- mass (kg ha ⁻¹)	Infiltra- tion (cm hr ⁻¹)	Level of significance ⁻¹			
			0.01	0.05	0.10	0.20
A. Antecedent soil water²						
1	2667	5.22	a	a	a	a
2	1432	4.62	a	a	ab	b
3	1020	4.35	a	ab	bc	b
4	627	3.66	a	b	c	c
B. Soil water near field capacity³						
1	2667	4.63	a	a	a	a
2	1432	3.60	a	ab	ab	b
3	1020	3.10	a	ab	b	bc
4	627	2.58	a	b	b	c

¹Means followed by the same letter within a soil water condition are not significantly different.

²Overall analysis of variance F(3, 4) = 7.37, p = 0.0416 for dry run.

³Overall analysis of variance F(3, 4) = 3.62, p = 0.1232 for wet run.

Terminal infiltration rates were highest in treatment 1, representing no utilization and a potential phytomass of 2,667 kg ha⁻¹ and 3,382 kg ha⁻¹ for years 1 and 2, respectively. The difference in mean terminal infiltration was much greater between treatment 1 and the rest of the treatments. This is probably because treatment 1 had a greater difference in residual phytomass compared to differences among the other treatments.

Infiltration rate near field capacity was lower than for antecedent soil water conditions in both years, and the difference in the means at soil water near field capacity was greater. This is attributed to the importance of antecedent soil water condition in the infiltration process. Infiltration rates are usually negatively correlated with soil water content. The soil water content was lower at the antecedent soil water condition; therefore, terminal infiltration rates are higher at antecedent soil water conditions than soil water near field capacity. However, the trend near field capacity is more important than at the antecedent soil water level. The effects of

Table 3. Treatment comparisons for terminal infiltration rates at the antecedent soil water level and near field capacity for year 2.

Treatment	Phyto-mass (kg ha ⁻¹)	Infiltration (cm hr ⁻¹)	Level of significance ⁻¹			
			0.01	0.05	0.10	0.20
A. Antecedent soil water²						
1	3882	6.81	a	a	a	a
2	1443	4.49	b	b	b	b
3	1037	3.36	b	bc	c	c
4	620	2.52	b	c	c	d
B. Soil water near field capacity³						
1	3882	6.20	a	a	a	a
2	1443	4.43	ab	a	b	b
3	1037	2.30	bc	b	c	c
4	620	0.92	c	b	d	d

¹Means followed by the same letter within a soil water condition are not significantly different.

²Overall analysis of variance F(3, 4) = 32.18, p = 0.029 for dry run.

³Overall analysis of variance F(3, 4) = 26.32, p = 0.0043 for wet run.

antecedent soil water condition can prevail for a shorter duration than at field capacity if the rainfall duration is greater.

Treatment means for both years at each soil water condition were in descending order from treatment 1 to treatment 4. A decrease in the phytomass level resulted in a corresponding decrease in terminal infiltration, which implies the residual phytomass can be used to reflect infiltration rates.

Orthogonal polynomial analysis was used to evaluate the linear, quadratic, and cubic effects for terminal infiltration. The linear effect was significant for year 1 at both soil water conditions. In year 2, only a linear effect was significant at antecedent soil water, while linear, as well as quadratic effects, were significant at soil water near field capacity. No cubic effect was significant in any year for any soil water level at the 0.10 level of significance.

Cumulative Infiltration

Cumulative infiltration is the total quantity of water absorbed through the soil surface during 30 minutes of simulated rainfall. During year 1, the F and p-values were 3.94 and 0.109 for soil water at antecedent level, while these values for soil water at field capacity were 6.38 and 0.053, respectively. During year 2, the F and p-values were 21.92 and 0.006 at antecedent soil water, these values were 18.58 and 0.008, respectively, for wet run.

Treatment 1 (exclosure) had the highest cumulative infiltration and treatment 4 had the lowest cumulative infiltration in both years (Tables 4 and 5). This was probably the result of the higher residual phytomass in treatment 1 as compared to treatment 4. Phytomass was positively correlated with infiltration rates; therefore, treatment 1 resulted in the highest cumulative infiltration.

