J. Range Manage.
54: 210–217 May 2001

Application of non-equilibrium ecology to rangeland riparian zones

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Abstract

Traditional theories of plant succession leading to a single equilibrium community are being re-evaluated. Alternative theories involving multiple steady states, and state-and-transition processes have been postulated to more adequately reflect the dynamics of rangeland ecosystems. The ecological literature provides examples of apparent thresholds in arid and semi-arid plant communities, however the literature is void of discussion of the applicability of non-equilibrium ecological theory to riparian areas contained within the rangelands of the world.

In arid and semi-arid environments the availability of soil water is critical in the determination of the composition of the plant community. In this study we hypothesized that the relationship between soil moisture and depth to groundwater within the riparian zone controlled the composition of the associated plant communities. These soil water, groundwater, plant community composition relationships were used to test the applicability of state and transition models to riparian zones.

Water table levels within an irrigated eastern Oregon riparian valley were monitored for 2 consecutive summers. The study area was mapped into 4 distinct plant community types on the basis of dominant graminoids. We measured depth to the water table, soil moisture content, relative species composition, litter, percent bareground and percent relative basal cover of key plant species and life forms. Relationships between water table levels, soil moisture content and plant communities were analyzed. Results indicated the 4 plant communities contained within this study area can be segregated on the basis of soil moisture content and/or depth to groundwater during the growing season. Ecological states and transition zones based on soil moisture content and/or water table depth were determined.

Key Words: riparian plant communities, groundwater, soil moisture, state and transition model

Resumen

Las teorías tradicionales de sucesión vegetal que conducen a una sola comunidad en equilibrio están siendo revaluadas. Para reflejar mas adecuadamente las dinámicas de los ecosistemas de pastizal se han postulado teorías alternativas que involucran estados estables múltiples y procesos de estado y transición. La literatura ecológica provee ejemplos de umbrales aparentes en comunidades vegetales áridas y semiáridas; sin embargo, esta literatura esta carente de discusión respecto a la aplicabilidad de la teoría ecológica de no-equilibrio en áreas ribereñas de los pastizales del mundo. En los ambientes áridos y semiáridos la disponibilidad de agua en el suelo es crítica en la determinación de la composición de la comunidad vegetal. En este estudio nosotros hipotetizamos que la relación entre la humedad del suelo y la profundidad del agua subterránea dentro de las zonas ribereñas controló la composición de las comunidades vegetales asociadas. Estas relaciones entre el agua del suelo, el agua subterránea y la composición de la comunidad vegetal se utilizaron para probar la aplicabilidad de los modelos de estado y transición en las zonas ribereñas. Durante 2 veranos consecutivos se monitorearon los niveles del agua fréatica dentro de un valle ribereño irrigado del este de Oregon. El área de estudio se mapeó dentro de 4 tipos distintos de comunidades vegetales que se distinguieron entre ellos por las gramíneas dominantes .Medimos la profundidad del manto fréatico, el contenido de humedad del suelo, la composición relativa de especies vegetales, el mantillo, el porcentaje de suelo desnudo y el porcentaje relativo de cobertura basal de las especies clave y formas de vida. Se analizaron las relaciones entre los niveles del agua fréatica, contenido de humedad del suelo y la comunidad vegetal. Los resultados indicaron que las 4 comunidades vegetales incluidas en el área de estudio pueden ser segregadas en base del contenido de humedad del suelo y/o la profundidad del agua subterránea durante la estación de crecimiento. Se determinaron zonas estados ecológicas y transición basadas en la humedad del suelo y/o profundidad del manto fréatico.

An important criterion of the applicability of a model or theory is its ability to predict the consequences of humans' activities with acceptable precision over timescales relevant to management. After 40 years of applying the quantitative climax model of Dyksterhuis (1949) to rangeland management, its predictive capabilities have come under scrutiny in disturbance based ecosystems. The inability of the model to handle multiple vectors of change (climatic variation, fire, plant introduction, grazing) have led some ecologists to abandon the model completely (Wilson 1984, Smith 1988). Traditional theories of plant succession leading to a single equilibrium community have been found to be inadequate for understanding the complex successional

Research was primarily funded by the USDA Sustainable Agriculture in Research and Education Grant with additional support provided by the Oregon Agricultural Experiment Station.

Paul S. Doescher, Warren P. Clary, and Jeanne C. Chambers provided insightful review.

This article is submitted as Technical Paper No. 11526 Oregon Agricultural Experiment Station, Corvallis, Ore.

Manuscript accepted 14 Jul. 2000.

pathways of semi-arid and arid rangeland ecosystems (Westoby 1980, Anderson 1986, Foran et al. 1986, Laycock 1991, Tausch et al. 1993). The recognition of this inadequacy has generated a search for an alternative theory that more adequately reflects the dynamics of rangeland ecosystems. Theories involving multiple successional pathways, multiple steady states, and state-and-transition processes are gaining in acceptance.

Westoby et al. (1989) proposed the use of a state-and-transition model as the basis for describing rangeland dynamics. A state is defined as an alternative, persistent vegetation community which is not simply reversible in the linear successional framework. Transitions between states are triggered by natural events (e.g., weather or fire) or by management actions. Transitions may occur very quickly, as in the case of fire, or slowly over an extended period of time as in the case of a shift in weather patterns. Regardless of the rate of change, the system does not come to rest halfway through a transition (Westoby et al. 1989). Transitions are also referred to as thresholds (Friedel 1991). Friedel suggested that environmental change can be discontinuous, with thresholds between alternative new states of species assemblages. Thresholds have 2 important characteristics: first they are the boundary in space and time between 2 states; and second, the initial shift across the boundary is not reversible on a practical time scale without significant inputs of energy and time.

