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SIMULATION OF PLANT BIOMASS ON A SHORTGRASS  
AND A TALLGRASS PRAIRIE WITH  
EMPHASIS ON BELOWGROUND PROCESSES

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## ABSTRACT

The paper reports on a mathematical model constructed to simulate various aboveground and belowground compartments of the producer subsystem for a shortgrass and a tallgrass prairie. Simulated aboveground compartments are live shoots, recent and old dead shoots, litter, and crowns. Major belowground compartments are live and dead juvenile and nonsuberized and suberized roots. The rooting depth has been divided into six layers and all of the belowground compartments are simulated for each layer. Driving variables in the model are: daily rainfall, daily maximum and minimum air temperatures, long-term monthly average cloud cover, relative humidity, and wind speed. The major processes linking the state variables are net photosynthesis, translocation to crowns and roots, death of shoots, crowns, and roots, production of litter, aging of roots, respiration of crowns and roots, and decomposition of litter, crowns, and roots.

Selected outputs from 3-year runs (1970-1972) of model are provided to illustrate the general dynamics of the system. Important differences in the functional properties of the shortgrass and tallgrass prairies at the producer level indicated by the simulation exercise are discussed.

## INTRODUCTION

Mathematical models have been proved to be useful in providing an abstraction of and in serving as means of organizing the available knowledge about complex systems. The model presented in this paper depicts intra- and interseasonal dynamics of various herbage compartments, both aboveground and belowground, in a shortgrass and a tallgrass prairie.

The temperate grasslands are characterized by the presence of massive root biomass that often accounts for more than 90% of total plant standing crop (Sims & Singh 1971). A knowledge of various processes associated with the root compartment is therefore a prerequisite to the understanding of the structure and function of grasslands. Recent field experimentation on shortgrass prairie plots using carbon-14 (Singh & Coleman 1973, 1974, ms. to be published) and root observation windows (Ares 1976) have yielded valuable information regarding the translocation of the photosynthate to crowns and roots, amount of metabolically functional root biomass, pattern of root growth and mortality, etc. Ares & Singh (1974) organized this information into the framework of a compartment model in which fluxes between compartments were time-varying functions controlled by the donor or recipient compartment. This model was driven by an unlimited amount of carbon pool available for translocation in the aboveground plant parts, and the various flows in the model were non-mechanistic. We have reorganized the model in order to put mechanism in the formulation of flows, and we have replaced the aboveground translocatory carbon pool with simulation of photosynthesis and aboveground biomass dynamics. Emphasis, however, is still on the belowground plant compartments and associated processes. The root compartment now is divided into six depth strata.

The model was first constructed for the shortgrass prairie at the Pawnee Site because more information and experience were available there. It was then adapted to tallgrass prairie at Osage. The Pawnee grassland is dominated by blue grama (*Bouteloua gracilis* (H.B.K.) Lag.) and the Osage Site by little blue stem (*Andropogon scoparius* Michx.). The climate, soil, community structure, and herbage dynamics for the two sites have been described respectively by Rasmussen (1971), Reuss (1971), Risser (1971), and Sims & Singh (1971). Experimental observations on photosynthesis of dominant species were available from Brown (1974) and Risser & Johnson (1973).

We would like to emphasize that, as perhaps in all models, the present model presents a collection of hypotheses. In fact, each equation is a hypothesis concerning the respective producer function and is based partly on data, partly on literature, and partly on inferences and conjectures. We hope that more experimental evidence will be forthcoming which will lead to confirmation, modification, or replacement of these equations.

#### DESCRIPTION OF THE MODEL

A compartmental representation of the herbage system is illustrated in Fig. 1, showing the flows and state variables considered in the model. All the state variables in the aboveground part of the system are represented in this figure. The live and dead root compartments are further subdivided into juvenile roots, nonsuberized roots, and suberized roots, following Ares (1976) and Ares & Singh (1974). Fig. 2 illustrates the flow diagram for the belowground part of the system. Each of the state variables shown in this figure is considered for six soil layers with corresponding flows for each layer. All state variables

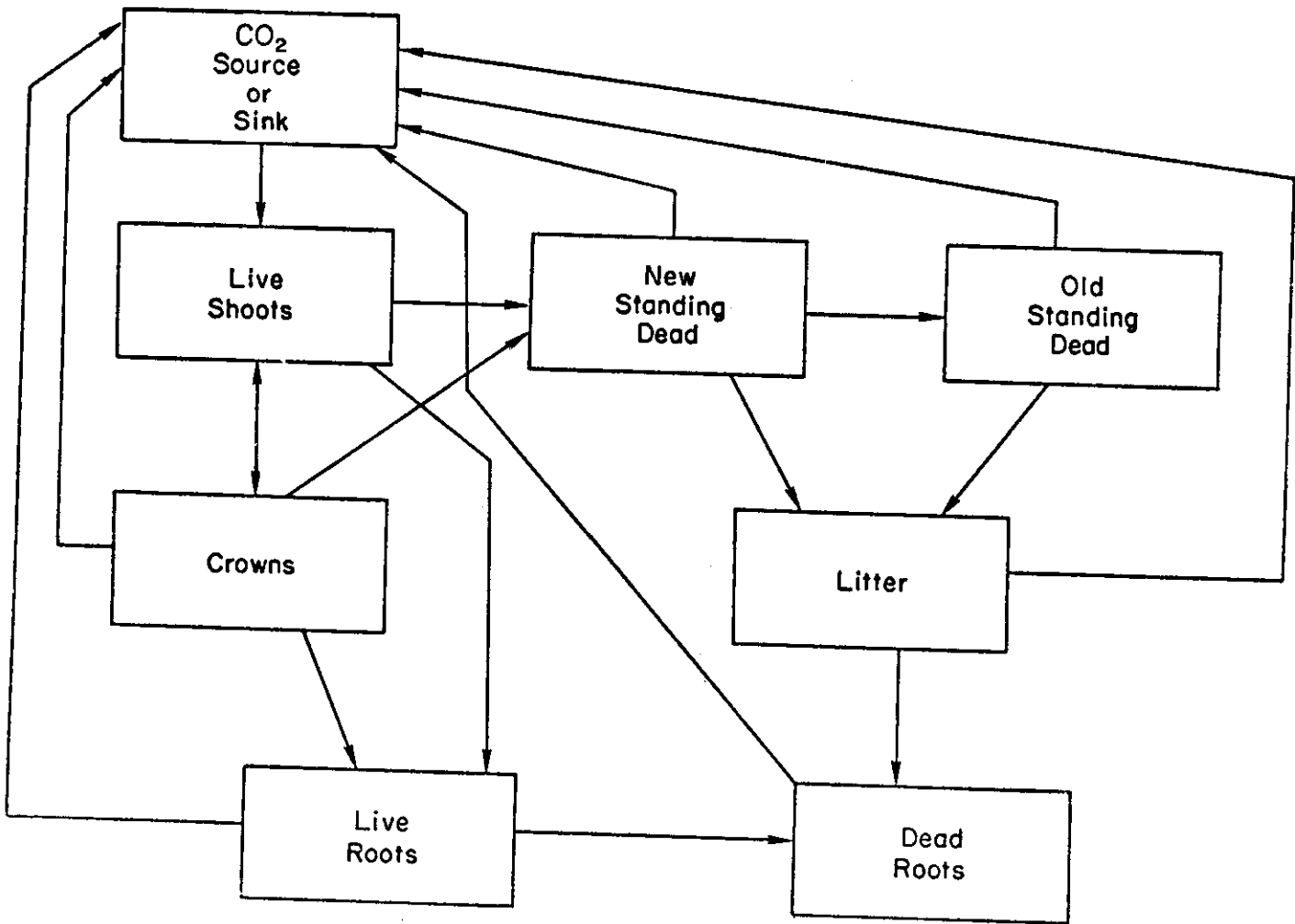


Fig. 1. Compartmental representation of the primary producer subsystem.

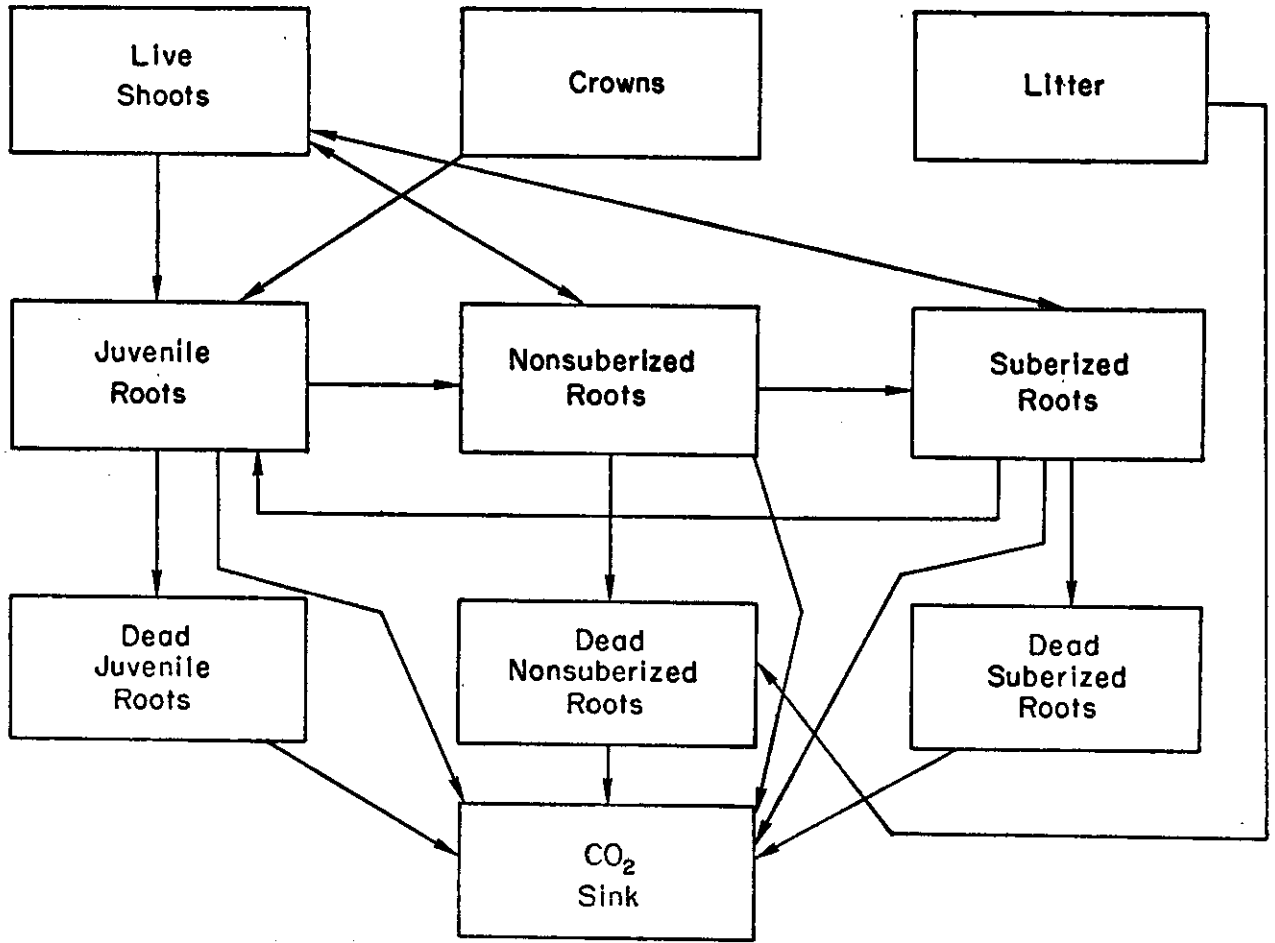


Fig. 2. Flow diagram for the belowground state variables.

and rate processes are in terms of dry weight. All the symbols for parameters used in the model are listed in the Appendix.

The abiotic section of the model consists of a water flow submodel and a temperature profile submodel. Figures 3 and 4 summarize the structure of these submodels. The water flow submodel simulates the flow of water through the plant canopy and the soil layers. The allocation of rainfall and the evapotranspiration of water are the important processes considered. The model is generalized to handle an arbitrary number of layers for soil water in which the depth and soil type are specified. The depth structure for soil water layers used in the Pawnee Site version of the model is shown in Fig. 3 while the soil layers were stratified into 0-5 cm, 5-10 cm, 10-15 cm, 15-30 cm, 30-45 cm, 45-60 cm, 60-75 cm, and 75-90 cm for the Osage Site version. The temperature profile submodel simulates the daily solar radiation, maximum canopy air temperature, the average daytime canopy air temperature, and the average daily soil temperature at 13 points in the soil profile (0 cm to 180 cm). The site specific parameters that define the structure of the abiotic model at the Osage and Pawnee Sites are shown in Table 1. A detailed description and validation of the Pawnee version of the abiotic submodel is given by Parton (1976).

The atmospheric driving variables that are required by the abiotic model include daily rainfall, maximum and minimum air temperature (2 m), and the long-term monthly average values of the cloud cover, relative humidity, and wind speed. The daily rainfall recorded at Foraker, Oklahoma (1970-1972), the daily maximum and minimum air temperature at Pawhuska, Oklahoma (1970-1972), and long-term average monthly values of cloud cover, relative humidity, and wind speed at Tulsa, Oklahoma



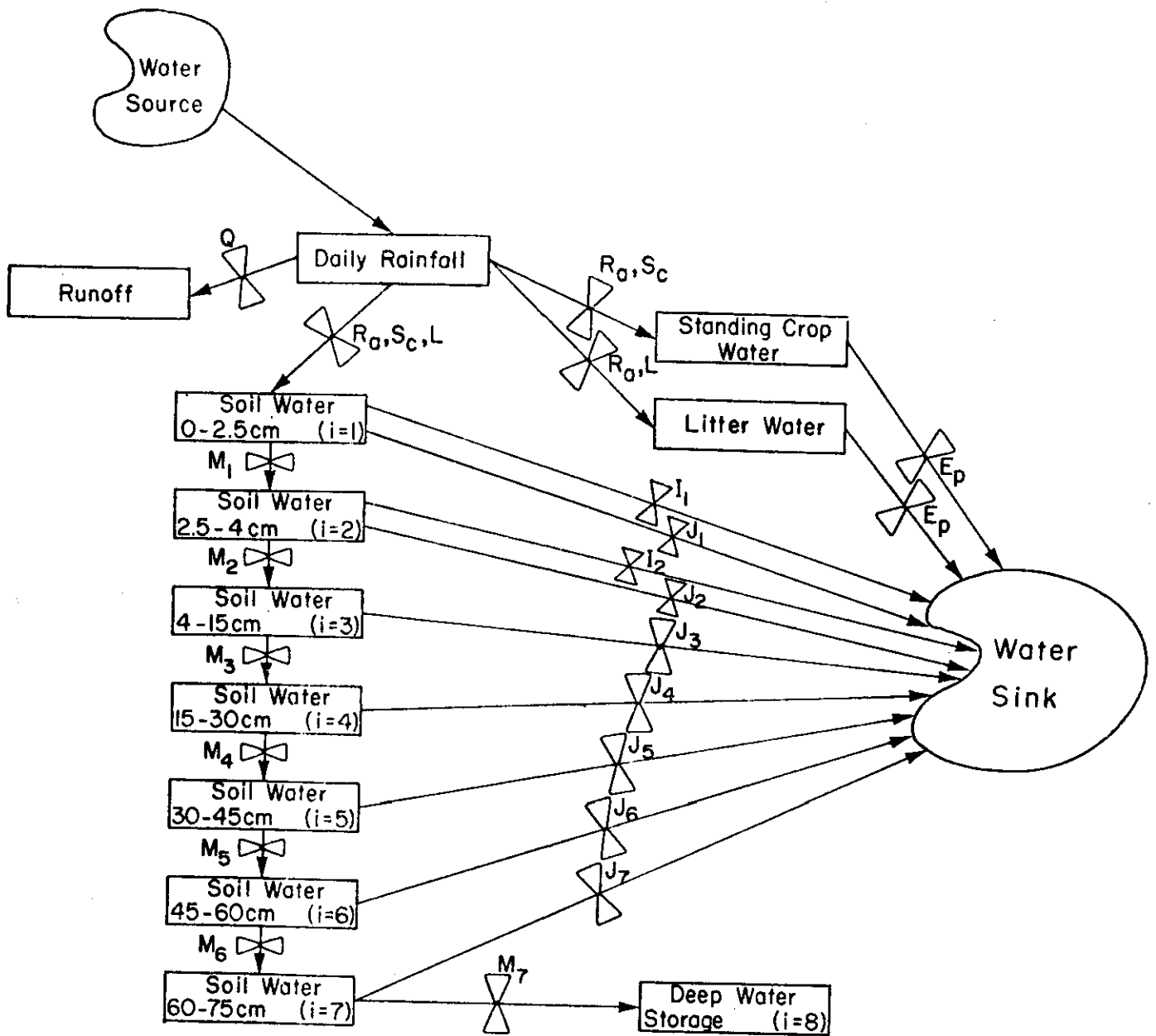


Fig. 3. Structure of the water flow submodel where  $I_i$  is the combination of  $M_i$ ,  $E_p$ ,  $G_i$ ,  $S_4$ , and  $B_1$ ;  $J_i$  is the combination of  $M_i$ ,  $E_p$ ,  $B_1$ ,  $H_i$ , and  $S_{75}$ ;  $R_a$  is the daily rainfall;  $M_i$  is the water content of the  $i^{\text{th}}$  layer;  $E_p$  is the potential evapotranspiration rate;  $S_4$  is the weighted average water tension in the 0-4 cm soil water layer;  $S_{75}$  is the weighted average water tension in the 0-75 cm soil water layer;  $B_1$  is the above-ground live shoot biomass;  $S_c$  is the shoot plus standing dead biomass;  $L$  is the litter biomass;  $Q$  is the flow set equal to zero;  $H_i$  is the water absorption coefficient for the live roots in the  $i^{\text{th}}$  layer; and  $G_i$  is the bare soil water loss for the  $i^{\text{th}}$  layer.

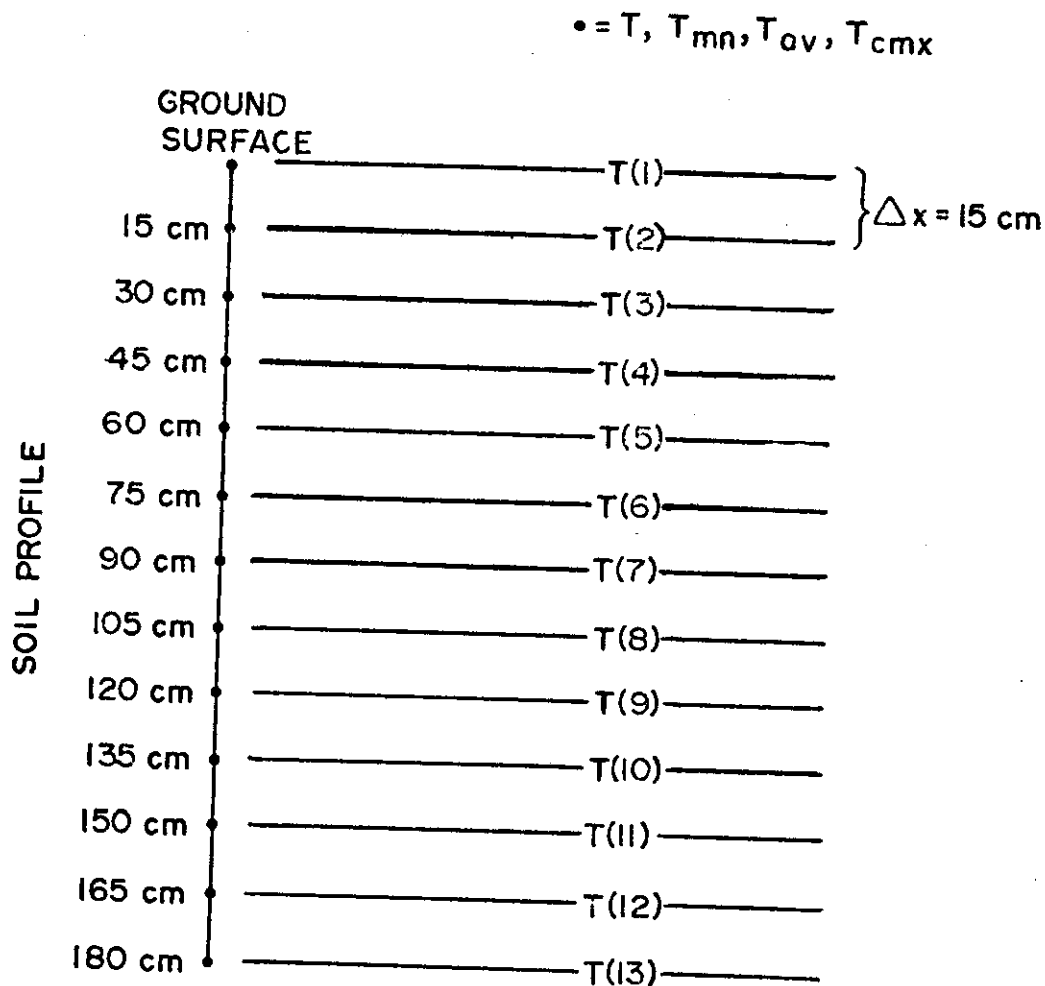


Fig. 4. Structure of the temperature profile submodel where  $T_{mx}$ ,  $T_{mn}$ ,  $T_{av}$ , and  $T_{cmx}$  are respectively the maximum and minimum air temperatures at 2 m, the average daytime temperature in the canopy, and the maximum canopy air temperature.  $T_i$  is the average daily soil temperature at the  $i^{\text{th}}$  point.