The difference between the cumulative infiltration means is greater between treatment 1 and treatment 2, compared to the difference among 2, 3, and 4. This is probably the result of differences in residual phytomass levels. This clearly supports the relationship between residual phytomass and cumulative infiltration. Overall, infiltration for treatment 1 was significantly different from that for the rest of the treatments at 0.05, 0.10, and 0.20 probability levels, as shown in Tables 4 and at all probability levels in Table 5. Orthogonal polynomials were used to examine the linear, quadratic, and cubic effects. The linear effect was significant, but no other effect was significant at 0.10 significance level at any soil water condition in any year.

Predictive Equations

Much hydrology research is devoted to modeling to describe how variables are related. A useful method of modeling the rela-

Table 4. Treatment comparisons for cumulative infiltration rates at the antecedent soil water level and near field capacity for year 1.

Treatment	Phyto-mass (kg ha ⁻¹)	Infiltration (cm hr ⁻¹)	Level of significance ⁻¹			
			0.01	0.05	0.10	0.20
A. Antecedent soil water²						
1	2667	7.16	a	a	a	a
2	1432	5.84	a	ab	ab	b
3	1020	5.41	a	ab	b	bc
4	627	4.61	a	b	b	c
B. Soil water near field capacity³						
1	2667	6.04	a	a	a	a
2	1432	4.30	a	ab	b	b
3	1020	4.05	a	b	b	b
4	627	3.36	a	b	b	b

¹Means followed by the same letter within a soil water condition are not significantly different.

²Overall analysis of variance F(3, 4) = 3.94, p = 0.109 for dry run.

³Overall analysis of variance F(3, 4) = 6.38, p = 0.053 for wet run.

Table 5. Treatment comparisons for cumulative infiltration at the antecedent soil water level and near field capacity for year 2.

Treatment	Phyto-mass (kg ha ⁻¹)	Infiltration (cm hr ⁻¹)	Level of significance ⁻¹			
			0.01	0.05	0.10	0.20
A. Antecedent soil water²						
1	3382	7.65	a	a	a	a
2	1443	5.67	ab	b	b	b
3	1037	4.57	b	bc	c	c
4	620	3.99	b	c	c	c
B. Soil water near field capacity³						
1	3382	6.89	a	a	a	a
2	1443	3.97	b	b	b	b
3	1037	3.09	b	b	b	b
4	620	2.96	b	b	b	c

¹Means followed by the same letter within a soil water condition are not significantly different.

²Overall analysis of variance F(3, 4) = 21.92, p = 0.006 for dry run.

³Overall analysis of variance F(3, 4) = 18.58, p = 0.0008 for wet run.

tionship between the variables is regression analysis.

The regression equations are of the following general form:

$$\hat{Y} = a + b_1 X_1 + \dots + b_n X_n \quad (1)$$

where \hat{Y} is the predicted dependent variable, a is the y-intercept, b is the estimated regression coefficient, and X is the independent variable influencing \hat{Y} . The predictive equations also identify the most important variables influencing a given dependent variable. The dry data for years 1 and 2 were combined and the wet data for years 1 and 2 were combined. A significance level of 0.15 was chosen for an independent variable to be included in the model. The regression equations are shown in Tables 6-7.

The predictive equation for terminal infiltration rate (cm hr⁻¹) for both years at the antecedent soil water level (Table 6) was:

$$\hat{Y}_1 = 2.046 + 0.012(X_1) + 0.042(X_9) - 0.026(X_{12}) \quad (2)$$

Where X₁ is standing phytomass, X₉ is soil depth, and X₁₂ is soil water from 0-5 cm depth. The overall F and R² for the selected model are 28.19 and 0.52, respectively.