Examples of thresholds in arid and semi-arid plant communities are recorded in the ecological literature (Archer and Smeins 1991, Friedel 1991, Laycock 1991), however, the discussion of the applicability of non-equilibrium based models for riparian areas within the arid and semi-arid rangelands of the world is just emerging. Weixelman et al. (1997) developed a state-and-transition model for a dry graminoid meadow located in central Nevada, however, the dominant species along with the meadow soil type does not classify the site as riparian. While riparian zones constitute only a small fraction (2–3%) of the areal extent of rangelands in the 11 western United States, they provide a disproportionate amount of the forage consumed by livestock and are vital for the support of fish and wildlife (Kauffman and Krueger 1984). Given the importance of riparian zones to livestock production as well as fish and wildlife habitat it is critical that proposed successional models be tested for accuracy in the prediction of riparian vegetation response to management.

Methods

Study Area

The study was conducted in Bear Valley in south central Grant County, Ore. Grant County, situated in the Central Blue Mountains of east-central Oregon, lies between 44° and 45° north latitude and 118° and 120° west longitude. Valley floor elevation ranges from 1,387 to 1,440 m. Climate is characterized by cold winters, moderate summers, and low precipitation. The 30-year average summer temperature in Bear Valley is 13.8°C and mean maximum temperature of 26.7°C occurs during July and August. Average winter temperature is –4.87°C with the mean minimum of –13.1°C occurring in January. Temperature extremes range from 37.8 to –44.4°C. Mean annual precipitation is 33.2 cm and occurs primarily from November through June with the majority of it coming in the form of snow. Mean annual snowfall is 162 cm.

Bear Valley is divided by Scotty Creek, a second-order stream, flowing from the west and Bear Creek, a third-order stream, flowing from the east. Both these streams join the Silvies River near the south central portion of Bear Valley. The valley floor is wide and unconstrained with slopes of less than 2%. The valley soil was classified at the series level as Damon silty clay loam. The soil is poorly drained, formed in mixed alluvium with a restrictive layer at 100 to 130 cm. Permeability is moderately slow, estimated at 1.5 to 5.0 cm hr^{-1}. Available water holding capacity is 18 to 25 cm and effective rooting depths are 75 to 100 cm (Stringham 1996).

A mosaic of private family-owned livestock ranches cover the valley floor within Bear and Silvies valleys, bordered by the surrounding Malheur National Forest. Cattle production is the primary economic enterprise. Subterranean irrigation, where water is diverted from the stream, carried by a ditch along the flood plain edge and allowed to return to the stream via subsurface interflow is applied to the privately owned riparian pastures to increase production of native and seeded grasses. Many meadows are hayed in late July for supplemental winter livestock feed.

Plant Community Designation

Initial reconnaissance of the study area indicated that 4 distinct plant community types representing a mesic to hydric moisture regime could be identified on the basis of dominant graminoids. Community types were identified by ocular assessment (Table 1). The number of plots of each type of community included in the study is noted.

Eleven, 1 ha plots were randomly located within the irrigated meadows straddling the associated stream channel. Seven of the plots were located along Bear Creek and 4 along Scotty Creek. All 4 Scotty Creek plots and 4 of the Bear Creek plots included areas on the uphill side of the irrigation ditch providing 8 replications of the dry bluegrass (DB) community type.

Table 1. Plant communities as defined by dominant graminoids.

	Plant Communities
Wet Meadow (WM) community replication = 7	*Carex nebrascensis Dewey* (Nebraska sedge) *Carex rostrata* Stokes (beaked sedge) *Deschampsia cespitosa* (L.) Beauv. (tufted hairgrass) *Beckmannia syzigachne* (Steud.) Fern. (slough grass) *Agrostis alba* L. (redtop)
Moist Meadow (MM) community replication = 8	*Alopecurus pratensis* L. (meadow foxtail) *Carex nebrascensis* Dewey (Nebraska sedge) *Juncus balticus* Willd. (baltic rush) and other grasses, rushes, and forbs
Moist Bluegrass (MB) community replication = 11	*Poa pratensis* L. (Kentucky bluegrass) *Phleum pratense* L. (timothy) *Bromus inermis* Leys. (smooth brome) *Alopecurus pratensis* L. (meadow foxtail) and annual and perennial forbs
Dry Bluegrass (DB) community replication = 8	*Poa pratensis L.* (Kentucky bluegrass0 *Bromus inermis* Leys. (smooth brome) *Koeleria cristata* Pers. (junegrass) *Poa sandbergii* Vasey (Sandbergs bluegrass) *Festuca idahoensis* Elmer (Idaho fescue) *Sitanion hystrix* (Nutt.) Smith (Squirreltail) *Chrysothamnus viscidiflorus* (Hook.) Nutt. (green rabbitbrush) *Artemisia tridentata* ssp. *vaseyana* Nutt. (mountain big sagebrush) and annual and perennial forbs and other grasses

Replication of the wet meadow (WM), moist meadow foxtail (MM), and moist bluegrass (MB) plant communities within the 11 plots was unbalanced with a total of 7, 8, and 11 replications, respectively.