Table 1. Site specific parameters for Osage and Pawnee Site versions of the abiotic submodel. The solar transmission coefficient and the soil diversity are respectively 0.84 and  $1.4 \text{ g} \cdot \text{cm}^{-3}$  at the Pawnee and 0.75 and  $1.50 \text{ g} \cdot \text{cm}^{-3}$  at Osage

	Soil layer 1	Soil layer 2	Soil layer 3	Soil layer 4	Soil layer 5	Soil layer 6	Soil layer 7	Soil layer 8
Soil depth								
Osage	0-5	5-10	10-15	15-30	30-45	45-60	60-75	75-90
Pawnee	0-1.5	1.5-4	4-15	15-30	30-45	45-60	60-75	--
Soil layers with bare soil evaporation								
Osage	yes	yes	no	no	no	no	no	no
Pawnee	yes	yes	no	no	no	no	no	--
Volumetric soil water content at the wilting point (percent)								
Osage	14.0	16.5	19.5	20.0	20.8	23.4	24.7	24.7
Pawnee	6.0	7.0	10.0	12.0	13.0	13.0	12.0	--
Volumetric soil water content at -3 bars soil water tension (percent)								
Osage	24.0	26.0	28.0	29.0	29.0	31.0	31.0	31.0
Pawnee	10.0	12.0	15.0	18.0	18.0	18.0	17.0	--
Volumetric soil water content at field capacity with no dead roots (percent)								
Osage	31.0	35.0	37.0	39.0	39.0	39.0	39.0	39.0
Pawnee	16.0	18.0	25.0	29.0	29.0	29.0	29.0	--
Bare soil water absorption coefficient (NOD)								
Osage	0.70	0.30	0.0	0.0	0.0	0.0	0.0	0.0
Pawnee	0.76	0.24	0.0	0.0	0.0	0.0	0.0	--
Transpiration water absorption coefficient (NOD)								
Osage	0.24	0.18	0.16	0.16	0.11	0.07	0.05	0.04
Pawnee	0.13	0.14	0.37	0.18	0.07	0.06	0.05	--
Fraction of dead roots								
Osage	0.17	0.15	0.10	0.25	0.17	0.10	0.04	0.02
Pawnee	0.45	0.15	0.08	0.15	0.10	0.05	0.02	--

(1966-1972) were used to derive the Osage version of the model. The Pawnee version used the daily rainfall values (1970-1972) from micro-watershed 2 at the Pawnee Site (Smith and Striffler 1969), the maximum and minimum air temperature observed at the Pawnee Site (1970-1972), and long-term average monthly cloud cover, relative humidity, and wind speed at nearby Cheyenne, Wyoming (1966-1972).

The Pawnee and Osage versions of the total model were run for a 3-year time period (1970-1972) using a compartmental flow-oriented simulation compiler (Gustafson and Innis 1973). The compiler uses a Fortran-like computer simulation language designed to ease the development and implementation of compartmental flows. Compartmental flow simulations are defined by specifying the flow rates between compartments and are represented in a difference equation form. The model uses a time step equal to 1 day. For the sake of clarity, the aboveground and below-ground components of the model are described separately.

#### *Aboveground system*

The processes involved in the aboveground part of system are: photosynthesis; translocation to crowns and roots; death of live shoots; transfer from standing dead to litter; decomposition of litter; mechanical mixing of litter; leaching of new standing dead, old standing dead, and litter; death and respiration of the crowns.

#### Net photosynthesis

Net photosynthesis ( $P_n = g \cdot m^{-2} \cdot day^{-1}$ ) is calculated as a function of the average daytime canopy air temperature, soil water, solar radiation (shortwave) above the canopy ( $S_r$ ), canopy height, phenological

stage, and the photosynthetically active biomass ( $B_a$ ) using the following equation:

$$P_n = M_p P_p C B_a \quad (1)$$

where  $M_p$  is the maximum photosynthesis rate ( $g \cdot g^{-1} \cdot day^{-1}$ ),  $P_p$  is the phenology control parameter for photosynthesis (NOD<sup>2/</sup>, 0 to 1), and  $C$  is the combined water tension and air temperature control parameter for photosynthesis (NOD, 0 to 1). The phenological stages are simulated by a phenology submodel described later in the text. The maximum net photosynthesis rate ( $M_p$ ) is calculated as a function of the solar radiation incident upon the live plant canopy ( $S_1$ ) and the peak net photosynthesis rate achievable per calorie of solar energy ( $P_m = g \cdot g^{-1} \cdot day^{-1} \cdot cal^{-1}$  in the absence of limiting factors:

$$M_p = S_1 P_m \quad (2)$$

The values for  $P_m$  were estimated from experimental data reported by Risser & Johnson (1973) and Brown (1974).  $P_m$  is set equal to 0.00033 for blue grama in the shortgrass prairie at Pawnee and 0.00030 for little blue stem in the tallgrass prairie at Osage. The solar radiation at the top of the live plant canopy ( $S_1$ ) is calculated as a function of the average height of live shoot biomass ( $H_1$ ) and the average height of the old standing dead biomass ( $H_0$ ) using the following set of equations:

$$S_1 = \begin{cases} = S_r & \text{if } H_1 \geq H_0 \\ = S_r (Z_q)^{L_a} & \text{if } H_1 < H_0 \end{cases} \quad (3)$$

---

<sup>2/</sup>NOD means no dimension throughout the text and figures.

$$Z_q = \begin{cases} 0.40 + (6 - P_d)0.10 & \text{if } P_d \leq 6 \\ 0.40 & \text{if } P_d > 6 \end{cases} \quad (4)$$

$$P_d = B_d/100 \quad (5)$$

$$L_a = P_d F_1 \quad (6)$$

where  $L_a$  is the leaf area index ( $\text{cm}^2 \cdot \text{cm}^{-2}$  of ground) of old standing dead that is above the average height of the live biomass,  $P_d$  is the leaf area index of old standing dead (NOD),  $B_d$  is the biomass of old standing dead,  $Z_q$  is the parameter that controls the extinction of light in the plant canopy, and  $F_1$  is the fractional leaf area of the old standing dead biomass above  $H_1$ . The average height of the live shoot biomass ( $H_1$ ) is calculated as a function of live plus recent standing dead (see Fig. 5) using a functional relationship that was derived from data presented by Conant (1972). The average height of the old standing dead is calculated as a function of the old standing dead biomass using the same relationship illustrated in Fig. 5 with the X axis replaced by the product of the old standing dead biomass multiplied by 0.25 (Conant 1972). The leaf area index conversion factor (eqn (5)) is based on observations of Conant (1972) and Brown (1974), while the fractional leaf area of old standing dead above  $H_1$  is calculated as a function of the ratio of  $H_1$  to  $H_0$  (see Fig. 6) using a relationship derived from Conant (1972). The light extinction control parameter  $Z_q$  is calculated as a function of the leaf area index of standing biomass (see eqn (4)) by assuming that increasing leaf area index results from leaves having a more horizontal orientation with less light penetrating into the plant canopy. This assumption is based upon visual observation of the plant canopy at the Osage and Pawnee Sites. Eqns (3) and (4) are partly based upon the findings of Cowan (1968). The effect of the phenological stage

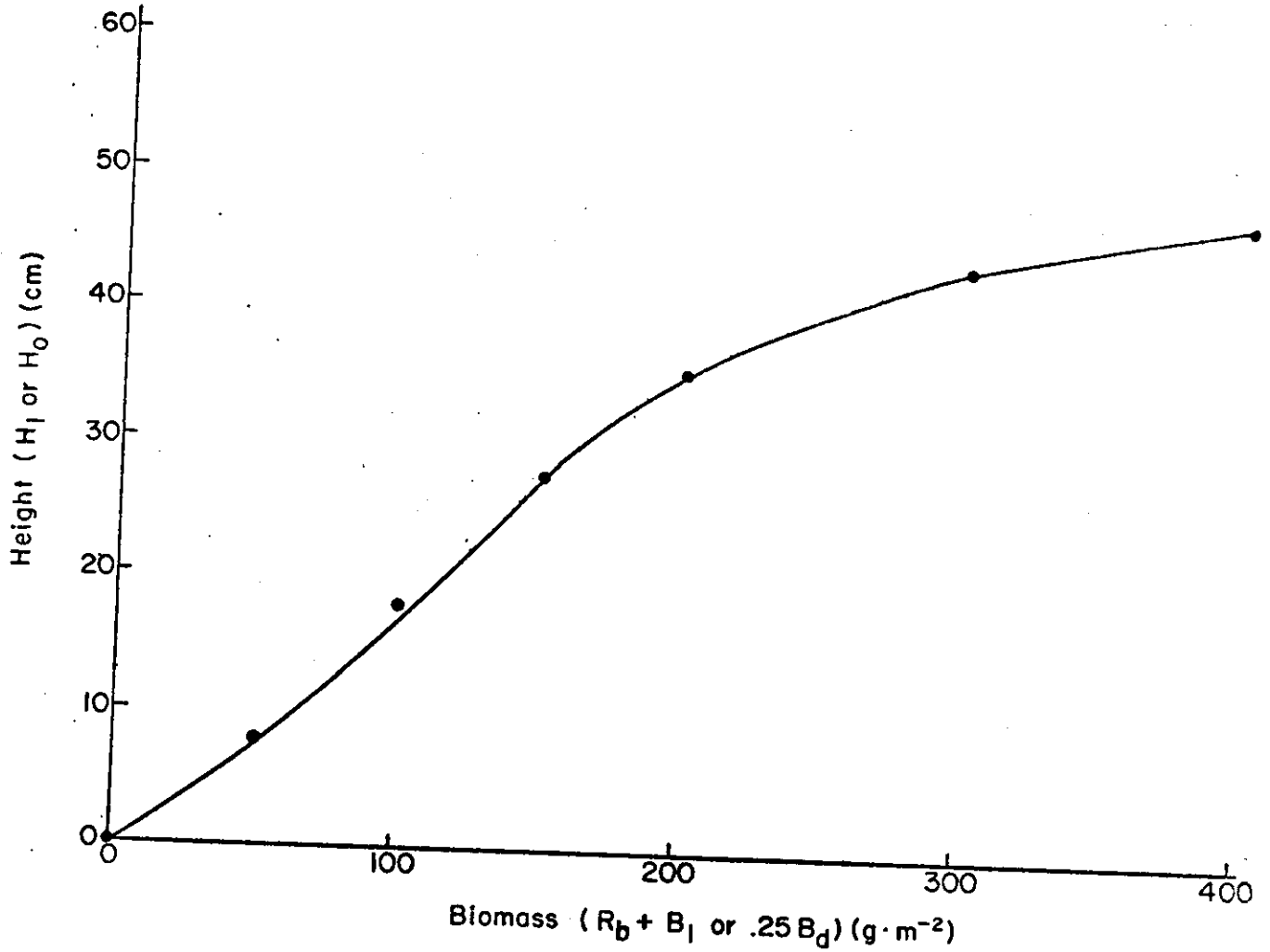


Fig. 5. Average height of the live plant canopy ( $H_l$ ) and the standing dead canopy ( $H_o$ ) as a function, respectively, of the sum of live shoot biomass ( $B_l$ ) and recent standing dead ( $R_b$ ), and the product of 0.25 times the old standing dead biomass.

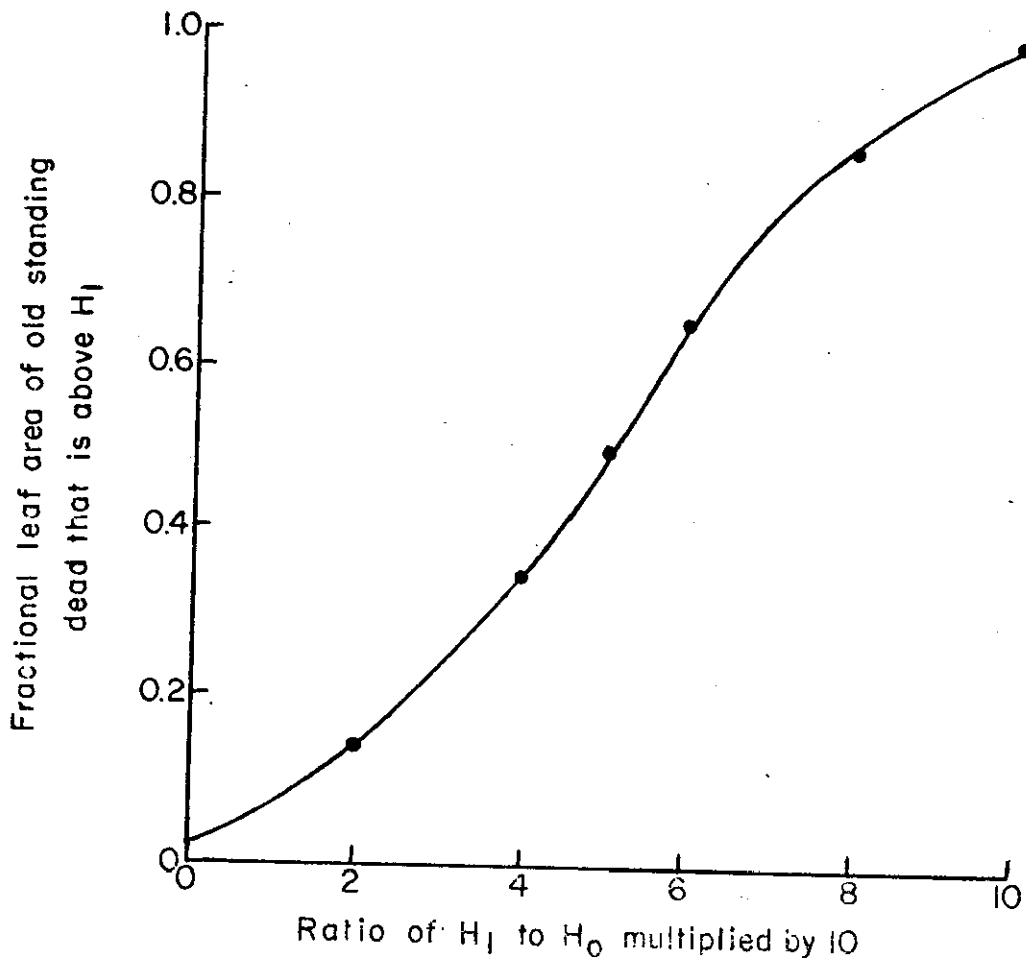


Fig. 6. Relationship of the fractional leaf area of old standing dead above  $H_1$  to the ratio of  $H_1$  to  $H_0$ .



of the plant on the phenology control parameter for photosynthesis ( $P_p$ ) is calculated (see Fig. 7) using the relationships derived from data presented by Brown (1974) and Risser (unpublished). The combined water tension and air temperature control parameter for photosynthesis ( $C$ ) is calculated as a function of weighted average soil water tension and the average daytime canopy air temperature using the relationship illustrated in Fig. 8. This formulation is also based on Brown's (1974) and Risser's (unpublished) studies. The weighted average soil water tension is calculated by using weight factors that decrease exponentially with soil depth. The photosynthetically active biomass ( $B_a$ ) is assumed to be equal to the live shoot biomass; however,  $B_a$  is not allowed to exceed  $150 \text{ g} \cdot \text{m}^{-2}$ ; this limit is set because of light extinction relations of the plant canopy (Cowan 1968).

#### Translocation to roots and crowns

Translocation from the live shoots to crowns ( $T_c = \text{g} \cdot \text{m}^{-2} \cdot \text{day}^{-1}$ ) is calculated as a function of the phenological stage of the plant ( $P$ , NOD), the ratio of shoot biomass to crown biomass ( $R_c$ , NOD) and the net photosynthesis rate ( $P_n$ ) using the following equation:

$$T_c = \begin{cases} R_c P_n A_c & \text{if } P < 4 \\ P_c P_n & \text{if } P \geq 4 \end{cases} \quad (7)$$

where  $A_c$  is a control constant for translocation to the crowns (NOD,  $A_c = 0.5$  for Pawnee and  $0.2$  for Osage),  $P_c$  is the fraction of  $P_n$  translocated to crowns (NOD), and  $P$  is the phenological stage.  $P_c$  is calculated as a function of phenological stage of the plant using a relationship (Fig. 9a) derived from data presented by Singh & Coleman (ms. to be published).

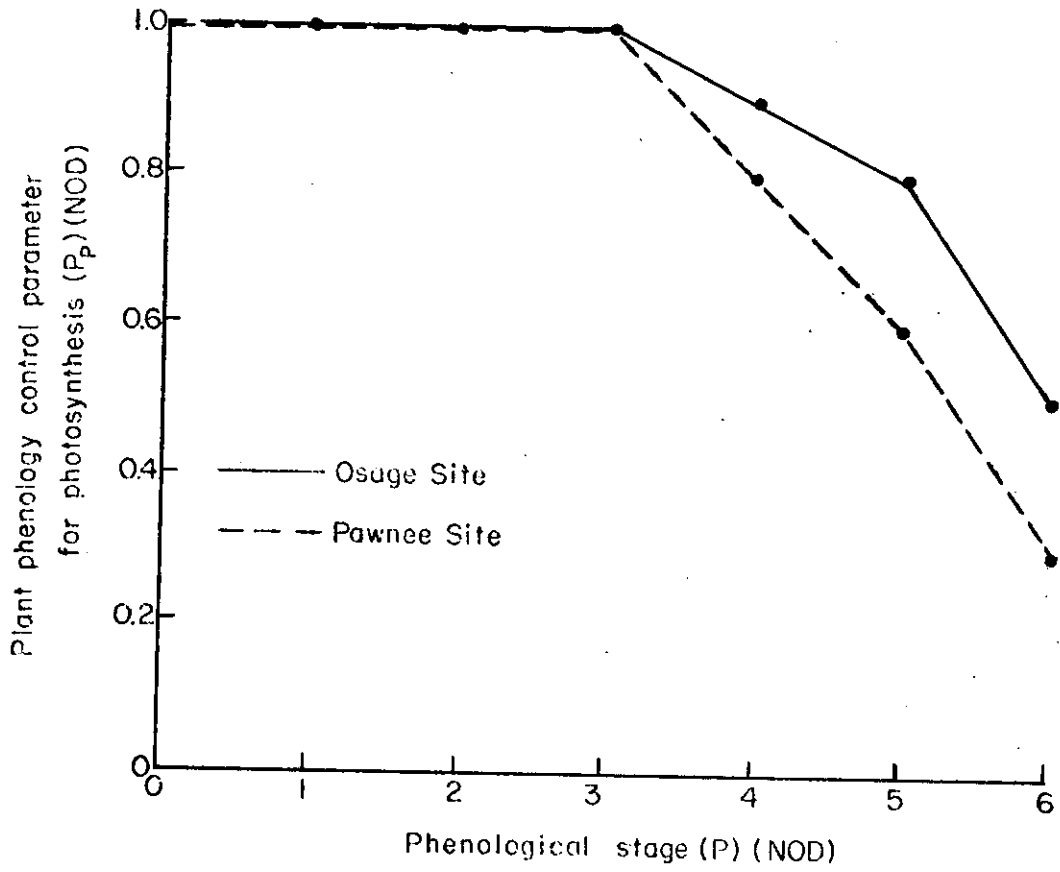


Fig. 7. The functional relationship of plant phenology control parameter for photosynthesis ( $P_p$ ) to the phenological stage ( $P$ ) of the plants at both Osage and Pawnee Sites.