The predictive equation for terminal infiltration for both the years at soil water near field capacity (Table 6) was:

$$\hat{Y} = 2.056 + 0.011(X_1) - 0.044(X_4) \quad (3)$$

Table 6. Multiple regression equations for total terminal infiltration for year 1 and year 2 with combined soil water conditions¹.

Year and condition	Regression equations	R ²
1987 and 1988 dry ³	$\hat{Y}_1 = 2.046 + 0.012(X1) + 0.042(X9) - 0.026(X12)$ (se = 0.001) ² (se = 0.025) (se = 0.013) (p = 0.0001) (p = 0.098) (p = 0.051)	0.52
1987 and 1988 wet ³	$\hat{Y}_2 = 2.056 + 0.011(X1) - 0.044(X4)$ (se = 0.002) (se = 0.020) (p = 0.001) (p = 0.033)	0.44

¹Sample size (n) = 96.

²Standard error and p-value for each regression coefficient have been given in parenthesis for each column, respectively.

X1 = Standing phytomass (g m²)

X4 = Litter cover associated with foliar cover (%)

X9 = Soil depth (cm)

X12 = Soil water (0–5 cm) depth, dry (%)

³Overall analysis of variance F(3, 77) = 28.19, p = 0.0001 for year 1 and year 2, dry.

Overall analysis of variance F(2, 77) = 30.35, p = 0.0001 for year 1 and year 2, wet.

Table 7. Multiple regression equations for cumulative infiltration for year 1 and year 2 with combined soil water conditions¹.

Year and condition	Regression equations	R ²
1987 and 1988 dry ³	$\hat{Y}_3 = 3.398 + 0.011(X1) + 0.034(X9) - 0.017(X12)$ (se = 0.001) ² (se = 0.021) (se = 0.011) (p = 0.0001) (p = 0.010) (p = 0.138)	0.52
1987 and 1988 wet ³	$\hat{Y}_4 = 2.362 + 0.013(X1)$ (se = 0.001) (p = 0.0001)	0.51

¹Sample size (n) = 96.

²Standard error and p-value for each regression coefficient have been given in parenthesis for each column, respectively.

X1 = Standing phytomass (g m²)

X9 = Soil depth (cm)

X12 = Soil water (0–5 cm) depth, dry (%)

³Overall analysis of variance F(3, 82) = 29.07, p = 0.0001 for year 1 and year 2, dry.

Overall analysis of variance F(1, 83) = 88.52, p = 0.0001 for year 1 and year 2, wet.

Where X1 is standing phytomass and X4 is litter cover associated with foliar cover. The overall F and R² are 30.35 and 0.44, respectively.

In general, standing phytomass, foliar cover and basal cover were the variables included in most of the models, and are important from a management point of view. The best model would be the one with most of these variables and high R² and F-values, with a low standard error and a low p-value.

Cumulative Infiltration

Cumulative infiltration equations are also important in hydrology. These equations help to identify the important variables that affect cumulative infiltration (Table 7).

The predictive equation for cumulative infiltration rate (cm hr⁻¹) for the combined data of year 1 and year 2 at antecedent soil water (Table 7) was:

$$\hat{Y} = 3.398 + 0.011(X1) + 0.034(X9) - 0.017(X12) \quad (4)$$

Where X1 is standing phytomass, X9 is soil depth, and X12 is soil water 0–5 cm depth. The overall F and R² for the selected model are 29.07 and 0.52, respectively.

The predictive equation for cumulative infiltration rate (cm hr⁻¹) for the combined data for year 1 and year 2 at soil water near field capacity (Table 7) was:

$$\hat{Y}_4 = 2.362 + 0.013(X1) \quad (5)$$

Where X1 is standing phytomass. The overall F and R² for the selected model are 88.52 and 0.51, respectively.

Summary and Conclusions

Like many other parts of the world, most Pakistan rangelands are overgrazed. Overgrazed rangelands not only affect the on-site productivity, but also negatively affect water quality and siltation of reservoirs. In Pakistan, moist temperate ranges are under heavy grazing pressure by local livestock and nomadic herds. The main reason for the deterioration is the lack of knowledge and poor socio-economic conditions of the people, and the lack of research, which leads to overgrazing.