Cover and Species Composition

Point sampling using the point intercept method as described by Pieper (1973) was used to estimate basal cover, species composition, litter, and bare ground. Five, 15 m transects, with points every 15 cm, were randomly located in each plant community within each plot. Determinations were made in mid-June 1994 and mid-June 1995.

Soil Classification

Fifteen soil pits were excavated with a backhoe in October 1995. Seven pits were located in the moist bluegrass community type, 3 each in the dry and meadow foxtail communities and 2 in the wet meadow type. At least 1 soil pit was located in each of the 11 plots. Horizons were described to a depth of 150 cm and the permeability estimated for each horizon.

Soil Moisture

Soil moisture was measured at 2 week intervals in each community type within each plot from late May through September. Gravimetric soil moisture content was determined using the method described by Gardner (1986). One sample from both the 30 cm and 45 cm depths were collected from each plant community within each plot. No soil moisture samples were collected from flooded communities, however, ponded conditions were noted.

Water Table Depth

Water table depth was measured on 10 day intervals from late May through September in each plant community within each plot. Five transects each consisting of 4 shallow groundwater access tubes were placed perpendicular to the creek in each of the plots for a total of 220 access tubes. The transects were located on both sides of the creek in an alternate fashion beginning at a randomly selected point. Within a transect, the first access tube was located within 1 m of the stream channel. The placement of the remaining 3 tubes was determined by plant community change and/or distance from the previous tube being greater than 8 m and less than 25 m. This resulted in transect length varying from 45 to 60 m.

Access tubes were chosen over piezometers to allow for measurement of the actual depth to groundwater instead of head pressure which may give a false indication of groundwater depth (Jury et al. 1991). Access tubes were constructed of 19 mm PVC pipe with 3 mm diameter holes drilled from the bottom of the tube to within 15 cm of the top. The access tube at creekside was placed at a depth of 120 cm or base flow level of the creek, which ever was greater. Differences in ground surface elevation from the creekside tube to the 3 additional tubes within the transect was determined using standard survey methods. Access tube depth for the remaining tubes within a transect was calculated based on the creekside tube depth plus or minus the change in ground surface elevation.

Statistical Analysis

Indicator species analysis was used to indicate the concentration of species abundance and faithfulness of occurrence of identified species within the specified plant communities (Dufrene and Legendre 1997). The method produces indicator values for each species in each group and tests the values for statistical significance using a Monte Carlo technique. Plant community designations on the basis of dominant graminoid were confirmed.

Soil moisture and percent basal cover by dominant plant species and life forms were analyzed between plant communities within years and across years. Eleven locations (1 ha plots) were included in the analysis. The design was blocked by location and a mixed model ANOVA was used to determine within year differences (SAS 1994). A nested ANOVA, with year nested within plant community was used to identify between year differences when no significant year interaction occurred.

All plant species with sparse distributions were not analyzed statistically (< 5% basal cover). However, the relative percent basal cover of the life form groups of forbs, other grasses, mosses, rushes/sedges, and shrubs were analyzed.

The pair-wise mean comparison method was applied to basal cover and soil moisture means when F-tests were significant at ($P \leq 0.10$). This allowed identification of plant community attributes that were significantly different across plant communities. Between year comparisons were made when F-tests of the year nested within plant community component of the model was significant at ($P \leq 0.10$). Simple linear regression was used to determine the relationship between soil moisture and depth to water table.

Results and Discussion

Climate data from the Oregon Climate Service weather station located in the south central portion of Bear Valley at Seneca, Ore. was used for this study. Annual precipitation for 1994 was 21.2 cm, 11.9 cm below the 30 year average and the mean maximum temperature was 1°C warmer. Annual precipitation for 1995 was 45.7 cm, 12.5 cm above the 30 year average (Oregon Climate Service 1995). Both years are representative of the extreme ends of the precipitation history for Bear Valley. This large variance in precipitation over the 2 years of the project provided an opportunity to study the response of the vegetative communities to different environmental conditions.

Indicator Species Analysis

Relative abundance and frequency by plant community type were utilized to calculate indicator values using the Dufrene and Legendre (1997) method. Indicator values range from 0 (no indication) to 100 (perfect indication). Perfect indication implies that the presence of a species points to a particular group without error given the current data set. Table 2 presents the indicator values for the combined 1994 and 1995 species data. Indicator values for the dry bluegrass community (Table 1)

Table 2. Indicator values for selected species by plant community. Values were determined using both 1994 and 1995 frequency data.

	Indicator Values			
Species	**DB**	**MB**	**MM**	**WM**
Alopecurus pratensis	1	5	**80**	1
Poa pratensis	**31**	**47**	3	5
Deschampsia cespitosa	0	0	2	**65**
Carex/Juncus spp.	3	12	18	**59**
Bromus pratense	7	18	0	0
Phleum pratense	1	**51**	3	6
other grass	**48**	6	1	8
Artemisia tridentata ssp. *vaseyana*	**40**	0	0	0

were highest for the mountain big sagebrush (*Artemisia tridentata* ssp. *Vaseyana* Nutt.), Kentucky bluegrass (*Poa pratensis* L.) and the other grass category which included species such as Idaho fescue (*Festuca idahoensis* Elmer), junegrass (*Koeleria cristata* Pers.), and sandbergs bluegrass (*Poa sandbergii* Vasey). The moist bluegrass community (Table 1) indicator values showed a dominance of Kentucky bluegrass and non-native timothy (*Phleum pratense* L.) whereas the moist meadow foxtail (*Alopecurus pratensis* L.) community (Table 1) indicator values were highest for non-native meadow foxtail. Tufted hairgrass (*Deschampsia cespitosa* (L.)) and the sedge/rush category showed the highest indicator values for the wet meadow community (Table 1). The indicator values for each species in each group were tested for statistical significance using a Monte Carlo technique with 1,000 permutations. All indicator values were found to be significant at the 95% level ($p < 0.05$).