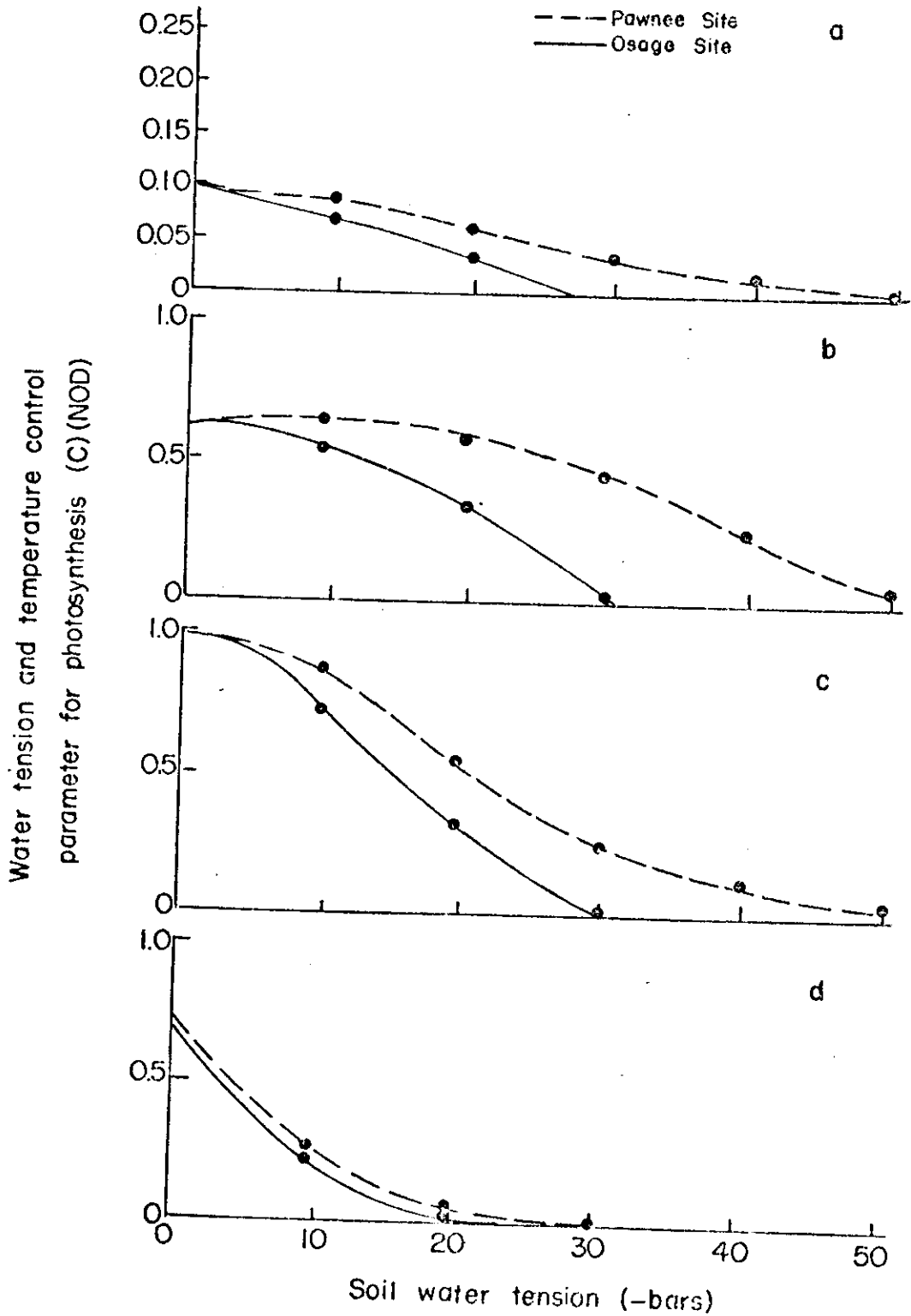


Fig. 8. The effect of canopy air temperature ((a) 10°C, (b) 20°C, (c) 30°C, (d) 40°C) and the weighted average soil water tension upon the combined water tension and air temperature control parameter for photosynthesis (C) at the Pawnee and Osage Sites.

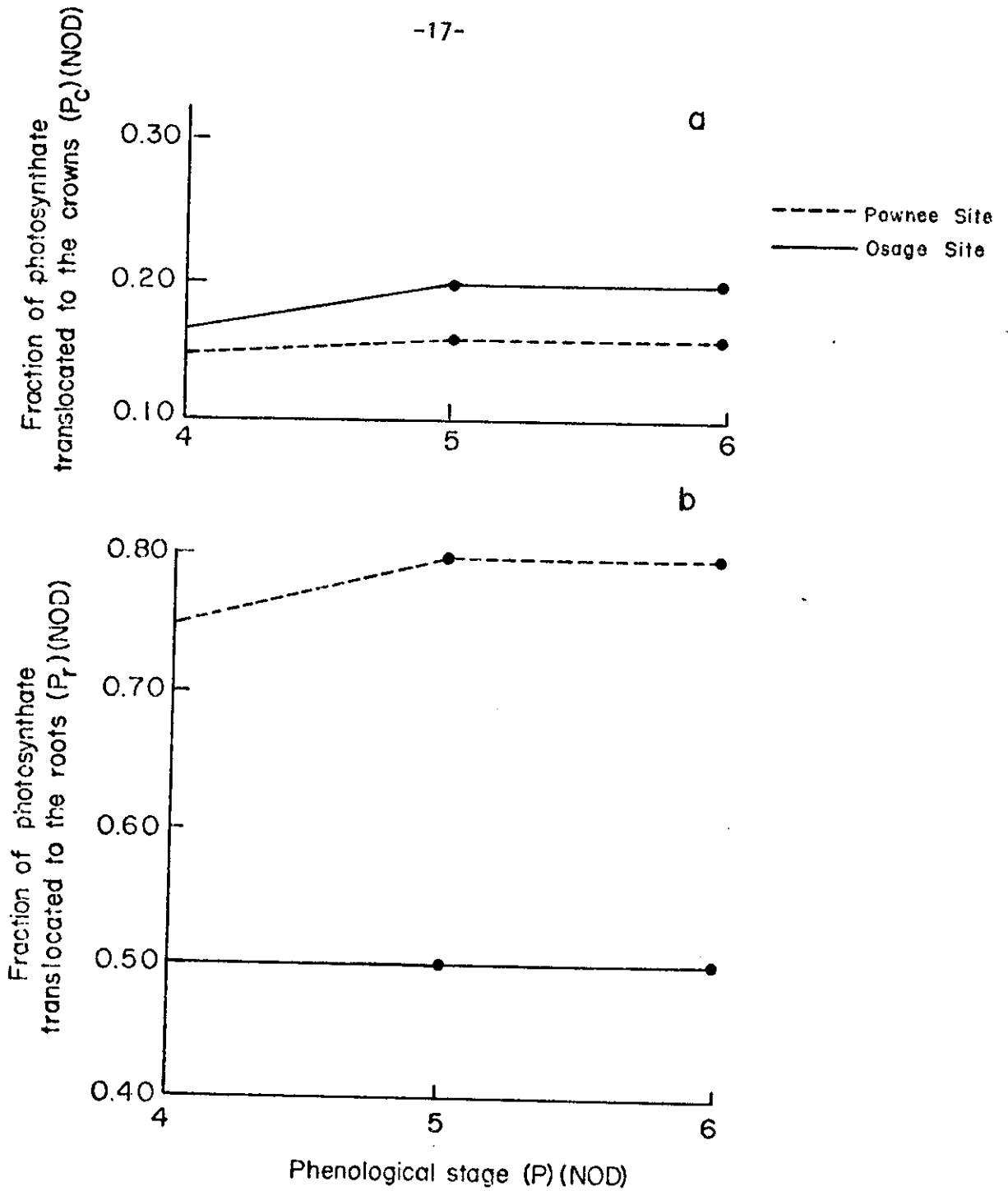


Fig. 9. Relationships between the fraction  $P_n$  translocated to (a) crowns and (b) live roots and the phenological stage of the plant. The information for the Pawnee Site is based on Singh and Coleman (ms. to be published). The lower values for the Osage Site are based on root:shoot ratios reported by Sims and Singh (1971).

The total amount of photosynthate translocated to the live root biomass ( $T_b = g \cdot m^{-2} \cdot day^{-1}$ ) is calculated as a function of the phenological stage of the plant ( $P$ ), the ratio of shoot biomass to the total live root biomass ( $R_r$ ), and the net photosynthate ( $P_n$ ) using eqn (8).

$$T_b = \begin{cases} R_r R_n A_r & \text{if } P < 4 \\ P_r P_n & \text{if } P \geq 4 \end{cases} \quad (8)$$

where  $A_r$  is the control constant for translocation to the roots (NOD,  $A_r = 4.0$  for Pawnee Site and 1.3 for Osage Site) and  $P_r$  is the fraction of  $P_n$  translocated to the live roots.  $P_r$  is calculated as a function of the phenological stage of the plant using a functional relationship (see Fig. 9b) calculated from data presented by Singh & Coleman (ms. to be published).

Transfer of stored carbohydrate material from the crowns and the live suberized and nonsuberized roots in the top two soil layers into the live shoot biomass occurs in the early part of the growing season which enables the initiation of shoot growth. This translocation to shoot is a function of the soil water tension in the appropriate layers and the mass of live shoots ( $B_1$ ), crowns ( $C_b$ ), and live suberized and nonsuberized roots and the ratio of solar radiation above the vegetation canopy to the solar radiation at the top of the live plant canopy ( $S_r/S_1$ ) using the following set of equations:

$$B_t = (C_b + R_{12} + R_{22} + R_{13} + R_{23}) \quad (9)$$

$$T_s = B \cdot 0.003 \cdot e^{[-B_1/(B_t \cdot 0.015)]} \cdot M \cdot (S_r/S_1) \quad (10)$$

where  $B_t$  is the sum of crown biomass and the live suberized and non-suberized root biomass in the top two soil layers,  $R_{i3}$  is the biomass of live suberized roots in the  $i^{\text{th}}$  layer,  $R_{i2}$  is the biomass of live nonsuberized roots in the  $i^{\text{th}}$  layer,  $T_s$  is the rate of transfer of stored carbohydrate to the live shoots from either  $C_b$ ,  $R_{12}$ ,  $R_{22}$ ,  $R_{13}$ , or  $R_{23}$ ,  $B$  is biomass of either  $C_b$ ,  $R_{12}$ ,  $R_{22}$ ,  $R_{13}$ , or  $R_{23}$ , and  $M$  is soil water tension control parameter for the translocation from either  $C_b$ ,  $R_{12}$ ,  $R_{22}$ ,  $R_{13}$ , or  $R_{23}$ . The soil water tension control parameter ( $M$ ) is calculated as a function of water tension in appropriate layer (crowns use water in the top layer only), using the functional form presented in Fig. 10. Eqn (10) assumes that translocation from crowns or roots to the live shoots is inversely proportional to the fraction of total solar radiation above the plant canopy that is incident on the live shoots (implying a shading effect from the standing old dead vegetation during the early part of the growing season) and the ratio of the live shoot biomass to the sum of crown and live root biomass. Translocation to the live shoot only occurs when the phenology stage ( $P$ ) is less than 4 and the 14-day moving average soil temperature ( $S_t$ , °C) from 0 to 15 cm is greater than a critical level ( $S_t \geq 4^\circ\text{C}$  Pawnee Site,  $S_t \geq 10^\circ\text{C}$  Osage Site). The translocation is assumed to occur only from roots in the first two soil layers because most of the surplus photosynthate is stored in these layers (Singh & Coleman 1974a).

#### Death of shoots

The death rate of live shoot biomass ( $D_s = g \cdot m^{-2} \cdot \text{day}^{-1}$ ) is a function of the weighted average soil water tension, the shoot biomass ( $B_1$ ), the minimum air temperature ( $T_m$ ), and the phenological stage of the plant using the following set of equations:

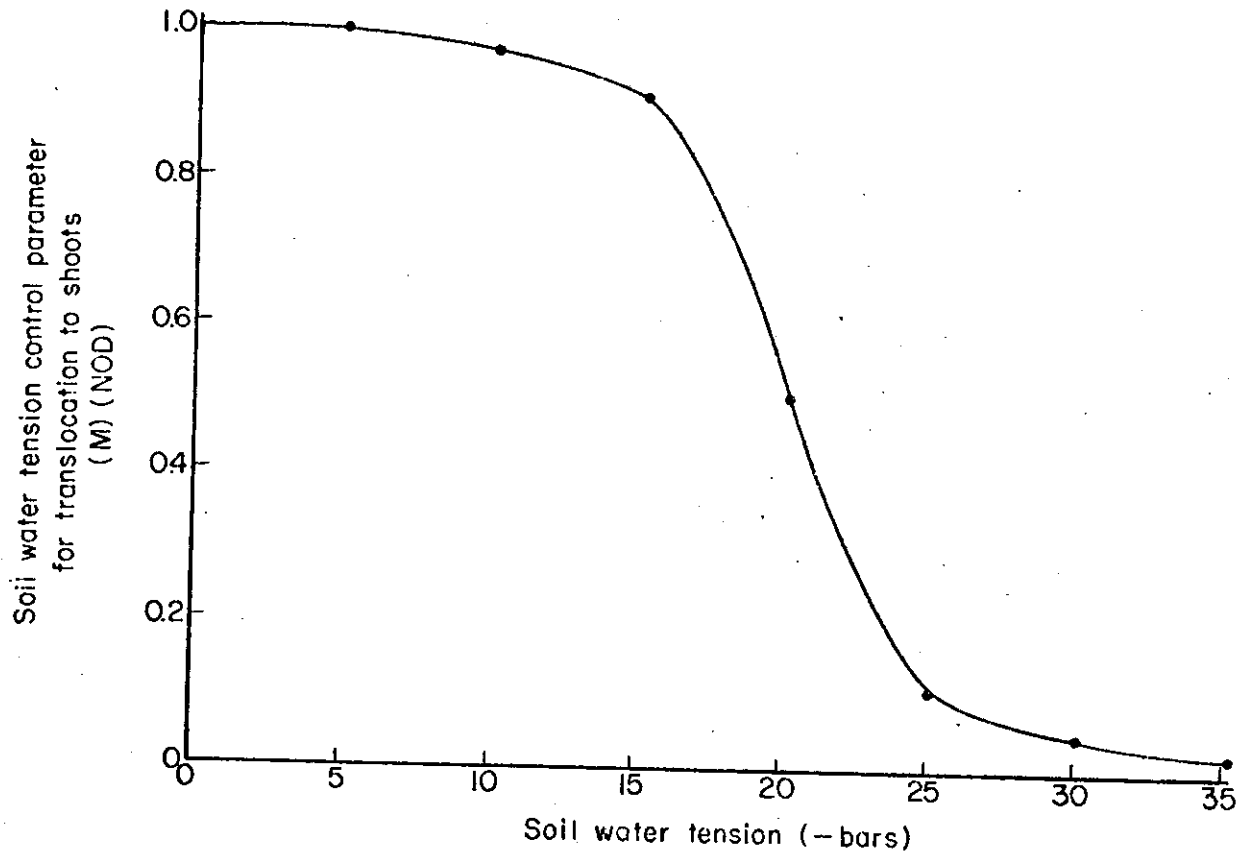


Fig. 10. Relationship between the soil water tension control parameter for translocation (M) to shoots and the soil water tension.

$$D_s = \begin{cases} (C_m e^{(-3 M_s)} + C_p) B_1 & \text{if } T_m \geq C_t \\ ((C_m e^{(-3 M_s)} + C_p) + 0.30) B_1 & \text{if } T_m < C_t \end{cases} \quad (11)$$

where  $C_p$  is the shoot turnover rate without soil water stress,  $C_m$  is the maximum shoot turnover rate produced by soil water stress,  $C_t$  is the minimum air temperature that will cause frost damage ( $C_t = -12^\circ\text{C}$  for Pawnee and  $-2^\circ\text{C}$  for Osage), and  $M_s$  is the water tension control parameter for shoot death.  $C_p$  and  $C_m$  are calculated as function of phenological stage of the plant (see Fig. 11a, b) while  $M_s$  is a function of the weighted average soil water tension (see Fig. 11c). The weighted average soil water tension is calculated using the transpiration water absorption coefficients (see Table 1) as weight factors).

Recent standing dead biomass is transferred to old standing dead at the beginning of the next simulation year. The transfer of both recent and old standing dead to litter ( $S_d^L$ ) are functions of the wind speed ( $W = \text{km} \cdot \text{hr}^{-1}$ ), daily rainfall ( $R_d = \text{cm} \cdot \text{day}^{-1}$ ), the long-term yearly average rainfall ( $R_y$ , Pawnee =  $30 \text{ cm} \cdot \text{yr}^{-1}$ , Osage =  $91 \text{ cm} \cdot \text{yr}^{-1}$ ), and the biomass of standing dead (see eqns (12) and (13)).

$$Q = 0.012 R_d \quad (12)$$

$$S_d^L = \begin{cases} (Q 30.5/R_y + 0.00013 W) B_s 0.67 C_d^L & \text{if } Q \leq 0.08 \\ (0.08 30.5/R_y + 0.00013 W) B_s 0.67 C_d^L & \text{if } Q \geq 0.08 \end{cases} \quad (13)$$

where  $Q$  is the fraction of standing dead biomass transferred to litter by daily rainfall ( $\text{day}^{-1}$ ),  $B_s$  is either the recent or old standing dead biomass, and  $C_d^L$  is average yearly turnover rate for the transfer of standing dead to litter ( $C_d^L = 0.7 \text{ yr}^{-1}$  at Osage,  $C_d^L = 1.5 \text{ yr}^{-1}$  at Pawnee).



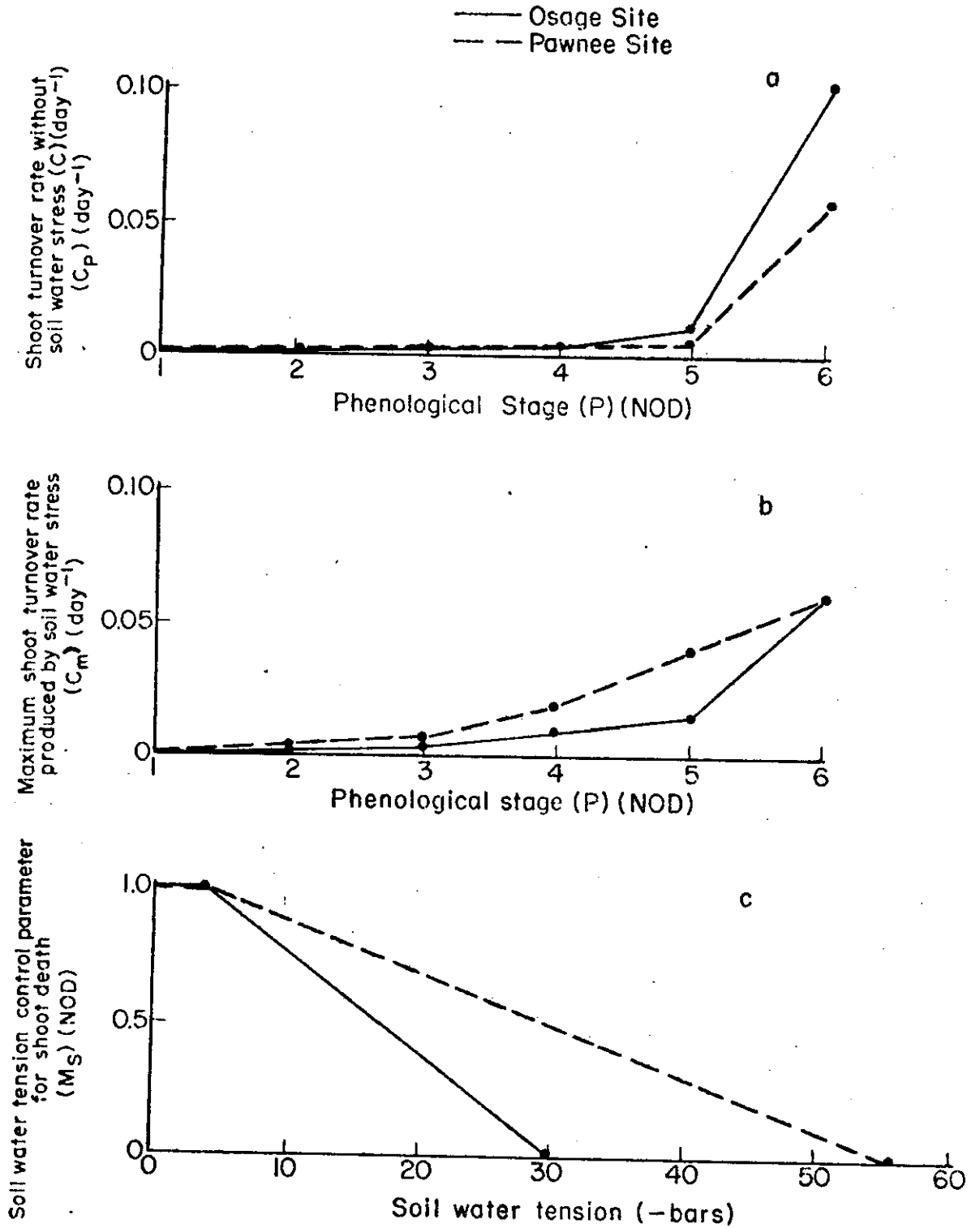


Fig. 11. The effect of phenological stage of the plant upon the shoot turnover rate without soil water stress (a), the maximum shoot turnover rate produced by soil water stress (b), and the effect of the weighted average soil water tension upon the soil water tension control parameter for shoot death (c).