To determine the severity of the runoff erosion caused by livestock grazing and to determine a reasonably good residual phytomass level both for livestock production, as well as to maintain and improve the watershed condition, this experiment was conducted in the temperate ranges of northwestern Pakistan. The experiment was continued for 2 growing seasons. The following conclusions are drawn from the results of this study:

- 1) Residual phytomass significantly affects infiltration rates.
- 2) The enclosure or no grazing treatment resulted in the highest infiltration rates among all the treatments.
- 3) The treatment with the lowest residual phytomass resulted in the lowest infiltration rates.
- 4) To protect and maintain the range sites, and for watershed management, at least 1,000–1,400 kg ha⁻¹ residual phytomass must be retained.
- 5) The potential phytomass changes from year to year; therefore, the watershed manager should rely on the residual phytomass level rather than removing a fixed percentage of forage.

In general, the decreased terminal and cumulative infiltration indicate treatment 4 was the least desirable condition of any of the grazing treatments, followed by treatments 3 and 2. Treatment 1 had the highest measured infiltration rates, but is not practical from the standpoint of livestock production.

To increase infiltration, one must consider a suitable residual phytomass level, which has a direct effect on this process. Although the enclosure (treatment 1) resulted in the highest infiltration rates, and is also most desirable from a watershed point of view, cultural and economic demands will not allow 100% protection of the phytomass. On the other hand, the lowest phytomass level of treatment 4 resulted in the lowest infiltration, and is not desirable for watershed protection. Thus, the land manager is left with treatment 2 and treatment 3, out of which to choose the residual phytomass level that will ensure proper utilization of the resource and proper protection of the watershed condition.

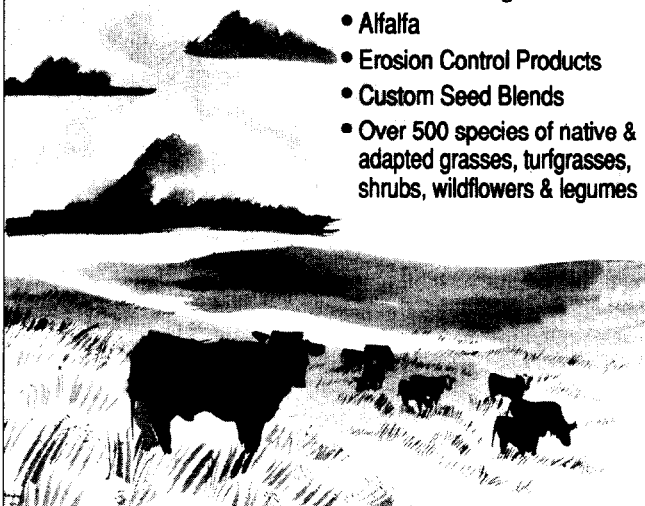
The choice for a given treatment will vary from site to site, and is greatly dependent on the major management objectives. If a range site is situated in a greatly disturbed riparian area, treatment 1 may be recommended for quick restoration. Similarly, if the range condition is good and there is great demand for forage, treatment 4 can also be recommended. In our view, the best choice would be treatment 2 or 3, rather than choosing the extremes. This helps assume high infiltration and will not adversely affect livestock production.

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Book Reviews

Toward a Unified Ecology. by T.F.H. Allen and Thomas W. Hoekstra. 1992. Columbia University Press, New York. 384 p. US \$45.00 hardbound. ISBN 0-231-06918-9.

This second volume of the 'Complexity in Ecological Systems' series aims at presenting a new conceptual framework to allow the development of a more holistic ecological theory, and promises to give a new perspective on the management of natural resources. T.F.H. Allen is professor of botany at the University of Wisconsin and coauthor of *Hierarchy: Perspectives for Ecological Complexity* (The University of Chicago Press, 1982) and *A Hierarchical Concept of Ecosystems* (Princeton University Press, 1986). It can thus be expected that many ideas from the above texts will be expanded within this book. Coauthor Thomas W. Hoekstra is Assistant Director for Research at the Rocky Mountain Forest and Range Experiment Station.