Table 4. Seasonal trends in average soil moisture content at 30 and 45 cm depth for 1994 within different plant communities. DB = dry bluegrass; MB = moist bluegrass; MM = moist meadow foxtail; WM = wet meadow. Comparisons are by date and depth across plant communities. Lower case superscripts are for 30 cm depths and upper case superscripts are for 45 cm depth.

	DB		MB		MM		WM*	
	30 cm	45 cm	30 cm	45 cm	30 cm	45 cm	30 cm	45 cm
	(%)							
16 Jun	25^{a}	28^{A}	42^{b}	48^{B}	51^{c}	58^{C}	62^{c}	72^{C}
26 Jun	27^{a}	31^{A}	34^{b}	38^{B}	45^{c}	49^{C}	46^{c}	64^{C}
7 Jul	22^{a}	27^{A}	31^{b}	35^{B}	34^{c}	46^{C}	48^{c}	56^{C}
16 Jul	18^{a}	21^{A}	25^{b}	31^{B}	28^{c}	37^{C}	39^{c}	41^{C}

*Sites with standing water were assumed to have 85% soil moisture.

Table 5. Seasonal trends in average soil moisture content at 30 and 45 cm depth for 1995 within different plant communities. DB = dry bluegrass; MB = moist bluegrass; MM = moist meadow foxtail; WM = wet meadow. Comparisons are by date and depth across plant communities. Lower case superscripts are for 30 cm depths and upper case superscripts are for 45 cm depth.

	DB		MB		MM		WM*	
	30 cm	45 cm	30 cm	45 cm	30 cm	45 cm	30 cm	45 cm
	(%)							
13 Jun	34^{a}	36^{A}	52^{b}	58^{B}	66^{c}	81^{C}	85^{d}	85^{C}
29 Jun	30^{a}	32^{A}	53^{b}	62^{B}	63^{c}	69^{C}	85^{d}	85^{C}
13 Jul	25^{a}	30^{A}	39^{a}	46^{B}	60^{c}	70^{C}	76^{c}	77^{C}
25 Jul	22^{a}	27^{A}	34^{a}	41^{A}	51^{b}	56^{B}	60^{b}	62^{B}

*Soil moisture content was not analyzed statistically due to a large number of sites with free standing water.

Basal Cover

Comparisons of the basal cover of individual key plant species and life forms by year are presented in Table 3. The wet meadow community had a significantly greater amount of tufted hairgrass and the combined sedge/rush category than the other 3 communities in both years. Meadow foxtail was found in significantly greater amounts in the moist meadow foxtail community for both years when compared to all other communities studied. The moist bluegrass community exhibited significantly more Kentucky bluegrass than the other 3 plant communities in 1994 and 1995. Although the dry bluegrass type had significantly less Kentucky bluegrass than the moist bluegrass type it had significantly more than the wet community and moist meadow foxtail community in 1994. In 1995, the same results occurred for the moist meadow foxtail community. Delineation of the 4 communities on the basis of dominant graminoid proved efficient and statistically significant.

Table 3. Mean percent basal cover of individual key species and life forms within the dry bluegrass (DB), moist bluegrass (MB), moist meadow foxtail (MM), and wet meadow (WM) communities. Standard error is in parentheses.

	DB		MB		MM		WM	
	1994	1995	1994	1995	1994	1995	1994	1995
	(%)							
Kentucky bluegrass	14.4 (±5.5)	5.4 (±3.1)	17.9 (±9.1)	10.4 (±3.4)				
Meadow foxtail			4.5 (±5.1)	.75 (±1.1)	27.1 (±10.8)	16.6 (±4.5)	1.2 (±1.5)	.43 (±.48)
Timothy			6.3 (±5.4)	4.6 (±2.9)				
Tufted hairgrass							10.3 (±13.0)	8.0 (±9.4)
Sedge/Rush			4.8 (±3.6)	1.9 (±1.9)	7.6 (±4.0)	3.2 (±1.5)	20.0 (±8.2)	13.7 (±3.8)
Moss					10.0 (±8.6)	14.1 (±15.2)	17.2 (±8.7)	30.1 (±10.1)
Forbs	10.3 (±3.3)	6.6 (±2.7	9.6 (±5.6)	8.3 (±3.5)	7.0 (±4.1)	2.1 (±2.6)	6.3 (±3.3)	2.3 (±1.8)
Shrubs	1.1 (±.5)	.31 (±.31)						
Total Grass	21.2 (±2.0)	11.6 (±2.8)	32.6 (±5.6)	17.8 (±3.7)	32.2 (±9.3)	19.2 (±3.0)	19.6 (±8.6)	13.0 (±7.3)
Total Basal Cover	34.2 (±8.8)	20.2 (±4.0)	47.1 (±7.5)	28.2 (±4.8)	46.8 (±9.3)	24.6 (±3.8)	34.2 (±8.8)	29.2 (±6.1)