### Leaching from standing dead

Leaching of soluble carbohydrate material from the standing dead biomass is calculated as a function of standing dead biomass ( $B_d$ ), the daily rainfall ( $R_d$ ), the long-term yearly average rainfall ( $R_y$ ), and the average yearly turnover rate for the transfer of standing dead to litter ( $C_d^L$ ) using the following equations:

$$Q_1 = R_d \cdot 0.36 / R_y \quad (14)$$

$$L_d = \begin{cases} Q_1 B_d \cdot 0.67 C_d^L & \text{if } Q_1 \leq 0.10 \\ 0.10 B_d \cdot 0.67 C_d^L & \text{if } Q_1 > 0.10 \end{cases} \quad (15)$$

where  $Q_1$  is the maximum possible fraction of standing dead leached by the rainfall and  $L_d$  is the leaching rate of recent or old standing dead ( $g \cdot m^{-2} \cdot day^{-1}$ ). Consideration of long-term yearly average rainfall was necessary to parameterize eqns (13), (14), (16), and (17) so that they could be used for both the sites. Leaching of litter biomass is calculated as a function of the litter biomass ( $L_b$ ),  $R_y$ , and the daily rainfall using eqn (16).

$$L_1 = R_d \cdot 0.048 L_b / R_y \quad (16)$$

where  $L_1$  is the leaching rate of litter biomass ( $g \cdot m^{-2} \cdot day^{-1}$ ). This model assumes that carbohydrates leached from the litter and standing dead is decomposed rapidly and returned to the atmosphere as  $CO_2$  within a day.

### Mixing of litter

The mechanical mixing of litter into the top soil layer ( $M_g = g \cdot m^{-2} \cdot day^{-1}$ ) is calculated as a function of the daily rainfall ( $R_d$ ), the long-term yearly average rainfall ( $R_y$ ), and the litter biomass (see eqn (17)).

$$M_g = R_d \cdot 0.048 L_b / R_y \quad (17)$$

This mechanical mixing transfers litter into the top soil layer. The respiration of crowns and decomposition of litter are included in the belowground section of the model.

*Belowground system*

Figure 2 shows all of the flows and state variables considered in the belowground section of the model. The six belowground state variables are calculated for each of the six soil layers. The biological processes illustrated by the flow diagram include respiration and death of the live suberized, nonsuberized, and juvenile roots, aging of the juvenile and nonsuberized live roots, juvenile root growth in the spring, translocation of carbohydrates from the live shoots to the live roots, and decomposition of the dead juvenile, suberized, and nonsuberized roots and litter.

Root and crown respiration

Respiration of the live juvenile, nonsuberized, and suberized roots are calculated as a function of the soil temperature and soil water tension using the following equations:

$$M_r = \begin{cases} (80 - S_w)/80 & \text{if } S_i \leq 76 \\ 0.05 & \text{if } S_i > 76 \end{cases} \quad (18)$$

$$T_r = 0.07(1.4)^{0.2T_i} \quad (19)$$

$$R_s = M_r T_r R_j R_{ij} \quad (20)$$

where  $M_r$  is the soil water tension control parameter for respiration,  $S_w$  is the soil water tension in the appropriate soil layer (-bars),  $S_i$  is the soil water tension in the  $i^{\text{th}}$  layer,  $T_i$  is the average daily soil

temperature in the appropriate soil layer ( $^{\circ}\text{C}$ ),  $R_j$  is the fraction of root biomass of the  $j^{\text{th}}$  type that is respired per day at  $40^{\circ}\text{C}$  with zero soil water tension ( $j = 1$  for juvenile root,  $j = 2$  for nonsuberized root,  $j = 3$  for suberized root,  $R_1 = 0.014$ ,  $R_2 = 0.009$ ,  $R_3 = 0.008$ ),  $R_{ij}$  is the biomass of live roots in  $j^{\text{th}}$  root type and the  $i^{\text{th}}$  layer,  $T_r$  is the temperature control parameter for respiration (NOD), and  $R_s$  is the respiration rate ( $\text{g} \cdot \text{m}^{-2} \cdot \text{day}^{-1}$ ) of  $j^{\text{th}}$  root type in the  $i^{\text{th}}$  layer. The above formulation makes the rate of root respiration dependent upon temperature, soil water, and tissue age. Unfortunately there is not much experimental information available on the respiratory rate of intact root systems. However, measurements of soil respiration (root + microbial respiration) at different temperatures have often yielded a  $Q_{10}$  of about 2 between  $10^{\circ}$  and  $20^{\circ}\text{C}$ ,  $10^{\circ}$  and  $40^{\circ}\text{C}$ , and  $20^{\circ}$  and  $40^{\circ}\text{C}$  (Lundegårdh 1927; Koepf 1953; Wiant 1967a); at higher temperatures the value declines. Harris & van Bavel (1957) measured respiration of intact root systems of tobacco, corn, and cotton plants at different times in the day and reported peak rates at about 4 pm when the air temperature was maximum. Available information indicates a sharp decrease in soil respiration at low soil water regimes (Wiant 1967b). Coleman (1973) reported pronounced increase in soil respiration of a grassland during August and attributed this increase to an increase in soil temperature or soil water content. In the shortgrass prairie at Pawnee, Clark & Coleman (1972) recorded a several-fold increase in  $\text{CO}_2$  output by intact soil-root cores following precipitation in September. Crapo & Coleman (1972) reported a pronounced increase in respiration rates for grass roots rinsed in water. Indirectly a very high level of soil water may adversely influence root respiration by diminishing soil aeration. That the root respiration is sensitive to oxygen concentration

has been demonstrated by Berry & Norris (1949). The younger roots are known to respire at a higher rate than older roots (Yemm 1965; Stoklasa & Ernest 1905). Osmon's (1971) data on juvenile wheat roots respiration are several-fold higher than those reported for mature communities (Newton 1924; Monteith & Yabuki 1965) and show a positive response to temperature.

The respiration rate of crowns is calculated by using eqns (18), (19), and (20) and replacing  $R_{ij}$  with the crown biomass,  $T_i$  with soil temperature at 0 cm, and  $S_i$  with the average soil water tension in the top 15 cm and by assuming that crowns respire at the same rate as nonsuberized roots ( $R_j = 0.009$ ).

#### Root and crown death

The death of live juvenile, nonsuberized, and suberized roots in each soil layer is calculated as a function of the soil water tension and soil temperature in the soil layer and the biomass of live roots using eqn (21).

$$D_{ij}^L = (\max(M_d, T_d)) R_{ij} D_j \quad (21)$$

where  $D_{ij}^L$  is death rate ( $g \cdot m^{-2} \cdot day^{-1}$ ) of live roots of the  $j^{th}$  root type that are in the  $i^{th}$  soil layer,  $M_d$  is water tension control parameter for root death,  $T_d$  is the temperature control parameter for root death,  $\max(T_d, M_d)$  is maximum value of  $M_d$  and  $T_d$ , and  $D_j$  is maximum fraction of live roots in the  $j^{th}$  category that will die per day ( $D_1 = 0.03$ ,  $D_2 = 0.0027$ ,  $D_3 = 0.0025$ ). Figure 12 shows the functional relationship of the water tension control parameter ( $M_d$ ) to soil water tension, and the relation of temperature control parameter ( $T_d$ ) to the soil temperature. Information on root mortality in grasslands is wanting. Recently Ares (1976) followed the pattern of root growth and

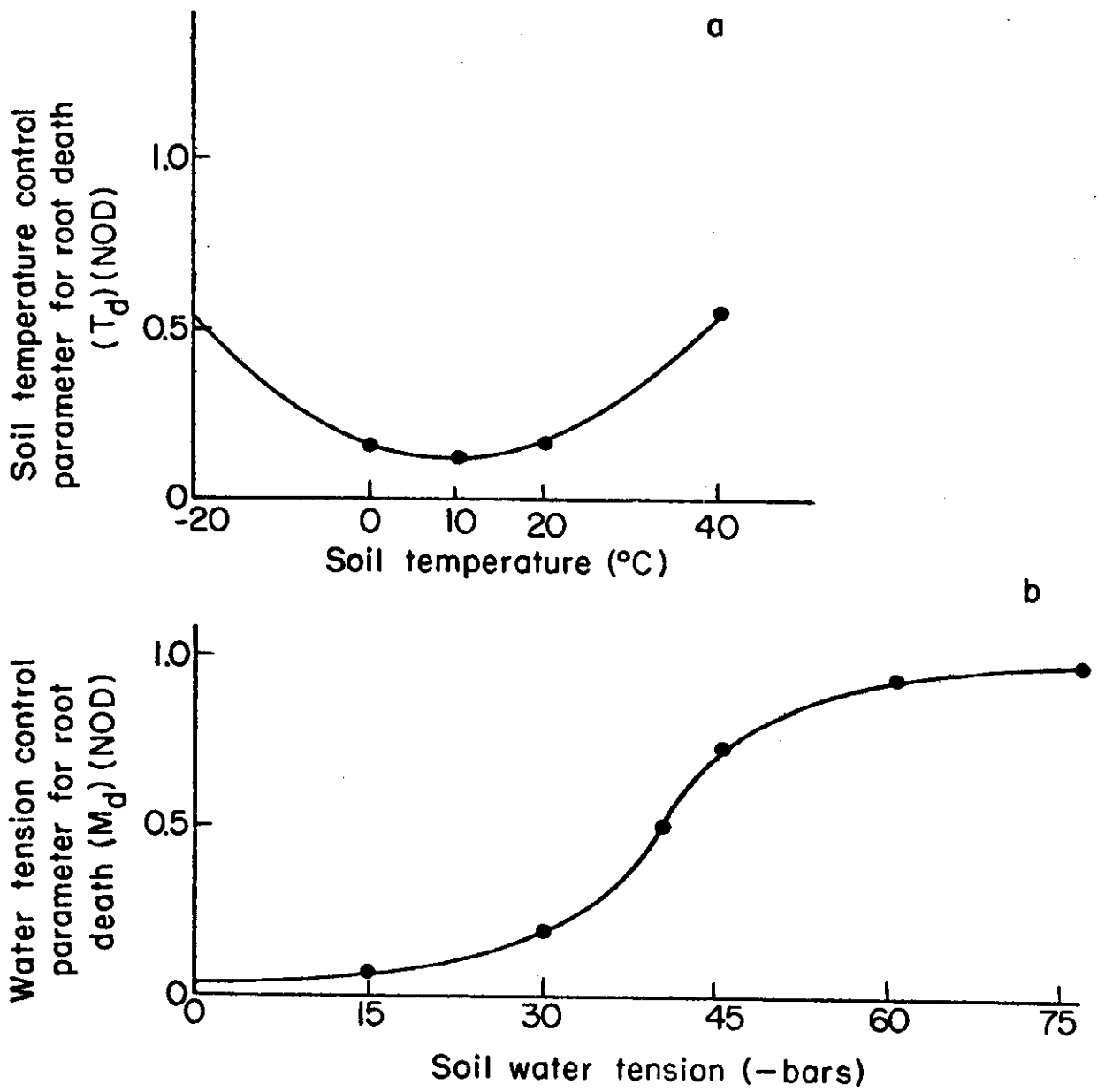


Fig. 12. Effect of soil temperature on the soil temperature control parameter for root death (a), and the effect of soil water tension on the water tension control parameter for root death (b).

death through root-observation windows at Pawnee Site and recorded greatest rate of mortality for juvenile roots and lower rates for the other two categories with death rates being related with the soil water tension and temperature. The model assumes that the suberized and nonsuberized roots in the deeper layers connected to dead suberized and nonsuberized roots in the top layers also die. Eqn (22), (23), and (24) show the functional relationships used to calculate this additional death of suberized, and nonsuberized roots in the deeper soil layers.

$$Q_j = \frac{\sum_{i=3}^6 R_{ij}}{\sum_{i=1}^6 R_{ij}} \quad (22)$$

$$D_j^T = (D_{1j} + D_{2j})Q_j \quad (23)$$

$$E_{ij} = D_j^T \left( R_{ij} / \sum_{i=3}^6 R_{ij} \right) \quad (24)$$

where  $j = 2, 3$  and  $i = 3, 4, 5,$  and  $6^{\text{th}}$  soil layer,  $Q_j$  is the ratio of the biomass of live roots of the  $j^{\text{th}}$  type in the bottom four layers to the total biomass of roots of the  $j^{\text{th}}$  type,  $D_j^T$  is the total additional death rate ( $g \cdot m^{-2} \cdot day^{-1}$ ) of live roots of the  $j^{\text{th}}$  type in the bottom four layers, and  $E_{ij}$  is additional death rate of live roots of the  $j^{\text{th}}$  type in the  $i^{\text{th}}$  soil layer.

The death rate of crowns is calculated as a function of the crown biomass and the average soil temperature and soil water tension in the top 15 cm of soil by using eqn (21) with  $R_{ij}$  being replaced by the crown biomass.

#### Aging of roots

The aging of juvenile roots (transfer to nonsuberized roots) is calculated as a function of the biomass of juvenile roots (see eqn (25)).

$$J_i^A = J_a R_{i1} \quad (25)$$

where  $J_i^A$  is the rate of transfer from juvenile roots to nonsuberized roots in the  $i^{\text{th}}$  soil layer,  $J_a$  is turnover rate of juvenile roots to suberized roots ( $J_a = 0.02 \text{ day}^{-1}$ ), and  $R_{i1}$  is the biomass of live juvenile roots.

The aging of nonsuberized roots (transfer to suberized roots) is determined as a function of the phenological stage of the plant and the biomass of nonsuberized roots using eqn (26).

$$N_i^A = N_a P_N R_{i2} \quad (26)$$

where  $N_i^A$  is the rate of transfer from nonsuberized roots to suberized roots in the  $i^{\text{th}}$  soil layer,  $N_a$  is the maximum turnover rate of non-suberized roots to suberized roots ( $N_a = 0.002 \text{ day}^{-1}$ ),  $P_a$  is a phenology control parameter for the aging of nonsuberized roots (NOD), and  $R_{i2}$  is the biomass of live nonsuberized roots. The effect of phenological stage upon  $P_a$  is shown in Fig. 13, while the functional relationship and constants used in eqns (25) and (26) are based upon data presented by Ares & Singh (1974).

#### Remobilization of reserve for initiation of juvenile roots

The transfer of stored carbohydrate from the suberized roots to the juvenile roots occurs in the spring for the initiation of juvenile root growth in the top two soil layers (Ares 1976, Singh & Coleman, ms. to be published). This flow from suberized roots is calculated as a function of the biomass of suberized roots, ratio of the shoot biomass to the sum of crown and live root biomass, and the soil water tension by using the functional relationship shown in eqns (9) and (10) and multiplying the



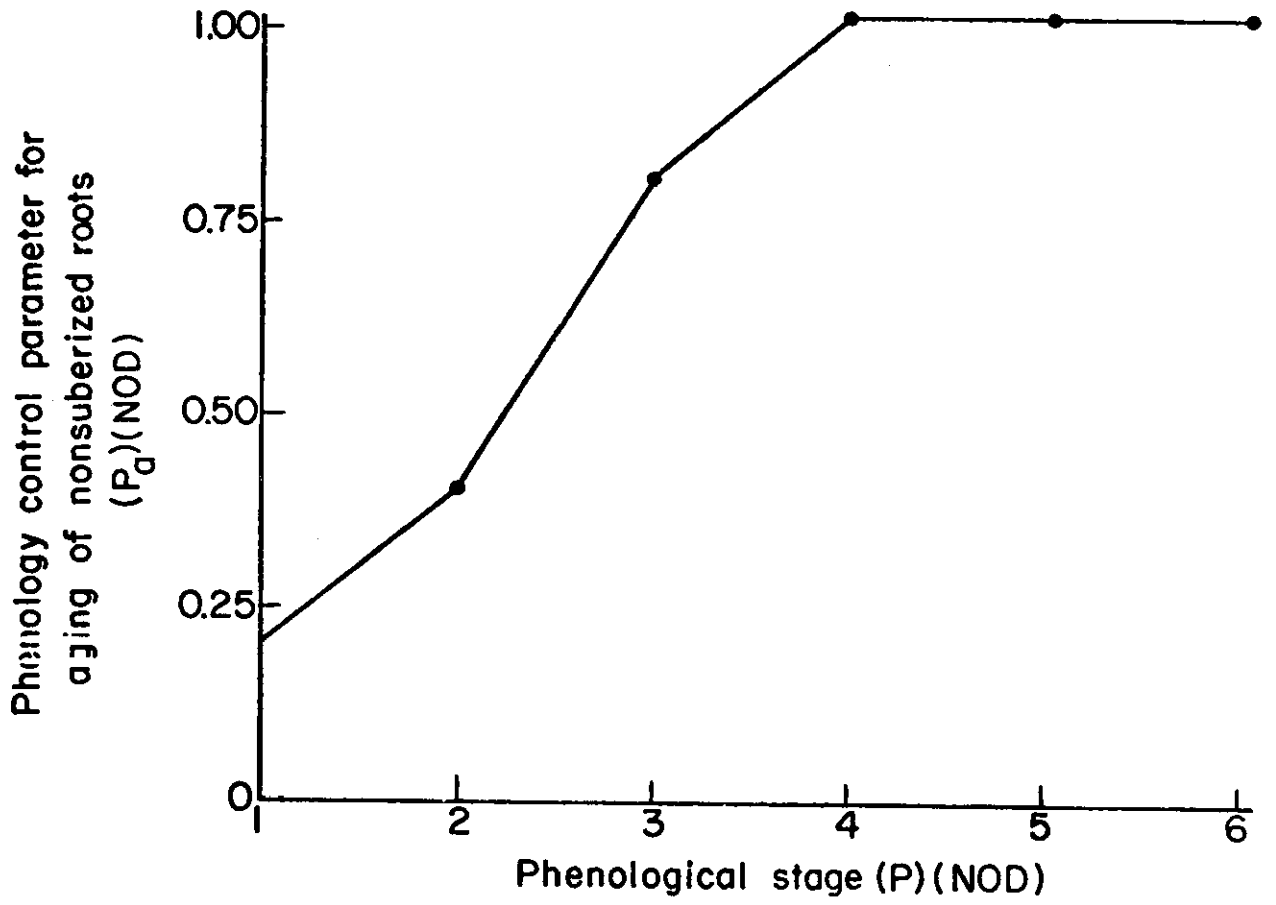


Fig. 13. The effect of phenological stage of the plant upon the phenology control parameter for aging of nonsuberized roots.

right side of eqn (10) by 5, and by dropping the ratio of  $S_r$  to  $S_1$  from the equation.

#### Translocation to roots

The total amount of photosynthate translocated to the roots ( $T_b = g \cdot m^{-2} \cdot day^{-1}$ ) is calculated in eqn (8), while the allocation of photosynthate to live juvenile, nonsuberized, and suberized roots in the  $i^{th}$  soil layer is calculated as a function of soil water tension by using the following set of equations.

$$A_i^T = M_i^1 W_i^A / \sum_{i=1}^6 M_i^1 W_i^A \quad (27)$$

$$A_{ij} = \begin{cases} M_i^2 & \text{if } j = 1 \\ (1 - M_i^2)0.87 & \text{if } j = 2 \\ (1 - M_i^2)0.13 & \text{if } j = 3 \end{cases} \quad (28)$$

$$T_{ij} = T_B A_i^T A_{ij} \quad (29)$$

where  $A_i^T$  is the fraction of total photosynthate sent to  $i^{th}$  soil layer,  $A_{ij}$  is the fraction of the photosynthate sent to the  $i^{th}$  layer that is allocated to the  $j^{th}$  root type ( $j = 1$ , juvenile roots;  $j = 2$ , nonsuberized roots; and  $j = 3$ , suberized roots),  $T_{ij}$  is the rate of transfer of photosynthate to the live roots of  $j^{th}$  type in the  $i^{th}$  soil layer ( $g \cdot m^{-2} \cdot day^{-1}$ ),  $M_i^1$  is soil water control parameter for the allocation of photosynthate to the  $i^{th}$  layer,  $W_i^A$  is the constant weight factor for the allocation of photosynthate to the  $i^{th}$  layer ( $W_i^A$ , NOD,  $W_i^A = 0.31, 0.43, 0.15, 0.06, 0.03, 0.02$  - Pawnee,  $W_i^A = 0.31, 0.22, 0.10, 0.14, 0.11, 0.12$  - Osage Site), and  $M_i^2$  is the fraction of photosynthate in the  $i^{th}$  layer allocated to the juvenile root type. This set of equations is based on the following assumptions: (1) the allocation of photosynthate

to the roots will decrease with soil depth (Singh & Coleman 1974), (2) relatively higher soil water content in a particular layer will cause more photosynthate to be allocated to that layer (Warembourg & Paul 1973), and (3) high soil water content will cause more of the photosynthate allocated to a layer to be sent to the juvenile roots (Ares 1974). The functional relationship of the soil water control parameter for the allocation of photosynthate ( $M_i^1$ ) and the fraction of photosynthate allocated to the juvenile roots ( $M_i^2$ ) to the soil water tension in the  $i^{\text{th}}$  layer is shown in Fig. 14. The value for  $W_i^A$  and eqns (27)-(29) are partially based on an analysis of the information presented by Ares & Singh (1974).