Chapter 1 introduces this new conceptual framework. The authors invoke hierarchy theory and address problems related to scale through the concepts of grain, extent, and scope. The fundamental units of the new theory are presented as "criteria", and include organism, population, community, ecosystem, landscape, and biome "criteria". These concepts are defined individually and then pieced together within an overall framework. The authors demonstrate the new insights and relations to be gained by giving readers a guided tour through a graphical depiction (a 'layer cake metaphor for ecological "criteria" and ecological scale') of their theory. The "criteria" are envisaged as being of equal importance, and can thus be related and compared directly to each other on the same and different ecological scales.

This process is adopted in each of the subsequent chapters (2-7) aimed at discussing individual "criteria" in detail. Repetition of this exercise from the perspective of different "criteria" ingrains the underlying process, while reinforcing the notions of flexibility and varied insight that these techniques bring. The quality of these chapters varies, presumably reflecting the interests of the authors (and the reader) as well as extant knowledge. For example, Chapter 4 (the Community "criterion") provides richer detail than other chapters on the history of development of science within that particular subdiscipline, different analytical approaches used, and important new areas of development (e.g., the application of fuzzy set theory to vegetation dynamics). Other chapters are relevant because the contrast and comparison technique does seem to yield some new perspective not previously apparent. The chapter (5) dealing with the organism "criterion" is particularly insightful, because it goes against conventional views. The authors point out that the physical tangibility of organisms has led to an anthropocentric view that clouds the relationship between organisms and their environment. Some chapters are particularly rich in their use of ecologically relevant examples. This is typified by the landscape "criterion" (Chapter 2), a rapidly growing field since the advent of readily accessible remotely sensed data and new analytical tools. A discussion of how organisms view landscapes differently, resulting in disparate scaling between organisms is another example of the inconsistency of organisms as a scaled unit. In some chapters, analogies are used in place of examples. I feel that this is not conducive to easy reading, and detracts somewhat from the 'unified' ecological theme, since models used in analogies are transferred from other disciplines and it is likely that readers will inadvertently transfer the assumptions and biases of those disciplines also. In general, it can be said that the chapters dealing with individual "criteria" do convey the process of the authors' metho-

dology clearly.

The final two chapters (8 and 9) discuss the management of ecological systems and present a 'unified approach to basic science'. The authors postulate that science would benefit greatly if it were able to combine the multi-"criteria" world of applied scientists with the ability to focus at specific and relevant scales the way basic researchers do. Multi-"criteria" worlds are more representative of the real world and floating scales allow one to focus sharply on questions. The authors show managers how to incorporate extant basic research into their multi-"criteria" world and supply basic researchers with a 'toolbox' for solving particular problems. These two subdisciplines of science are clearly integrated within the new conceptual framework.

Of some concern is the recurring use of concepts such as stability and equilibrium throughout the text. This concern stems from their many nuances and intuitive (and thus broad) meaning to the uninformed. The authors do not give an operational definition of these concepts, in spite of their admonitions. Recent texts (Botkin, 1990. *Discordant Harmonies: A New Ecology for the Twenty-First Century*. Oxford University Press.; Peters, 1991. *A Critique for Ecology*. Cambridge University Press.; Pimm, 1991. *The Balance of Nature? Ecological Issues in the Conservation of Species and Communities*. The University of Chicago Press) give detailed descriptions of these concepts, as well as lucid accounts of the problems arising from their use. A second general criticism concerns the lack of mention of the work conducted by Pimm (1991), surely a definitive work on communities. Pimm (1991) has attempted to integrate multiple "criteria" within his community outlook over ecologically relevant (and little researched) spatial and temporal scales. His work is also aimed at bridging the gap between theory and applied science, at least in the field of conservation biology.