Soil Moisture

Seasonal trends in soil moisture content for 1994 and 1995 at the 30 and 45 cm depth for the 4 plant community types are presented in Tables 4 and 5. Korpela (1992) measured soil moisture content in similar plant communities in a non-irrigated riparian area in northeastern Oregon. Results for the moist bluegrass and dry bluegrass communities were quite similar to the current study with the moist bluegrass community averaging at least 10% greater soil moisture content throughout the growing season. Pairwise comparisons of soil moisture averages within years across plant communities by date and depth showed significant differences in moisture content existed between the dry bluegrass and all other communities and moist bluegrass and all other communities. These results were consistent for both years. The soil moisture content within the moist meadow foxtail community was not significantly different than the wet meadow soil moisture early in the season, how-

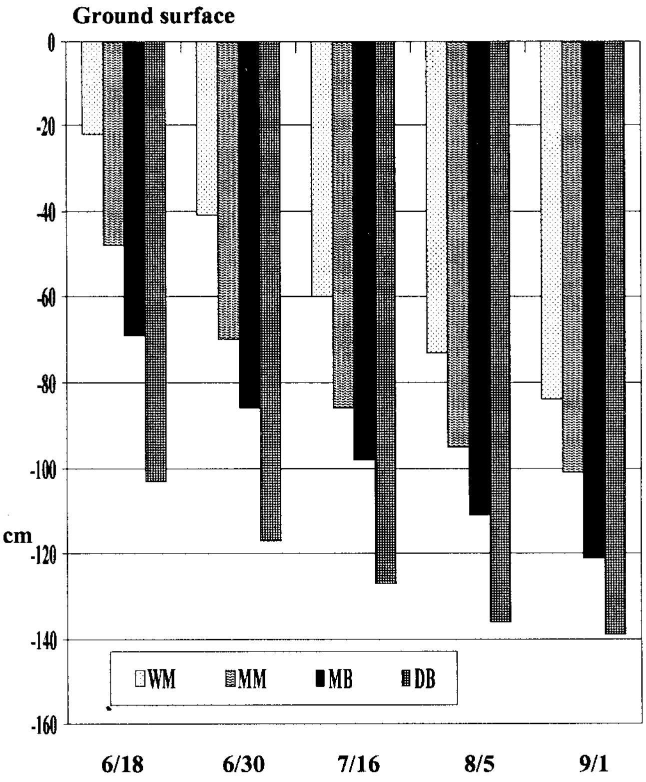

Fig. 1. Seasonal trends in average depth to the water table for 1994 within different plant communities designated as follows: MB = moist bluegrass, DB = dry bluegrass, MM = moist meadow foxtail, and WM = wet meadow.

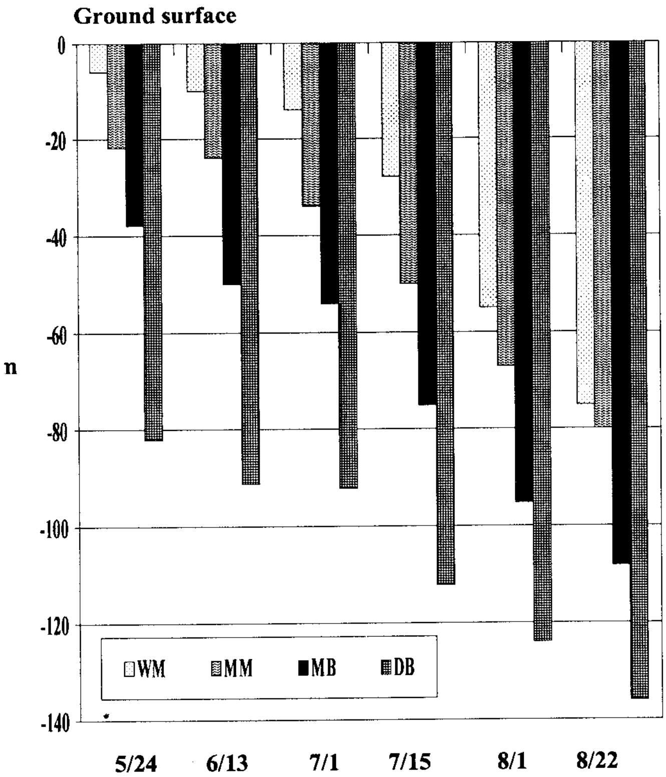

Fig. 2. Seasonal trends in average depth to the water table for 1995 within different plant communities designated as follows: MB = moist bluegrass, DB = dry bluegrass, MM = moist meadow foxtail, and WM = wet meadow.

ever a difference did exist at the 30 cm depth by mid-June in 1995. Sampling began in mid-June 1994 and we assume that due to extremely dry conditions this relationship was not observed but may have existed earlier in the season.

Water Table Depth

Trends in depth to the water table for the 4 plant communities are illustrated in Figures 1 and 2. Padgett (1982) monitored water table levels in several plant community types in central Oregon and found that the water table level in Kentucky bluegrass communities was generally 50 cm or more below the surface. Korpela (1992) studied water table trends in a dry bluegrass, moist bluegrass and wet meadow communities in northeastern Oregon. He reported water table depths of 50 cm or more for the moist bluegrass community and 100 cm or more for the dry bluegrass during the growing season. Water table depths for these communities within this study area were similar to Korpelas' during the 1994 growing season but were generally 20 cm closer to the surface during the 1995 growing season. This result can be attributed to the increased water available for irrigation during 1995. Padgett (1982) found that the water table in wet meadows dominated by beaked sedge (*Carex rostrata* Stokes) or water sedge (*C. aquatilis* Wahl) was at or near the ground surface until mid-summer, similar to trends for wet meadow communities within this study.