#### Root and litter decomposition

The root decomposition process is influenced by root mass, soil temperature, soil water, and root age (Klein & Clark 1973). Nyhan (1972) investigated the effect of soil water and temperature on the decomposition of  $^{14}\text{C}$  labeled blue grama material under laboratory conditions and was able to account for 85% of the variability in decomposition rate with temperature and water. Temperature as it regulates microbial respiration would seem to be an index of decomposition rate in moist soil. Decomposers are more active under moist conditions (Pilat 1969), and young roots decompose more rapidly than older roots (Klein & Clark 1973) presumably because they contain a lower proportion of resistant lignin and cellulose. Based on these studies the decomposition of dead root biomass is calculated as a function of soil water tension, soil temperature, and the biomass of dead roots by the following equation:

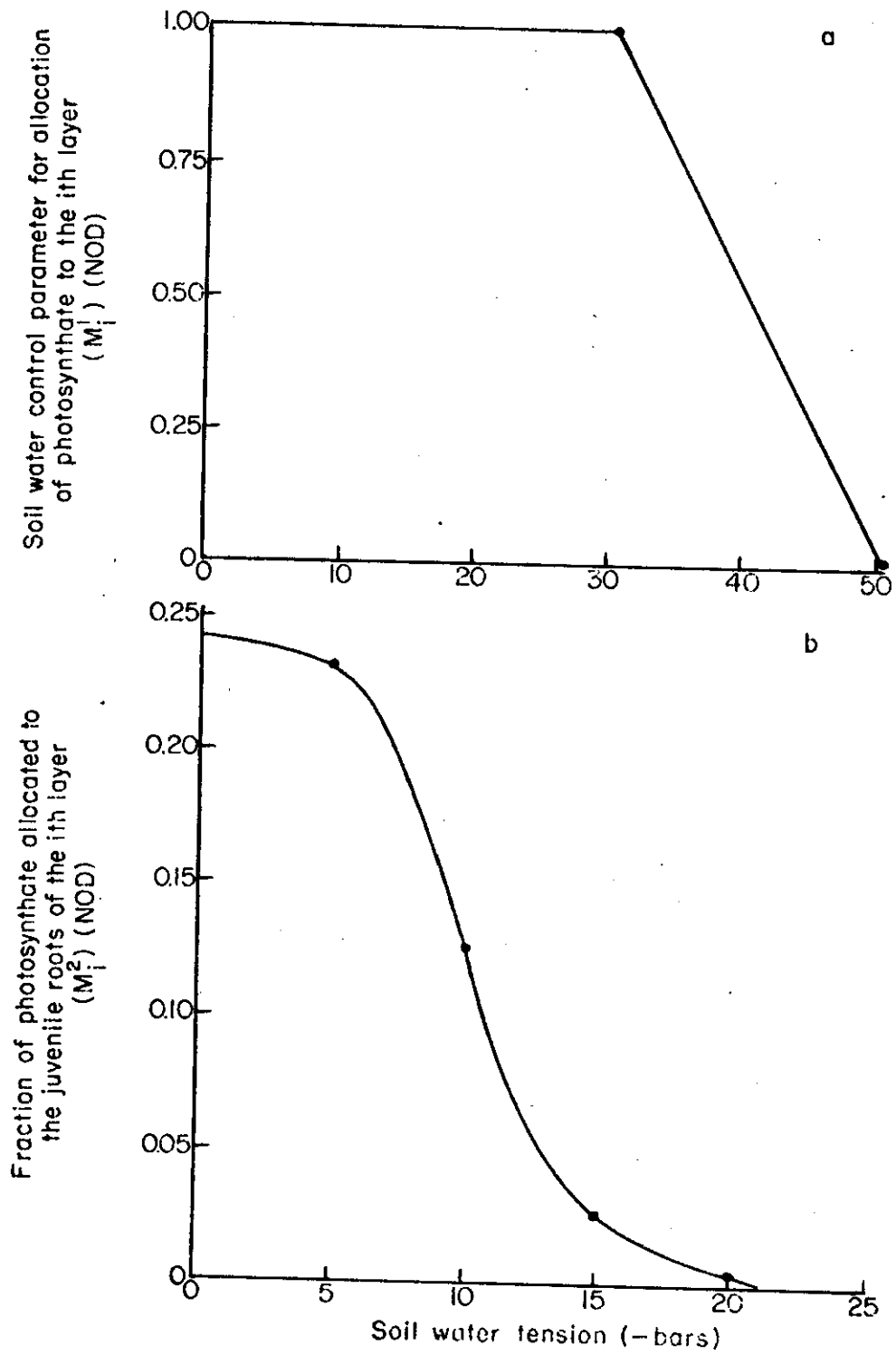


Fig. 14. Relationships of soil water control parameter for the allocation of photosynthate to the *i*th layer (a) and the fraction of photosynthate sent to juvenile roots (b) to the soil water tension of the *i*th layer.

$$R_{ij}^D = D_j (\min (M_i^D, T_i^D)) D_{ij} D_i^D \quad (30)$$

where  $R_{ij}^D$  is decomposition rate ( $g \cdot m^{-2} \cdot day^{-1}$ ) of dead roots of the  $j^{th}$  type in the  $i^{th}$  layer,  $D_j$  is the maximum turnover rate for dead roots of the  $j^{th}$  type ( $D_j = 0.5$  (juvenile),  $0.25$  (nonsuberized),  $0.06$  (suberized)  $day^{-1}$  Pawnee;  $D_j = 0.36$  (juvenile),  $0.05$  (nonsuberized),  $0.025$  (suberized)  $day^{-1}$  Osage).  $\min(M_i^D, T_i^D)$  is the minimum value of  $M_i^D$  and  $T_i^D$ ;  $M_i^D$  is soil water control parameter for decomposition in the  $i^{th}$  layer,  $T_i^D$  is temperature control parameter for decomposition in the  $i^{th}$  layer,  $D_{ij}$  is biomass of dead roots of the  $j^{th}$  type in the  $i^{th}$  layer, and  $D_i^D$  is the depth control parameter for decomposition in the  $i^{th}$  layer ( $D_i^D$  (NOD) = 1., 0.2, 0.1, 0.05, 0.02, 0.02 for the six layers - Pawnee;  $D_i^D = 1.0, 0.2, 0.15, 0.10, 0.06, 0.06$  - Osage). The functional relations of the soil water control parameter to soil water tension and of the temperature control parameter to soil temperature (Hunt 1976) are shown in Fig. 15.

The value for the maximum turnover rate of dead roots ( $D_j$ ) is based upon information presented by Ares & Singh (1974), and the value of depth control parameter for decomposition ( $D_i^D$ ) is based upon the assumption that the intrinsic decomposition rate of root biomass will decrease with depth. This seems to be a valid assumption as most of the microbial biomass and activity as well as substrate are limited to comparatively shallow depths.

The decomposition of litter biomass is calculated as a function of the litter biomass, the soil water tension in the top soil layer, and the soil temperature at 0 cm by using eqn (30), and assuming that decomposition rate of litter is equivalent to one half, the decomposition rate of nonsuberized dead roots in the top soil layer.

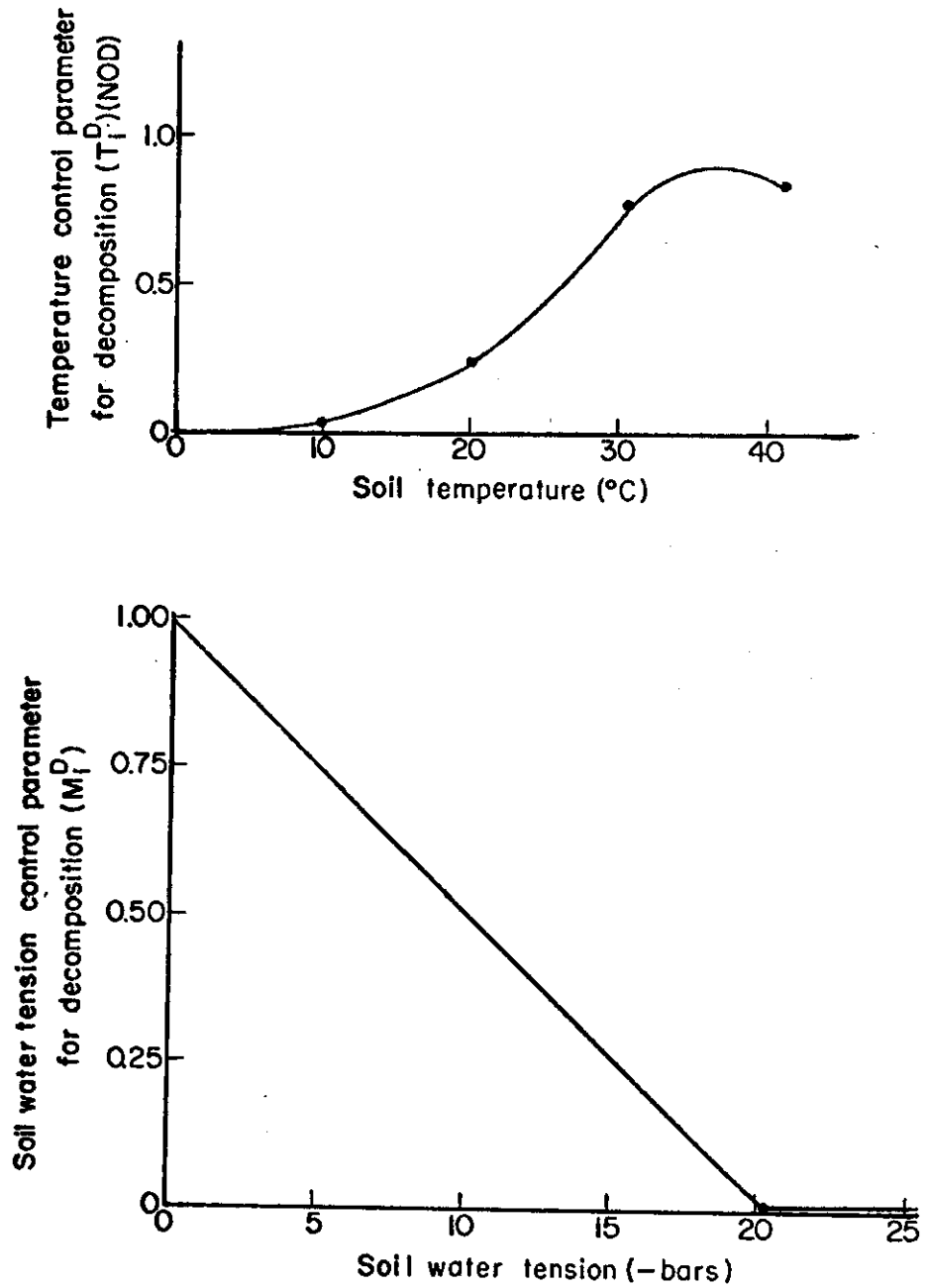


Fig. 15. The effect of soil temperature on the temperature control parameter for decomposition (a) and the effect of water tension on the soil water tension control parameter for decomposition (b).

*Phenology submodel*

The phenology submodel simulates the phenological stage of a warm season grass through the current growing season. The six phenological stages defined in this model include:

- (1) early vegetative growth
- (2) middle vegetative growth
- (3) full vegetative growth
- (4) reproductive growth
- (5) fall regrowth
- (6) senescence

The observable phenomena at the beginning of each of these stages is, respectively (1) first visible growth, (2) middle leaves fully visible, (3) middle leaves fully expanded, (4) developing floral buds, (5) ripe fruit, and (6) plant dormancy. The phenological progression of a plant through these stages is calculated as function of the cumulative sum of the product of the temperature control parameter for photosynthesis ( $T_p$ , NOD) times the soil water control parameter for phenological progression ( $P_m^H$ , NOD) through the growing season (eqns (31) and (32)):

$$P_m^H = \begin{cases} P_m^1 & \text{if } P < 3 \\ P_m^2 & \text{if } P \geq 3 \end{cases} \quad (31)$$

$$C_t^P = C_{t-\Delta t}^P + T_p P_m^H \quad (32)$$

where  $C_t^P$  and  $C_{t-\Delta t}^P$  are respectively the cumulative sum of the product of  $T_p \cdot P_m^H$  at time  $t$  and  $t-\Delta t$  ( $\Delta t = 24$  hours) during the growing season ( $C_t^P$ ,  $C_{t-\Delta t}^P$ , NOD), while  $P_m^1$  and  $P_m^2$  are the soil water control parameters for phenological progression during, respectively, phenology stages less than three (vegetative growth) and greater than or equal to three (full

vegetative and reproduction growth). The soil water control parameters for phenological progression ( $P_m^1, P_m^2$ ) are calculated as functions of the weighted average soil water tension using the functional relationship shown in Fig. 16, while the effect of canopy air temperature and the weighted average soil water tension upon the temperature control parameter for photosynthesis ( $T_p$ ) is shown in Fig. 17. The influence of soil water tension on phenological progression is based upon concepts presented by Sauer (1976), while Fig. 17 is based on data presented by Brown (1974). The use of the temperature control parameter for photosynthesis as a partial control for phenological progression is based on the concept that the phenological stages of plants follow cumulative heat sums through the growing season (Lindsey & Newman 1956; Jackson 1966). The phenological stage of the plant ( $P$ ) is a function of  $C_t^P$ , the shortwave solar radiation ( $S_s$ ) and the 5-day moving average of minimum air temperature at 2 m ( $T_m^5$ ) as shown in the following equation.

$$P = \begin{cases} i + (P_{i+1}^C - C_t^P) / (P_{i+1}^C - P_i^C) & \text{if } P_{i+1}^C > C_t^P \geq P_i^C \\ & \text{for } i = 1, 2, 3, 4 \\ 5 + (S_5^P - S_s) / (S_5^P - S_s^6) & \text{if } C_t^P \geq P_5^C \text{ and } S_s \geq S_s^6 \\ 6 & \text{if } S_s < S_s^6 \text{ and } C_t^P > P_5^C \\ 6 & \text{if } T_m^5 < T_m^C \end{cases} \quad (33)$$

where  $P_i^C$  is the value of the cumulative sum of  $C_t^P$  at the beginning of the  $i^{\text{th}}$  phenological stage,  $S_5^P$  is the value of  $S_s$  during the first day that  $C_t^P$  is greater than or equal to the value of  $P_5^C$ ,  $S_s^6$  is the value of  $S_s$  when plant dormancy starts, and  $T_m^C$  is the air temperature when live shoots will freeze. This equation is based on the assumption that the



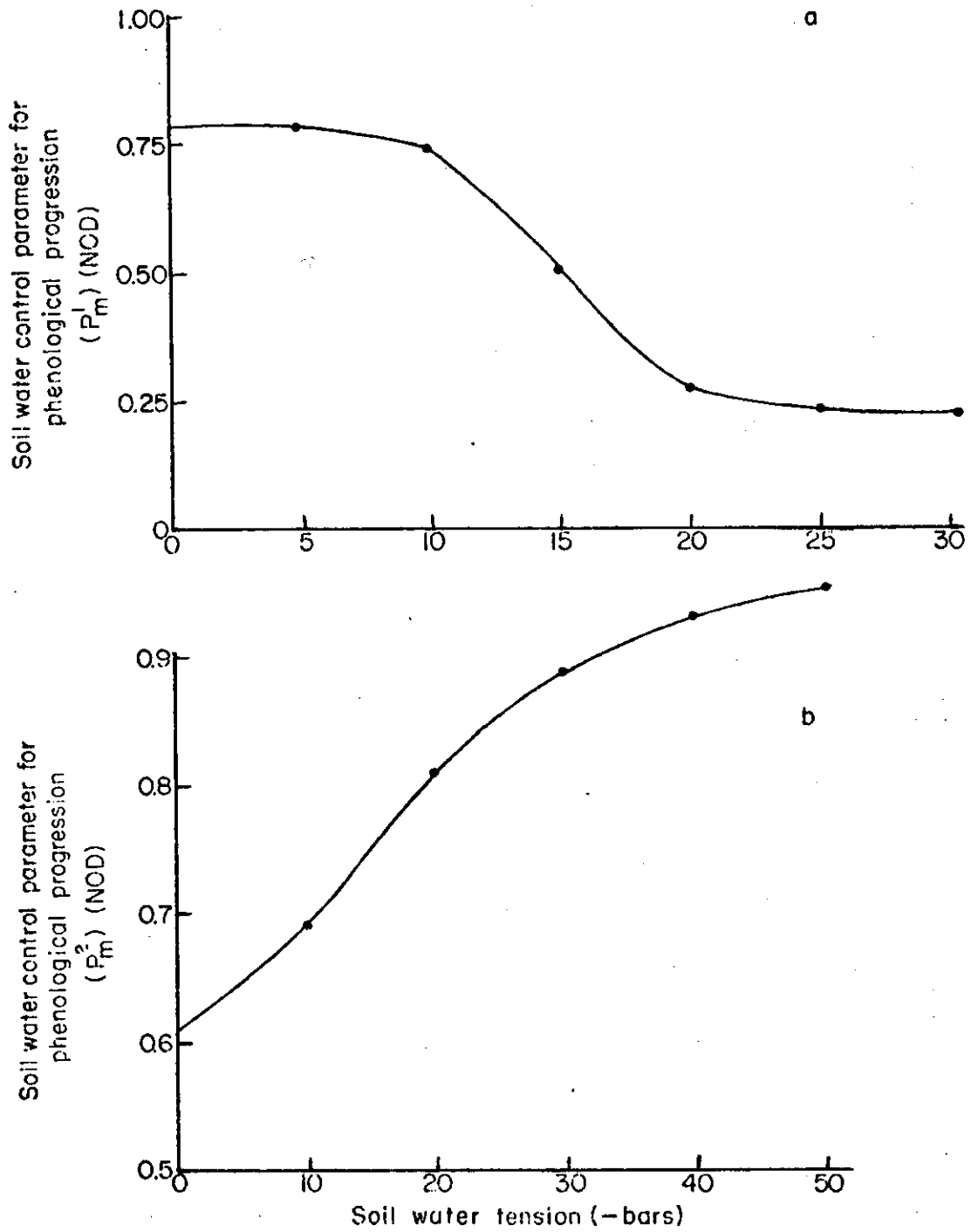


Fig. 16. The effect of the weighted soil water tension on the soil water control parameter for phenological progress where the phenological stage is less than 3 ( $P_m^1$ , (a)) and greater than or equal to 3 ( $P_m^2$ , (b)).