These criticisms should not dissuade anyone interested in ecology from reading this book. A measure of success for this new conceptual framework is its ability to defuse some of the age old disputes within ecology. Although there are no recipes for improving management and the quality of science, these new perspectives may lead to a more holistic ecology, increase our ability to solve problems, and allow a better understanding between basic and applied researchers. This book certainly does achieve its objectives, although applying these ideas routinely is another matter.—Paul E. Hosten, Department of Range Science, Utah State University, Logan, Utah.

Vegetation and Climate Interactions in Semi-arid Regions.

Edited by A. Henderson-Sellers and A.J. Pitman, with 20 text contributors. 1991. Kluwer Academic Publishers, Dordrecht. 238 p. US \$180.00 hardbound. ISBN 0-7923-1061-6.

The local and global effects of climate-vegetation interactions are receiving increasing attention because of phenomena such as desertification and global warming. *Vegetation and Climate Interactions in Semi-arid Regions* is a selection of papers presented at a conference at Macquarie University, Sydney, Australia, in January, 1990. That conference, entitled *Degradation of Vegetation in Semi-Arid Regions: Climate Impact and Implications* brought together those working in land degradation with researchers in climate and climatic change as a first step in interdisciplinary interaction.

Three introductory chapters provide an overview of the book. Three sections follow entitled Measurement, Modeling and Man-

agement, which were the three major themes of the conference. Most of the modeling papers are more climatic in emphasis while the management papers are naturally more terrestrial. Several of the modeling papers are quantitative, but with one exception are well related to vegetation. The complexity is not extreme, but the impression is still that the causes of climatic and vegetational change are profoundly simpler than the explanations and predictions.

An interesting consensus (more or less) of the contributors is that are our rangelands are being overutilized by domestic livestock, and are inexorably degrading. The estimates of carrying capacity and stocking numbers (animal-units) used by the authors are based on thoroughly inadequate concepts for sound technical use (ref., *J. Range Manage.*, 1990, 43:553-555.), but the authors' conclusions seem reasonable, and unless stocking levels are reduced, increasingly sophisticated management and greater unsustainable inputs will likely be needed to maintain livestock production from rangelands.

Several authors express the urgent need to better measure long-term vegetational changes on rangelands. Few would deny the

inadequacy of our efforts in long-term monitoring in the past several decades. The apparently impending climatic changes give this work a new urgency, and improved remote sensing techniques provide some new tools. We are very late.

The chapters contain other research suggestions such as the use of three-dimensional enclosures for gas-exchange testing, and management suggestions such as the elimination of dryland cropping on marginal lands. The role of government policies of taxation subsidies and drought relief in encouraging continued degradation of rangelands is discussed. Most problems of rangeland management are viewed as social rather than technical. The papers are largely technical, however, and some political objectivity characterizes the discussions.

Range scientists will find this collection broadening in that it will give global perspective to their local work. In it are many of the likely themes of rangeland research of the next century.—*David L. Scarneccia*, Washington State University, Pullman, Washington.

The PROCEEDINGS OF THE IVth INTERNATIONAL RANGELAND CONGRESS WHICH CONVENED IN MONTPELLIER, FRANCE, 22-26 April 1991, are now available. They consist of three volumes with a total of 1,280 pages. Vol. 1 and 2 are 592 and 401 pages long, respectively. They contain the 255 original articles accepted by the Scientific Committee and presented at the Congress by regularly registered participants. These articles are gathered into 16 different subject matter symposia. Vol. 1 includes symposia 1 to 8 dealing with: Ecological Bases of Range Science (11 articles), Dynamics of Rangeland Ecosystems (32 art.), Functioning and Productivity of Rangeland Ecosystems (16 art.), Ecophysiology of Range Plants (17 art.), Range Resources (11 art.), Ecological Adaptation and Phylogenetic Resources (24 art.), Plant/Animal Interactions (19 art.), Descriptive and Geographic Aspects of Woody and Herbaceous Range (20 art.).

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