Ponded conditions occurred at 26% of the 46 wet community sampling sites in mid-June 1994 and 67% had a water table ≤ 30 cm below the soil surface. The moist meadow foxtail community had a water table within 30 cm of the surface at 17% of the sampling sites in mid-June 1994. In 1995, ponding occurred at 50% of the wet meadow and 6% of the moist meadow foxtail sites in late May. By mid-June ponding had ceased in the moist meadow foxtail community while 41% of the wet meadow sites remained ponded. Ponding continued through mid-July at 10% of the wet community sites. The water table was within 30 cm of the ground surface during mid-June 1995 for 91% of the wet meadow sites and 63% of the moist meadow foxtail sites. By mid-July only 8% of the moist meadow foxtail sites had a water table ≤ 30 cm below the surface while the wet community had 63%.

State and Transition Determination

Depth to groundwater during the growing season was pivotal in the definition of states for 3 of the plant communities at the peak of the growing season. Due to the differences in precipitation amounts between the 2 years of the study, mid-June 1994 average depth to groundwater was compared with late-June 1995 data. The average depth to groundwater by plant community is presented in Table 6. Significant differences in depth to the water table during the growing season were found between all the plant communities for both 1994 and 1995. Although there exists a significant difference in depth to the water table between the moist bluegrass and dry bluegrass community this environmental variable was not utilized to determine the states and transitional zone between these 2 communities. Soil moisture content within the top 45 cm of the soil profile was considered to have a greater influence on species composition for the dry bluegrass community than depth to groundwater.

Table 6. Average water table depth for the wet meadow, moist meadow foxtail, moist bluegrass, and dry bluegrass communities at the peak of the growing season (cm). Comparisons are within year across plant communities. Standard errors in parentheses.

	Wet Meadow	Moist Meadow Foxtail	Moist Bluegrass	Dry Bluegrass
	(cm)			
16 Jun 94	23^{a} (.28)	49^{b} (1.9)	70^{c} (2.0)	104^{d} (3.0)
28 Jun 95	14^{a} (2.1)	34^{b} (2.4)	59^{c} (1.7)	98^{d} (.3.0)

Table 7. Average soil moisture content in percent for the moist meadow foxtail, moist bluegrass, and dry bluegrass communities at 30 and 45 cm depth at the peak of the growing season. Comparisons are within a year and depth across plant communities. Standard errors in parentheses.

	Moist Meadow Foxtail	Moist Bluegrass	Dry Bluegrass
	(%)		
16 Jun 94 30 cm	51^{a} (2.8)	42^{b} (2.8)	25^{c} (3.3)
28 Jun 95 30 cm	63^{a} (5.8)	46^{b} (2.3)	30^{c} (.3.1)
16 Jun 94 45 cm	58*	45^{b} (2.6)	28^{c} (2.8)
28 Jun 95 45 cm	69*	62*	32^{c} (4.7)

Average soil moisture content in mid-June 1994 and late-June 1995 for the dry bluegrass, moist bluegrass, and meadow foxtail communities contained within this study area are presented in Table 7. Significant differences in soil moisture content during the growing season were found between the dry bluegrass and moist bluegrass communities at the 30 cm and 45 cm depth for 1994 and the 30 cm depth for 1995. Greater than 30% of the soil moisture measurement sites within the moist bluegrass community in 1995 at the 45 cm depth exhibited free standing water, therefore, soil moisture comparisons were not made. Due to the difficulty with accurately measuring soil moisture content in saturated soils additional comparisons between plant communities were not made.

The extreme differences in precipitation during the 2 years of the study was expressed in the soil moisture content and water table depth within plant communities across years (Tables 6 and 7). This range in soil water components provided critical information in the determination of plant community ecological thresholds. States were conservatively estimated by the difference between the wet (1995) and dry (1994) year average soil water component for the specified plant community. Transitions between states were determined by the difference in the average soil water component plus or minus the standard error between the two specified plant communities.

The threshold between the moist bluegrass community and the dry bluegrass community was distinct. The ranges in average soil moisture for these 2 plant communities did not overlap. The average soil moisture content in the moist bluegrass community during the dry year was 12% greater than the average soil moisture content in the dry bluegrass community during the wet year (Table 7). The dry bluegrass state occurs within the 25 to 30% soil moisture range at 30 cm depth at the peak of the growing season, whereas, the moist bluegrass state occurs within the 42 to 46% soil moisture range at 30 cm depth. Thus, the transition zone between the dry bluegrass community and the moist bluegrass community lies between 33.1 and 39.2% soil moisture at the 30 cm depth.