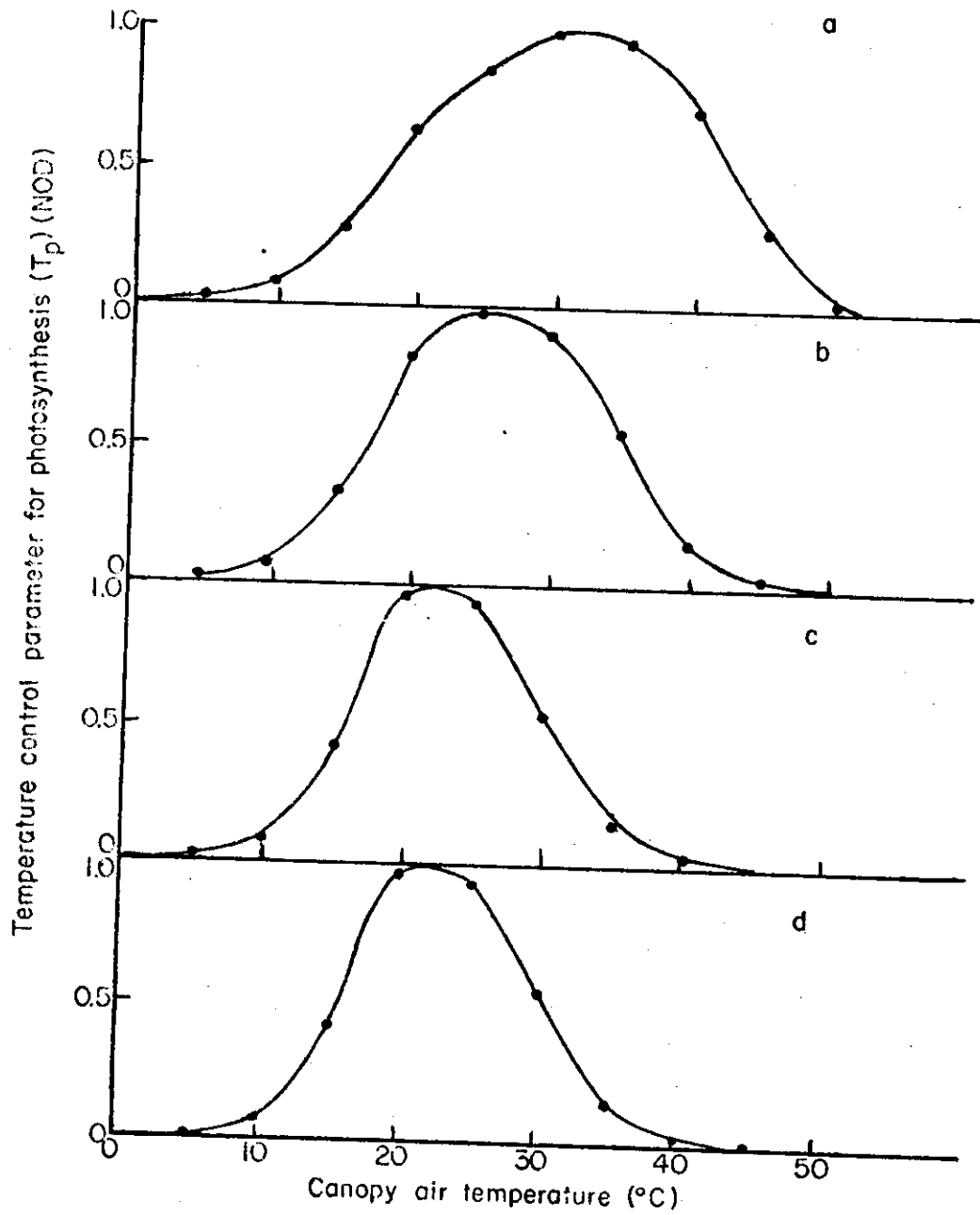


Fig. 17. The effect of weighted average soil water tension (a) -0, (b) -15, (c) -30, and (d) -45 bars and the average daytime canopy temperature upon the temperature control parameter for photosynthesis.

advance of phenology is a function of  $C_t^P$  for phenology stage less than five and that the senescence of the plant occurs at a specified date (when  $S_s < S_s^6$ ) or when plant death is caused by freezing. The value of  $P_i^C$  for the Osage and Pawnee Sites is specified in Table 2,  $S_s^6$  is equal to  $300 \text{ langley} \cdot \text{day}^{-1}$  for both Osage and Pawnee Sites, and  $T_m^C$  is equal to  $0^\circ\text{C}$  and  $-6^\circ\text{C}$  for the Osage and Pawnee Sites, respectively.

Initiation of plant growth at the beginning of the growing season ( $C_t^P = 0.0$ ,  $P = 1.0$ ) is started if the following conditions are satisfactory:

- (1) the phenological stage equals six at time  $t - 24$  hours,
- (2) the 7-day average value of the combined water tension and air temperature control parameter for photosynthesis is greater than 0.40 at Pawnee and 0.50 at Osage, and
- (3) the 14-day average soil temperature in the top 15 cm is  $\geq 4^\circ\text{C}$  at Pawnee and  $\geq 10^\circ\text{C}$  at Osage. The above set of conditions were determined by an analysis of observed data at the Pawnee and Osage Sites.

## RESULTS AND DISCUSSION

Of any modeling exercise, the completed model itself is the result. However, in this section some model outputs for a 3-year run (1970-1972) are provided to show the general dynamics of selected state variables in the two grassland systems. Also, estimates of certain functional properties of the systems resulting from the simulation are provided. Differences in these properties in the two systems as viewed through simulation model will be emphasized.

### *Shortgrass prairie at Pawnee*

The standing crop of aboveground live shoots increases sharply at the advent of the growing season (20 April, 15 April, and 25 March,

Table 2. The values of  $C_t^P$  at the beginning of the  $i^{th}$  phenology stage for both the Pawnee and Osage Sites

Site	Phenological stage				
	1	2	3	4	5
Osage	0.0	7.0	16	50	85
Pawnee	0.0	7.0	16	40	68

respectively, in 1970, 1971, and 1972) to a peak within about 90 days and then declines gradually as live material is transferred into new dead compartment (Fig. 18). Consequently there is a time-lag in the peak of recent dead material, although transfer from live to dead continues to occur throughout the growing season. The 1971 simulation indicated two adjacent peaks in the recent dead compartment; the trough between the two coincided with a shoulder in the live biomass curve occurring late in the season in response to late rainfall (6 cm between 28 August and 4 October). The crown biomass shows an initial decline at the beginning of the growing season, then after a considerable amount of live shoots have been generated, a sharp rise, the peak coinciding with the peak of live shoots. Later there is a gradual decline in the biomass indicating greater respiratory loss as compared to input of photosynthate through translocation. The model thus depicts an early replenishment of crowns as reported by Singh & Coleman (ms. to be published) who observed a greater storage of photoassimilated carbon-14 in crowns early in the season. The year 1972 was comparatively wet (measured precipitation at Pawnee during 1972 growing season was 324 mm as compared with 149 mm in 1970 and 222 mm in 1971), and as a result a greater amount of live biomass was present for a longer period of time. The curve for live biomass shows a distinct shoulder soon after the peak value in response to the rainfall event. This second shoulder resulted in a second peak in crown biomass because of sustained photosynthate translocation into crowns.

The growth of the three age-classes of roots follows a characteristic lag pattern. The peak in juvenile roots is followed by that of the nonsuberized roots which in turn is followed by that of the suberized roots (Fig. 18). The peak in juvenile roots precedes the peak of

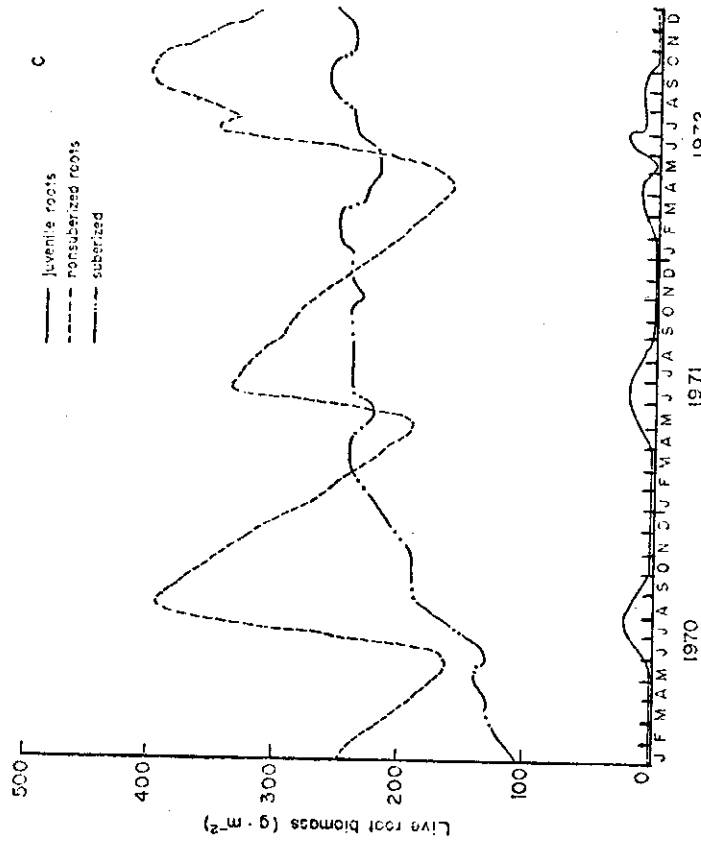
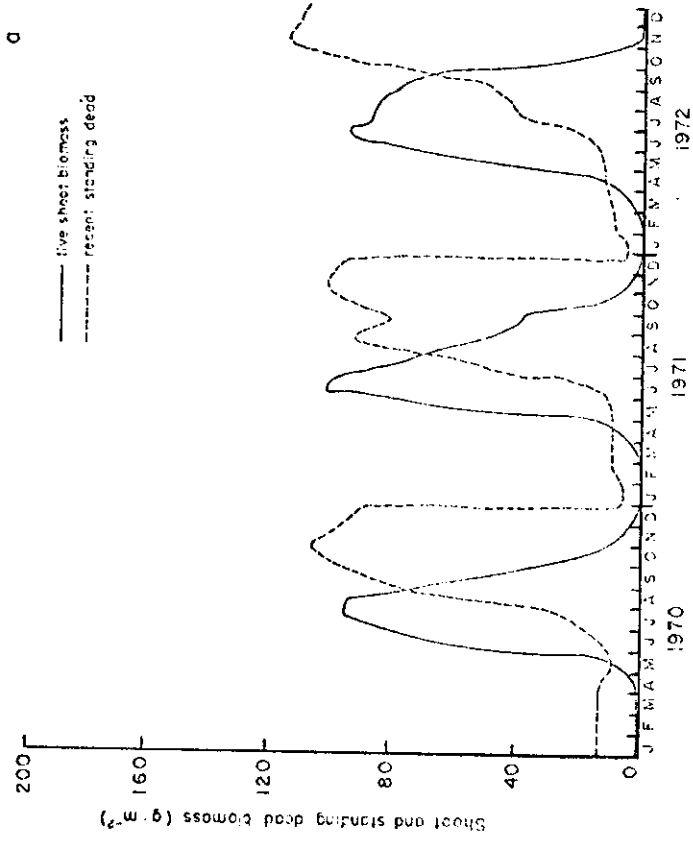
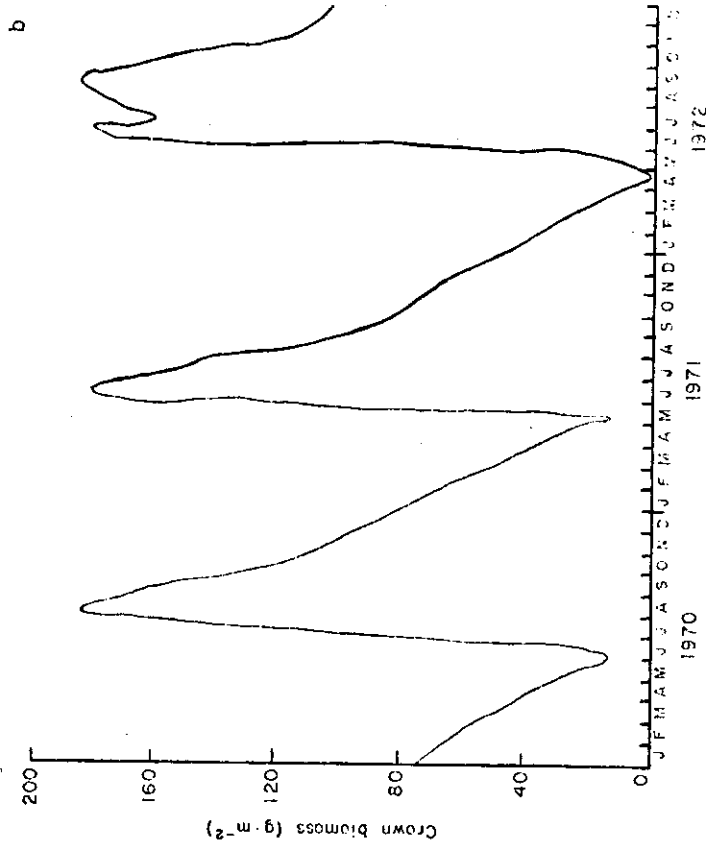


Fig. 18. Three-year simulated time series at the Pawnee Site of (a) recent dead and live shoot biomass, (b) recent dead and live crown biomass, and (c) recent dead and live biomass and total live biomass of juvenile suberized and nonsuberized roots.

aboveground live biomass (some early production of juvenile roots is due to a transfer from nonsuberized roots, see Ares & Singh 1974) and the peaks in the other two categories of roots follow that of aboveground live biomass. This pattern is consistent with the observations of Ares (1976) on Pawnee grassland. As stated earlier the growing season rainfall in the 3 years followed the order, 1970 < 1971 < 1972. This continuous improvement in the rainfall resulted in some net accumulation of live roots over the 3 years.

The standing crop of the old dead compartment continues to decline throughout the growing season as a result of transfer of material into the litter compartment and leaching (Fig. 19). This compartment is replenished each year as current dead is transferred in bulk into it at the beginning of the next year. The transfer from the old dead compartment is reflected by an increase in litter standing crop, but later in the season when most of the old dead has been transferred into this compartment, decomposition and leaching more than compensate for input resulting in a decrease in the standing crop of litter. There was considerably greater loss in litter compartment during the comparatively moist 1972 growing season.

The younger roots (juvenile and nonsuberized) show more intra-seasonal dynamics than the older suberized roots in response to favorable rainfall pulses within a growing season (Fig. 20-22). Ares (1976) observed a fast response of growth and mortality of young roots to fluctuations in the soil water potential under field conditions. There is relatively greater biomass of live roots in the 4 to 30 cm depth stratum where soil water conditions remain comparatively favorable throughout the growing season; also the shallow depths show more intra-seasonal dynamics than the deeper layers. There is a continuous

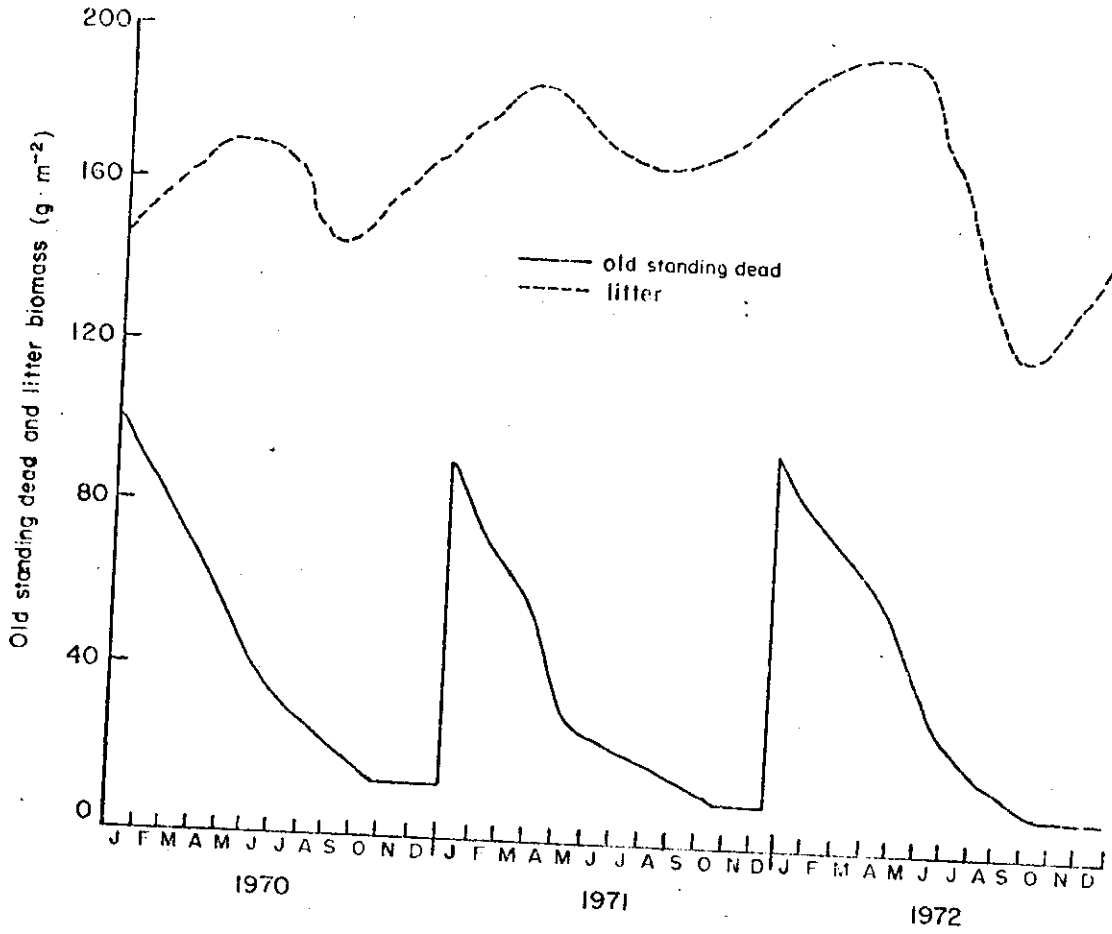


Fig. 19. Three-year simulated time series of the old standing dead and litter biomass at the Pawnee Site.



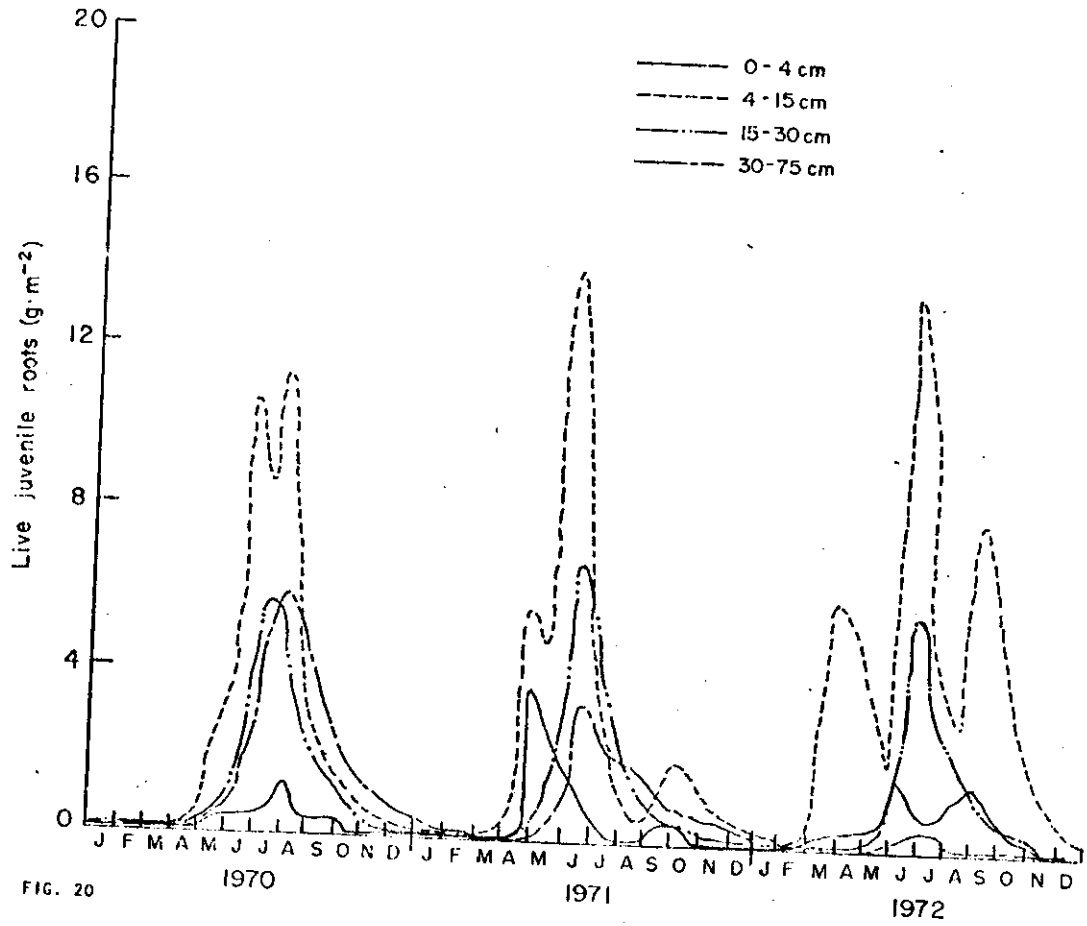


FIG. 20. Three-year simulated time series of the live juvenile roots for the 0-4 cm, 4-15 cm, 15-30 cm, and 30-75 cm soil layers at the Pawnee Site.