The states and transition zones for the other 3 community types were determined using the depth to groundwater data for June. The transition zone between the moist meadow foxtail and moist bluegrass community as determined by depth to groundwater was distinct. The average

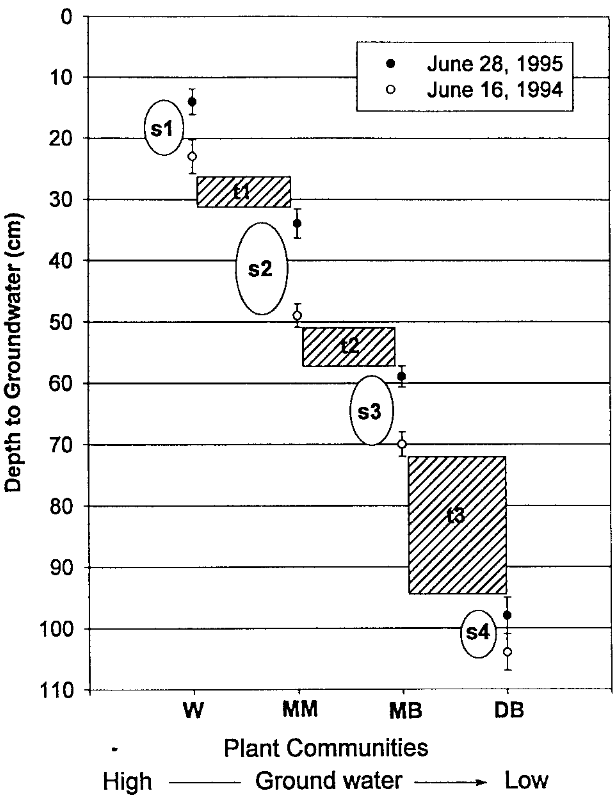

Fig. 3. Conceptual model of changes in plant community as a function of changing water table level. Plant community states are indicated by "s" and transitions between states by "t". The apparent ecological amplitude of a community is portrayed by the vertical height of the ellipse. The time or energy required to move from 1 plant community state to the next is illustrated by the vertical height of the transition box. Average mid-June depth to groundwater by plant community for 1994 and 1995 is presented. States were determined by the average plus or minus the standard eror. Transitions between states were determined by difference in ground water depth between the driest (1994) and the wettest (1995) years data for sl and s2, s2 and s3, s3 and s4. W = wet, MM = meadow foxtail, MB = meadow K. bluegrass, DB = upland K. bluegrass.

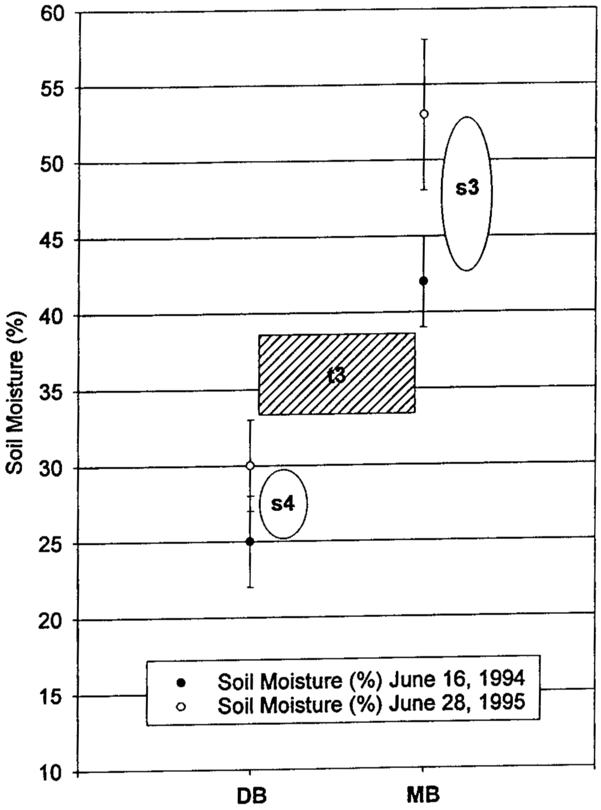

Fig. 4. Conceptual model of changes in plant community as a function of growing season soil moisture. Plant community states are indicated by "s" and transitions between states by "t". The apparent ecological amplitude of a community is portrayed by the vertical height of the ellipse. The time or energy required to move from 1 plant community state to the next is illustrated by the vertical height of the transition box. Average mid-June soil moisture for the dry bluegrass (DB) and moist bluegrass (MB) communities for 1994 and 1995 is presented. States were determined by the average plus or minus the standard error. Transitions between states were determined by the difference in soil moisture between the driest (1994) and wettest (1995) years data for s3 and s4.

depth to groundwater within the moist bluegrass community for the wet year was 59 cm whereas the average depth to groundwater for the moist meadow foxtail community during the dry year was 49 cm (Table 6). Thus, the transition zone was estimated to lie between 50.1 cm and 57.3 cm in depth to groundwater in mid to late June. The moist bluegrass state exists between a depth to groundwater of 59 to 70 cm whereas the moist meadow foxtail state lies between a water table depth of 34 to 49 cm. During the dry year the depth to groundwater within the wet meadow community averaged 23 cm and during the wet year 14 cm. The transition zone between the wet meadow and the moist meadow foxtail communities was estimated to occur between water table depths of 25.8 and 31.6 cm.

Conclusions

Our results suggest that models of vegetation dynamics based on the concepts of non-equilibrium ecology are appropriate tools for predicting change within the riparian zone. State-and-transition models specify a "state" as an alternative, persistent vegetation community which is not simply reversible in the linear successional framework. In addition, transitions are defined as the boundary in space and time between 2 states with the initial shift across the boundary permanent, on a practical time scale, without significant inputs of time and energy. Two conceptual models using the results of this research are presented in Figures 3 and 4. Plant community states are indicated by "s" and transitions between states by "t". The apparent ecological amplitude of a community is portrayed by the vertical height of the ellipse. The time or energy required to move from one plant community state to the next is illustrated by the vertical height of the transition box. The vertical height of the transition between the dry bluegrass and moist bluegrass communities based on depth to water table is relatively large (Fig. 3). Since this exceeds the potential rooting depth of the herbaceous component of the dry bluegrass community it was not considered a correct threshold. The appropriate model for the relationship between these 2 communities was based on soil moisture content and is presented in Figure 4.

The process of plant community change with respect to soil water components appears to be step-wise rather than linear. This implies a community may be stable and resistant to change up to a critical threshold. Once this threshold is crossed, changes can be dramatic and potentially irreversible over a time frame relevant to management. The semi-arid West contains examples of riparian zones which have been dewatered through the gullying of the associated alluvial stream channel. However, these models suggest that minor changes of 10 to 20 cm in the depth to groundwater can produce profound change in the associated riparian plant community. Further testing of these concepts across a variety of soils and climates is needed for verification and refinement of the proposed model.

Literature Cited

Anderson, J.E. 1986. Development and structure of sagebrush steppe plant communities, pgs. 10–12. *In:* P.J. Joss, P.W. Lynch, and O.B. Williams (eds.), Rangelands: A resource under siege—Proceedings of the Second Internat. Rangeland Congr. Aust. Aca. of Sci., Canberra, Aust.

Archer, S. and F.E. Smeins. 1991. Ecosystem-Level Processes, pgs. 109–139. *In:* K. Rodney and Jeffery W. Stuth (eds), Grazing Management. an Ecological Perspective.

Dufrene, M. and P. Legendre. 1997. Species assemblages and indicator species: The need for a flexible asymmetrical approach. Ecol. Monogr. 67(3):345–366.

Dyksterhuis, E.J. 1949. Condition and management of rangeland based on quantitative ecology. J. Range Manage. 2:104–115.

Foran, B.D., G. Bastin, and K.A. Shaw. 1986. Range assessment and monitoring in arid lands: the use of classification and ordination in range survey. J. Environ. Manage. 22:67–84.

Friedel, M.H. 1991. Range condition assessment and the concept of thresholds: A viewpoint. J. Range Manage. 44(5):422–426.

Gardner, W.H. 1986. Water content, pp. 493–544. *In:* A. Klute (ed.), Methods of Soil Analysis. Part 1. Monograph 9, Amer. Soci. of Agron., Madison, Wisc.

Jury, W.A., W.R. Gardner, and W.H. Gardner. 1991. Soil Physics. John Wiley & Sons, Inc., New York, N.Y.

Kauffman, J.B. and W.C. Krueger. 1984. Livestock impacts on riparian ecosystems and streamside management implications...a review. J. Range Manage. 37(5):430–7.

Korpela, E.J. 1992. Modeling Riparian Zone Processes: Biomass Production and Grazing. Diss. Dept of Rangel. Resources, Oregon State Unive., Corvallis, Ore.

Laycock, W.A. 1991. Stable States and thresholds of range condition on North American rangelands: A viewpoint. J. Range Manage. 44(5):427–433.

Oregon Climate Service. 1995. Taylor, G.H., State Climatologist. Oregon State Univ., Corvallis, Ore.

Padgett, W.G. 1982. Ecology of Riparian Plant Communities in the Southern Malheur National Forest. M.S. Thesis. Oregon State Univ., Corvallis, Ore. 145pp.

Pieper, R.D. 1973. Measurement Techniques for Herbaceous and Shrubby Vegetation. New Mexico State University, Las Cruces, N.M.

SAS Institute Inc. 1994. SAS User's Guide: Statistics, Version 6 Edition. SAS Institute Inc., Cary, N.C. 956 pp.

Smith, E.L. 1988. Successional concepts in relation to range condition assessment (chapter 6), pp. 113–133. *In:* P.T. Tueller (ed.), Vegetation science applications for rangeland analysis and management. Kluwer Academic Publishers, Boston, Mass.

Stringham, T.K. 1996. Application of Nonequilibrium Ecology to Managed Riparian Ecosystems. Diss. Oregon State Univ., Corvallis, Ore. pp.156.

Tausch, R.J., P.E. Wigand, and J.W. Burkhardt. 1993. Viewpoint: plant community thresholds, multiple steady states, and multiple successional pathways: legacy of the Quaternary? J. Range Manage. 46:439–47.

United States Dept. of Agriculture. 1995. Soil Descriptions, Bear Valley, Oregon. Nat. Resource Consev. Serv., Baker City, Ore.

Westoby, M. 1980. Elements of a theory of vegetation dynamics in rangelands. Israel J. Bot. 28:169–194.

Westoby, M., B. Walker, and I. Noy-Meir. 1989. Range management on the basics of a model which does not seek to establish equilibrium. J. Arid. Environ. 17:235–239.

Weixmelman, D.A., D.C. Zamudio, K.A. Zamudio, and R.J. Tausch. 1997. Classifying ecological types and evaluating site degradation. J. Range Manage. 50(3):315–321.

Wilson, A.D. 1984. What is range condition: development of concepts in Australia. Bull. Ecol. Soc. Amer. 65:171.