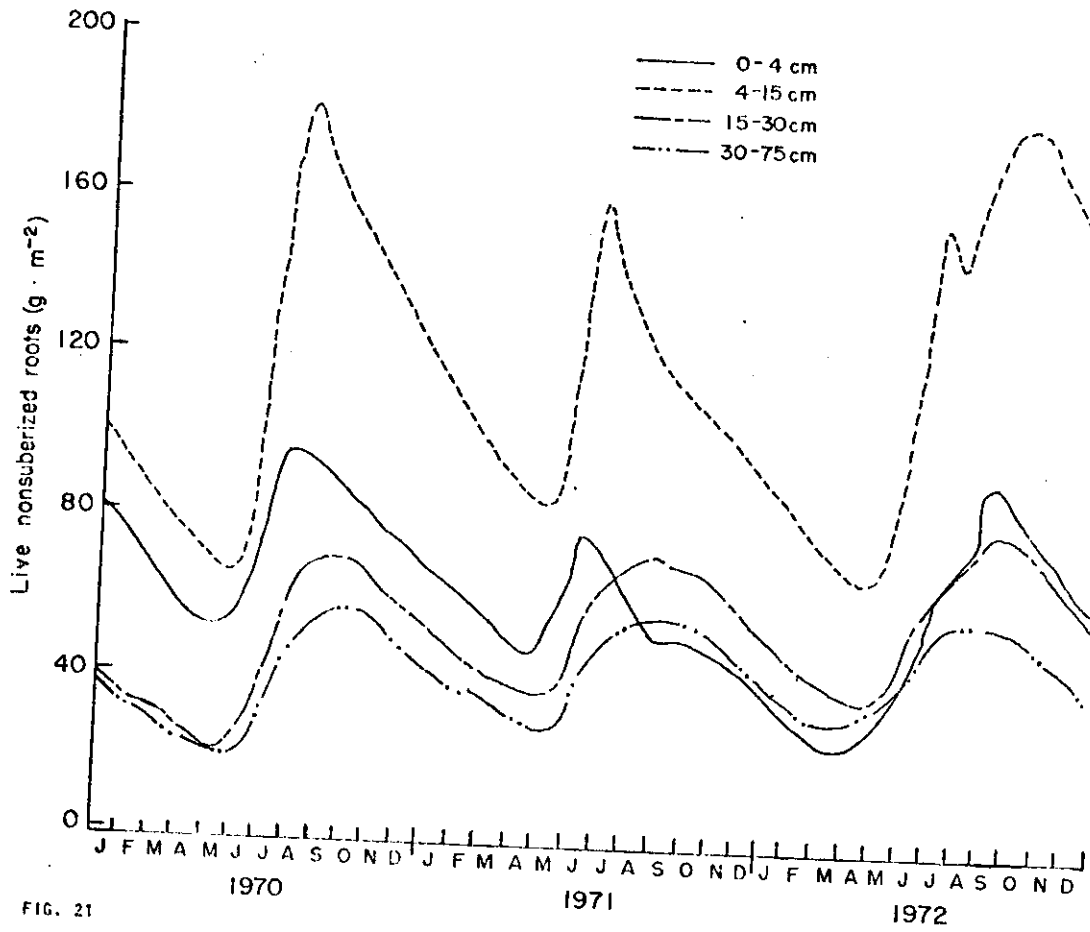


FIG. 21

Fig. 21. Three-year simulation time series of the live nonsubersized roots for the 0-4 cm, 4-15 cm, 15-30 cm, and 30-75 cm soil layers at the Pawnee Site.

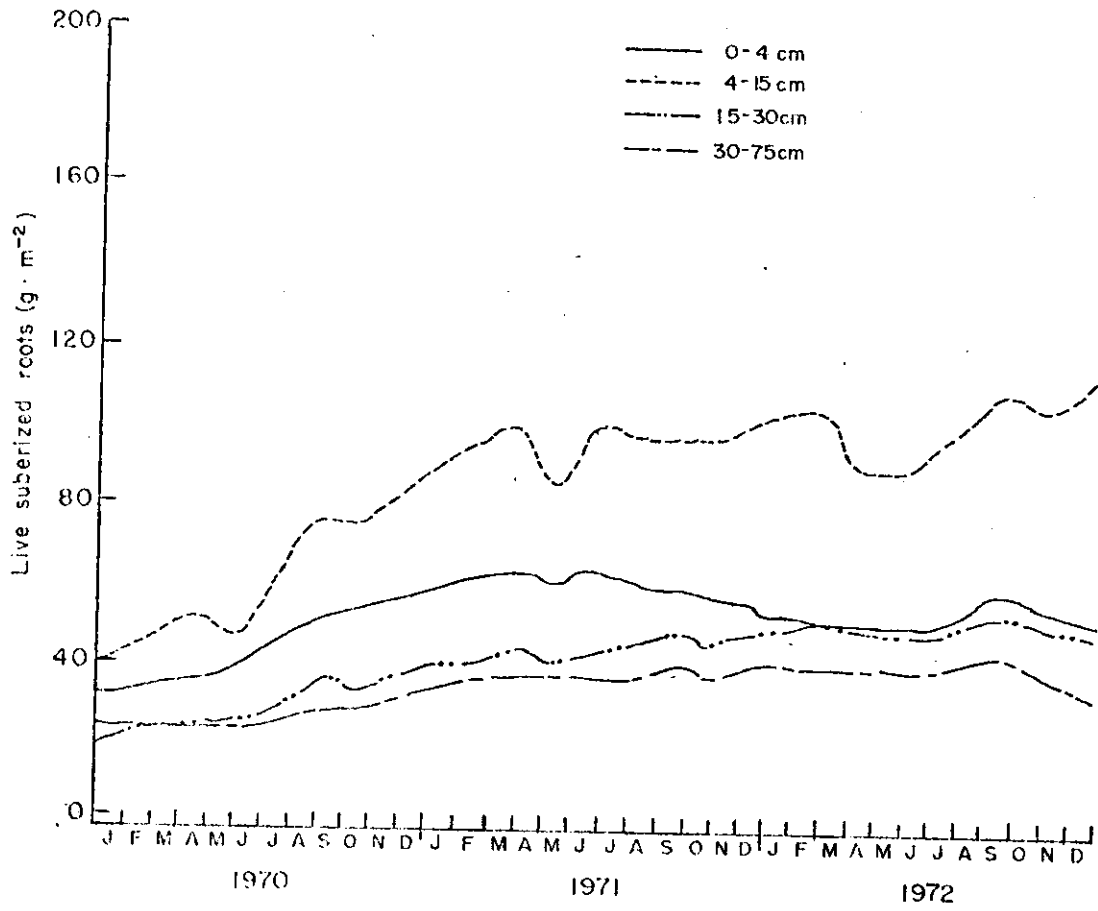


Fig. 22. Three-year simulated time series of the live suberized roots for the 0-4 cm, 4-15 cm, 15-30 cm, and 30-75 cm soil layers at the Pawnee Site.

transfer of live to the dead root compartment, although the peaks of dead biomass follow the peaks of live biomass of respective root category. Figure 23 indicates that the dynamics in total roots, total live roots, and total dead roots is not as marked as are the dynamics of roots of different age categories; relatively, however, the total live root compartment is more dynamic than the total dead root compartment, showing a peak in each growing season. This points out to the fact that infrequent sampling of total root biomass (live + dead) in field may show few changes, thus providing little or no clue to the functioning of the belowground system. The percent live root biomass also shows some intraseasonal fluctuation being maximum during the middle of the growing season. The shallow layers have a higher percent of living roots than deeper layers (Fig. 24). This conforms to the observation of Singh & Coleman (1974) who used carbon-14 to detect functional root biomass in this prairie.

Decomposition of dead biomass (litter and dead roots) is the major pathway of dissipation of energy accumulated in the net production. Fig. 25 shows, that more root material is decomposed each year than litter because of a greater root biomass. The rate of decomposition of both the components is fast during early growing season when favorable soil temperature and soil water conditions exist. Decomposition is negligible during the coldest winter periods.

#### *Tallgrass prairie at Osage*

The results of a 3-year run (1970-72) of the Osage version of the model (Fig. 26-30) show that the above- and belowground state variables follow similar patterns as those simulated for Pawnee Site. The difference between the two sites are mainly caused by the fact that the

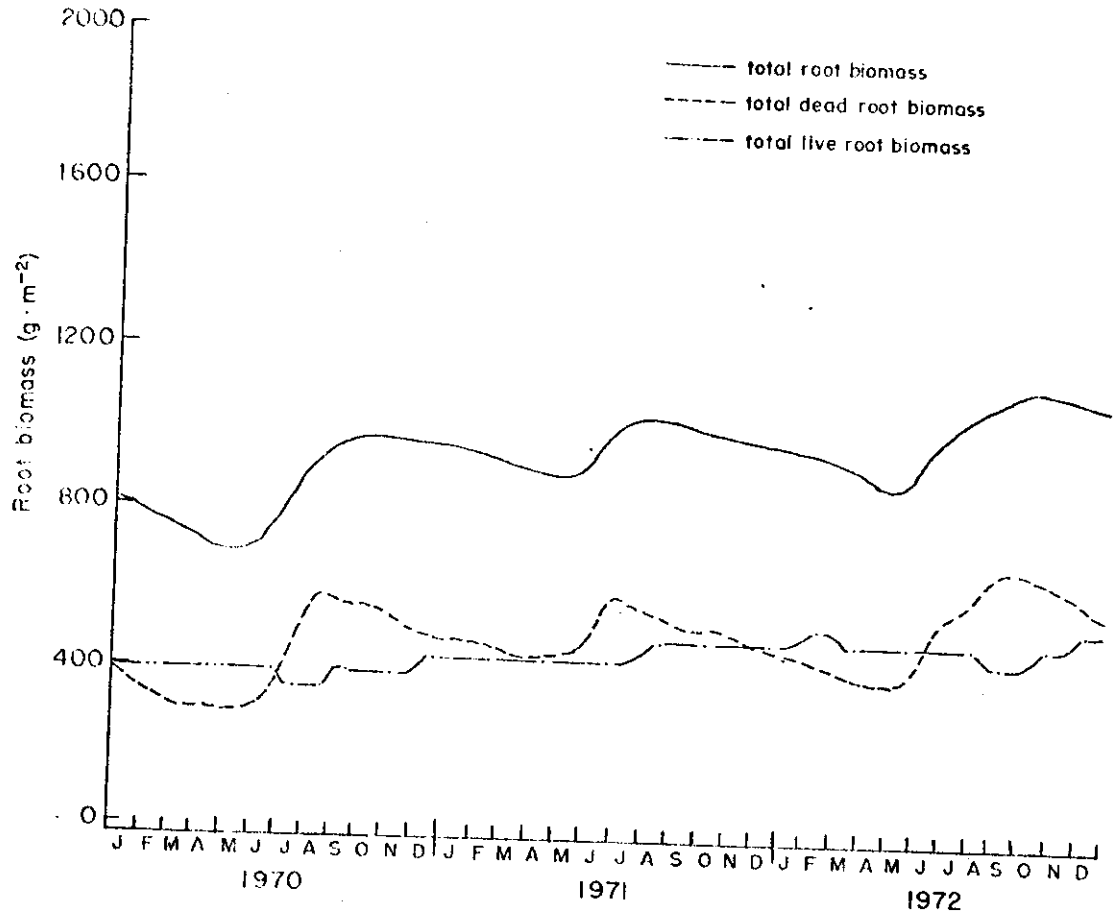


Fig. 23. Three-year simulated time series of the total root biomass and the total live and dead root biomass at the Pawnee Site.

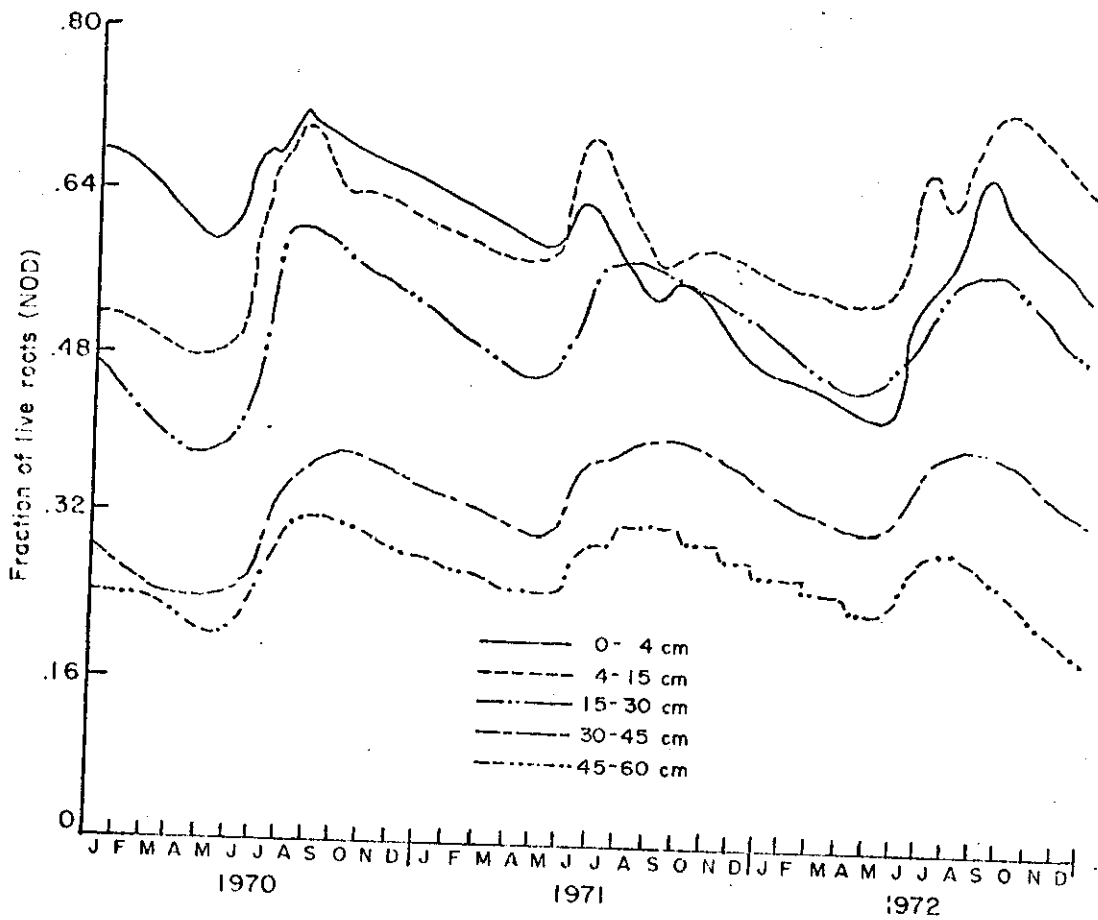


Fig. 24. Three-year simulated time series of the fraction of live root in 0-4 cm, 4-15 cm, 15-30 cm, 30-45 cm, and 45-60 cm soil layers at the Pawnee Site.

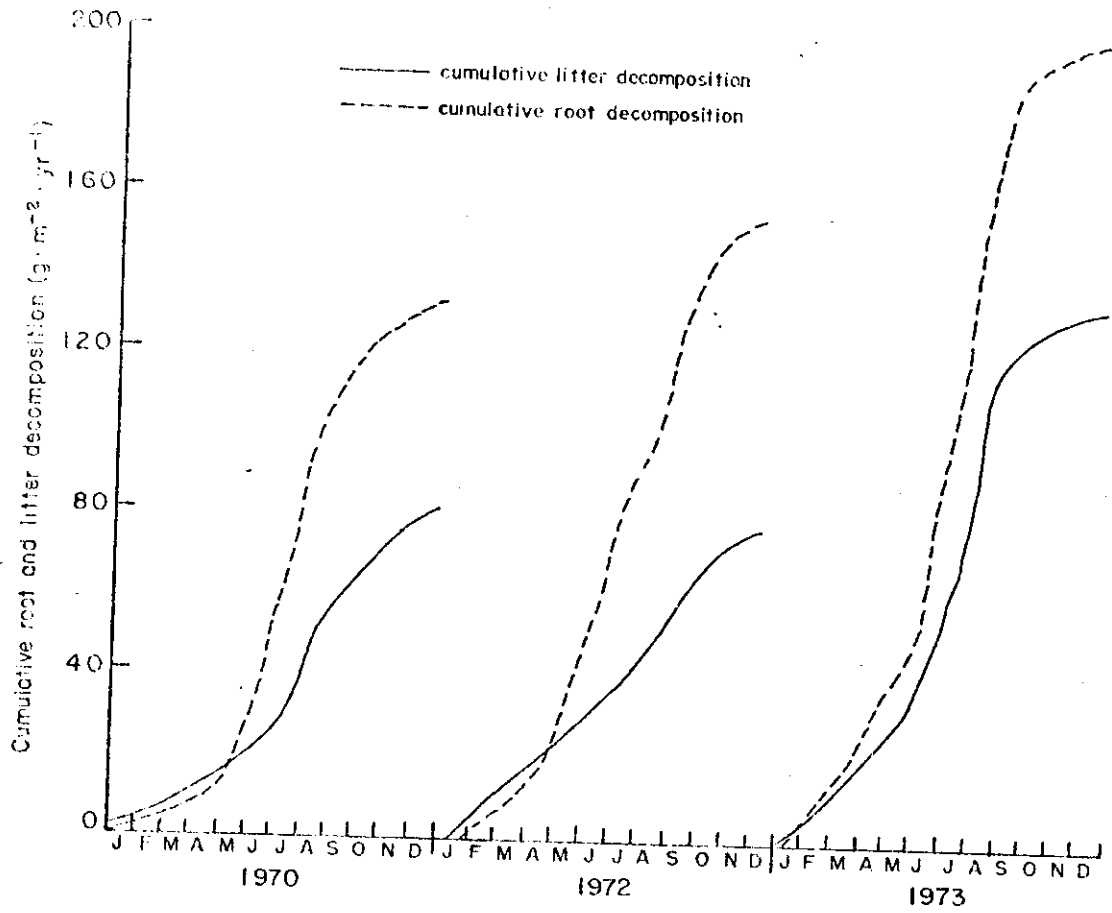


Fig. 25. Three-year simulated time series of the cumulative decomposition of litter and dead roots at the Pawnee Site.

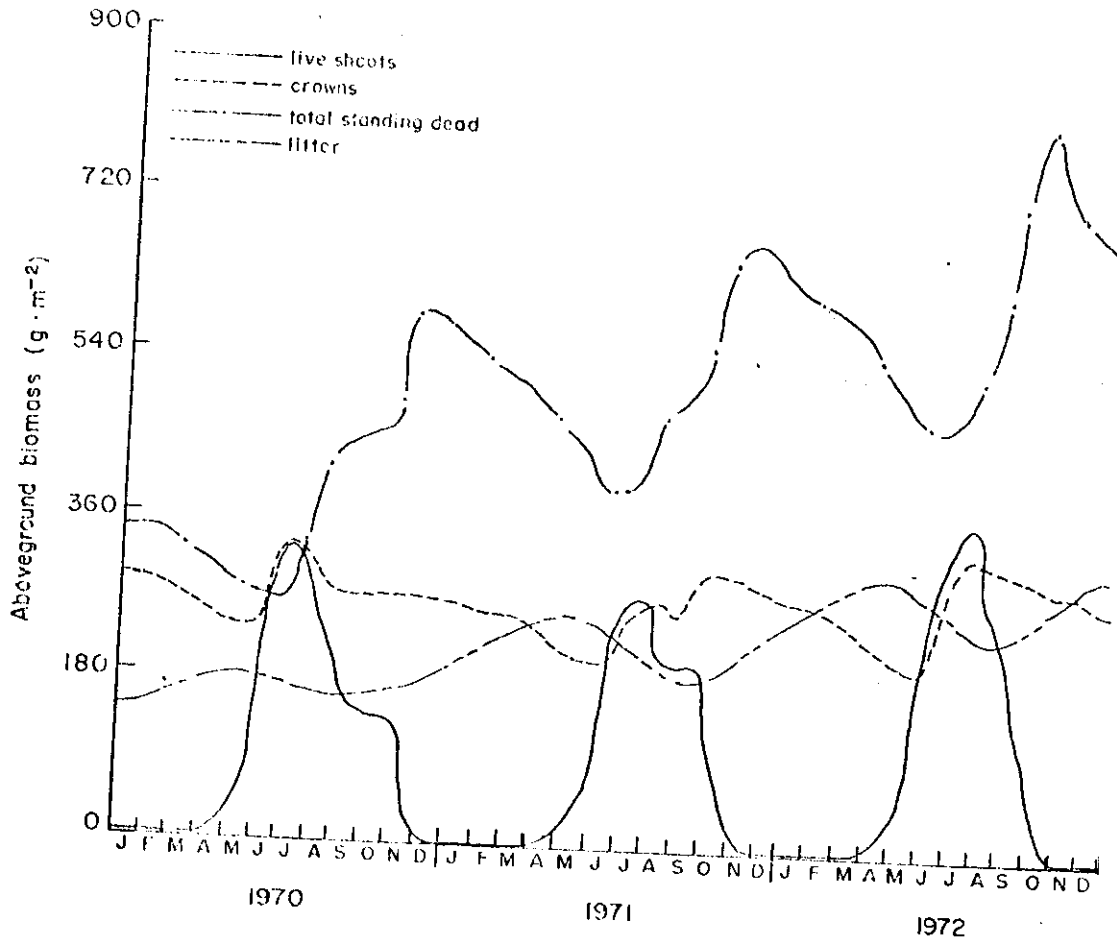


Fig. 26. Three-year simulated time series of the live shoot, crown, total standing dead, and litter biomass at the Osage Site.



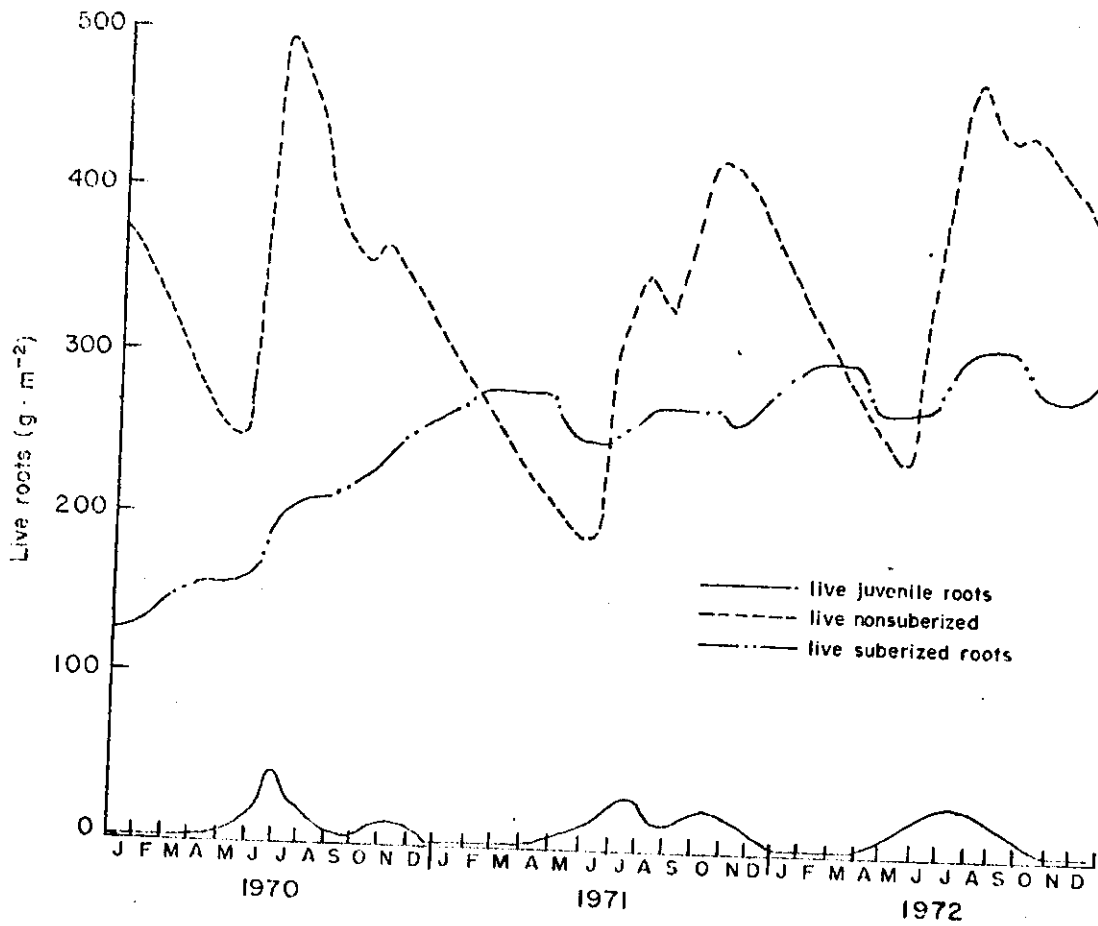


Fig. 27. Three-year simulated time series of the live juvenile, nonsuberized, and suberized roots at the Osage Site.

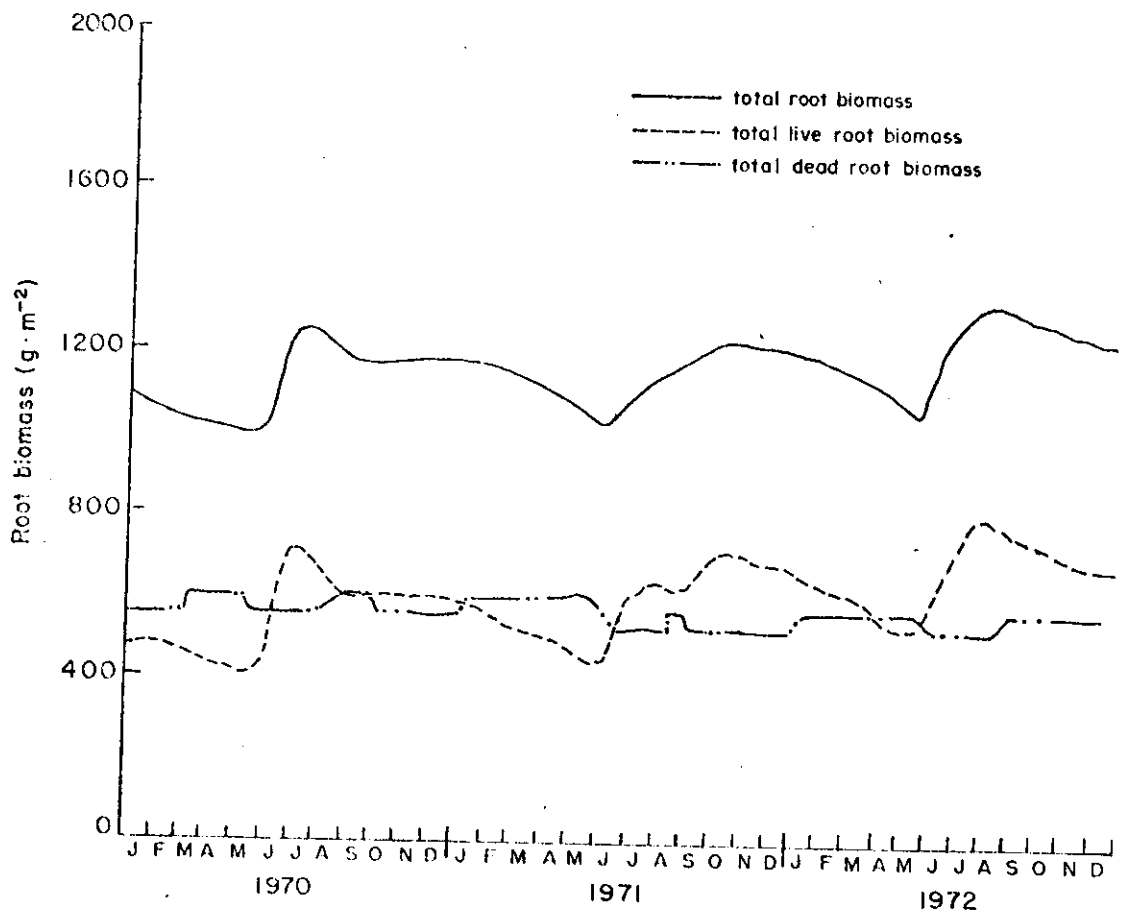


Fig. 28. Three-year simulated time series of total root biomass, total live root biomass, and total dead root biomass at the Osage Site.



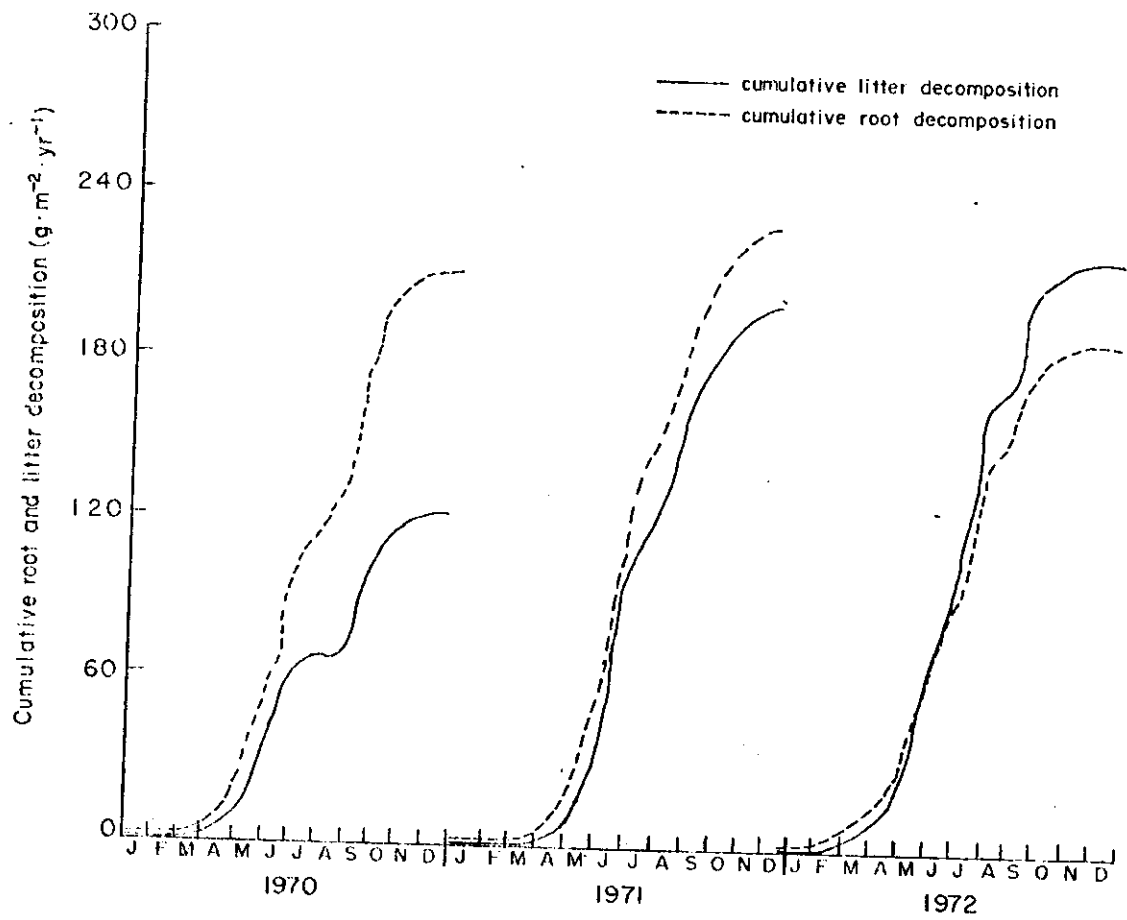


Fig. 30. Three-year simulated time series of litter and dead root decomposition at the Osage Site.

average growing season air temperature and the growing season rainfall are greater at the Osage Site. The increased rainfall and higher air temperature cause an increase in total production with a greater percentage going to aboveground production (61% (Osage) vs. 22% (Pawnee)). This increased production results in a large increase in the peak standing crop of live shoots and standing dead biomass compared to the Pawnee Site. This increased aboveground production causes a significant increase in the fraction of total biomass in the system that is decomposed as litter (see Fig. 30). The percentage of live roots during the growing season is significantly greater at the Osage Site. This is presumably caused by more favorable conditions (higher soil water content) for decomposition of dead roots at the Osage Site during the period of time when the greatest amount of carbohydrate is translocated to the roots.

#### *Model verification*

The degree of similarity between the simulation output and estimates of certain state variables through harvest is shown in Table 3 for 1972. The harvest data for all the three years were directly or indirectly used in the construction of the model, but more extensive use was made of 1970 and 1971 data than of 1972 observations.<sup>3/</sup> A perusal of Table 4 suggests a fair degree of agreement between simulation and harvest

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<sup>3/</sup>The time-series harvest results for the 3 years both for Pawnee and Osage are available in the US/IBP Grassland Biome Data Library at the Natural Resource Ecology Laboratory, Colorado State University, Fort Collins, Colorado.

Table 3. *Certain functional properties of the system*

	Pawnee			Osage		
	1970	1971	1972	1970	1971	1972
Net photosynthesis	717	597	816	1190	1271	1251
Net root production	306	173	321	287	256	228
Net crown production	50	49	75	55	82	82
Net aboveground production	128	126	142	457	525	542
Standing dead to litter	131	127	130	200	307 <sup>1/2</sup>	358
Death of root	155	201	212	214	160	207
Death of crown	45	56	54	68	44	54
Total net production	484	348	538	799	863	852
Total Biomass Disappearance	518	599	689	855	1090	1096

Table 4. A comparison of simulated and observed values of certain state variables for 1972

Date	Aboveground live (g · m <sup>-2</sup> )		Total standing dead (g · m <sup>-2</sup> )		Litter (g · m <sup>-2</sup> )		Crowns (g · m <sup>-2</sup> )		Total live + dead roots (g · m <sup>-2</sup> )	
	Simulated	Observed	Simulated	Observed	Simulated	Observed	Simulated	Observed	Simulated	Observed
Pawnee Site										
5 June	69	72	52	59	191	204 <sup>a/</sup>	162	212 <sup>a/</sup>	940	793 <sup>a/</sup>
12 July	97	110	50	54	166	135	223	73 <sup>b/</sup>	1093	999
7 August	91	87	60	39	146	208	220	132	1086	1031
11 September	78	97	57	68	124	209	224	283	1125	918
Osage Site										
6 June	167	128	470	510	248	250	229	228	1140	--
5 July	334	203	482	550	228	261	314	479 <sup>c/</sup>	1330	842 <sup>d/</sup>
7 August	348	254	502	461	205	339	341	332	1385	550
2 September	213	222	643	563	223	274	320	540 <sup>e/</sup>	--	--

a/ These values are for 26 June. No appropriate data for 5 June were available.

b/ On 26 June the measured crown biomass was 212 g · m<sup>-2</sup>.

c/ Measured crown biomass on 6 June was 228 and 8 August 332 g · m<sup>-2</sup>.

d/ The observed root biomass is only up to 50 cm depth while simulated values are up to 90 cm. Estimates on the basis of 1970 observed values indicate 200-300 g · m<sup>-2</sup> root material within 50 to 90 cm depth.

e/ Variations in crown and root biomass measurements were too large. For example, for this date crown biomass was 540 ± 201 (1SE).

estimates. There are two notable exceptions which merit attention, however. On the Osage Site except for the later part of the growing season, the model indicates a higher live biomass than clipped data. In fact, the harvest data show a lower peak biomass ( $254 \text{ g} \cdot \text{m}^{-2}$ ) in 1972 than in 1970 ( $270 \text{ g} \cdot \text{m}^{-2}$ ) or 1971 ( $336 \text{ g} \cdot \text{m}^{-2}$ ). The rainfall during the thermal-potential growing season (when day temperature averaged  $\geq 4.4^\circ\text{C}$  for a fortnight) in 1972 was 805 mm as opposed to 782 in 1971 and 435 in 1970. The annual rainfall was 652 mm in 1970, 947 in 1971, and 867 in 1972. Even if we consider that a considerable amount of thermal-potential growing season rainfall (about 19%) occurred too late to affect plant growth, the residual moisture from 1971 high rainfall and good, if not better, rainfall during the early part of the 1972 growing season should result in better plant growth in 1972, contrary to clipping results. This fact is illustrated by the model.

The second area of apparent disagreement is in the total root biomass values on the Osage (Table 4). The sampling was implemented only up to 50 cm while the model simulates biomass up to 90 cm depth. Field observations on the root biomass were quite variable. To illustrate the variability we give the following values which were recorded on the site. In 1970 up to 50 cm depth 960 to  $1209 \text{ g} \cdot \text{m}^{-2}$  roots were recorded. On 24 November 1970 the value was  $1021 \text{ g} \cdot \text{m}^{-2}$ . In 1971 on 3 March  $1618 \text{ g} \cdot \text{m}^{-2}$  roots were recorded. This value decreased to 881 on 18 June 1971, 683 on 15 May 1972 and 634 on 11 November 1972 with little intraseasonal dynamics. This calls for more precise measurements of the root biomass in the field which would also help refine the parameters in the model.



*Certain functional properties of the system*

Some of the functional properties of the system as evidenced by the simulation are listed in Table 3. The net root production in the short-grass prairie varies between  $171 \text{ g} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$  (1971) to  $320 \text{ g} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$  (1972). Singh & Coleman (ms. to be published) estimated net root production at the Pawnee grassland in 1972 to be  $300 \text{ g} \cdot \text{m}^{-2}$  using carbon-14. The value of  $142 \text{ g} \cdot \text{m}^{-2}$  for net aboveground production in 1972 is very close to the value obtained by summing up peak live weights of species from harvest data for 1972 ( $138 \text{ g} \cdot \text{m}^{-2}$ ). In 1970 and 1971, the harvested material was not separated into live and dead components so any aboveground net production estimate from harvest data was questionable. Root mortality varied from  $155 \text{ g} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$  (1970) to  $213 \text{ g} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$  (1972). Using experimental data of Singh & Coleman (1974) for 1972, root mortality can be calculated to be  $195 \text{ g} \cdot \text{m}^{-2}$ , thus there seems to be a reasonably close correspondence in value obtained through simulation and through field experiments. The results also indicate that except for 1971, the total net photosynthesis was higher than the sum of all losses from the system. This has resulted in some accumulation of belowground biomass over the three simulation years and suggests that there may not be an exact balance of input and output from year to year. Perhaps stability should be defined using several years.

We would like to make some comments on the comparability of the estimates of production from harvest data and the simulation process. If the net crown production and net root production are calculated as the sum of significant positive increments within the growing season, by depth, from the harvest data, belowground production (crowns + roots) estimate ranges from  $400$  to  $680 \text{ g} \cdot \text{m}^{-2}$  in the 3 years, giving a total

net production (above + belowground) of about  $600$  to  $900 \text{ g} \cdot \text{m}^{-2}$  (Sims & Singh, unpublished). The maximum total net production that we obtain through simulation is  $538 \text{ g} \cdot \text{m}^{-2}$  resulting from net photosynthesis of  $816 \text{ g} \cdot \text{m}^{-2}$ . So either the harvest technique overestimates production or the present simulation underestimates it. The major constraint in the simulation of net photosynthesis was the amount of soil water. We assumed that photosynthesis was essentially zero if water potential was  $\leq -55$  bars. We think that this is the lower limit for photosynthesis, and any extension of this would probably be unrealistic. However, we ran the model by allowing photosynthesis up to  $-70$  bars water potential. This resulted in an increase in the net photosynthesis to  $993 \text{ g} \cdot \text{m}^{-2}$  (in 1972 simulation), resulting in total net production of  $692 \text{ g} \cdot \text{m}^{-2}$ . This increased estimate was still short of the  $900 \text{ g} \cdot \text{m}^{-2}$  assumed from the harvest technique. Perhaps further rigorous field experimentation to study the net photosynthesis relations in the shortgrass prairie and more precise biomass measurements are needed.

In the tallgrass prairie simulation resulted into  $800$  to  $860 \text{ g} \cdot \text{m}^{-2}$  total annual net production (Table 3) out of which  $36\%$  to  $43\%$  is realized in the production of belowground parts. Net photosynthesis varies from  $1190$  to  $1271 \text{ g} \cdot \text{m}^{-2}$ , i.e., about one and one-half times that of shortgrass prairie. This is not surprising because Osage has about three times more annual precipitation ( $\sim 90$  cm) than Pawnee ( $\sim 30$  cm). Estimates of total net production from harvest techniques for this site range from  $850$  to  $900 \text{ g} \cdot \text{m}^{-2}$  (Sims & Singh, unpublished) which seem to be reasonably close to the simulation results. The difference in the two estimates is that, while from simulation net crown production ranges from  $55$  to  $82 \text{ g} \cdot \text{m}^{-2}$ , from harvest technique it lies between  $70$  and  $400 \text{ g} \cdot \text{m}^{-2}$ . Consequently aboveground net production from simulation

(457 to 525 g · m<sup>-2</sup>) is higher than from harvest estimate (331 to 416 g · m<sup>-2</sup>). In the harvest technique the amounts of aboveground biomass and crown biomass depend to a great extent on the height of clipping and even little variation in the latter is likely to cause a marked variation in the estimate of the two components. However, if crowns and shoots are taken together, the estimates from simulation and harvest technique become reasonably close.

We now wish to comment on the most important differences in the functioning of the two prairie systems as evidenced through this simulation exercise. These are mainly based on the differences in principal parameters and processes that we had to alter in adapting the model to two contrasting sites.

Maximum photosynthetic efficiency (peak net photosynthesis rate per calorie of solar energy under optimal conditions) for Pawnee plants is slightly higher than for Osage plants. Dominant plants on both the sites are C-4 plants, but the Pawnee Site is more water-stressed than the Osage Site. It would therefore seem that in a water-stressed environment the successful plants adapt themselves in such a way as to harvest maximum amount of energy in the presence of adequate soil water. This is further indicated by experiments of Brown (1974) who found considerable net photosynthesis in blue grama at  $\leq -50$  bars while Risser (personal communication) observed positive net photosynthesis in little blue stem only up to -25 bars. Photosynthetic efficiency of the plant canopy in the tallgrass prairie may also be lower because of greater shading effect and a higher amount of structural material. It was also inferred that higher water tensions at Osage will result into a faster transfer of biomass from live to dead compartment as compared to the naturally water-stressed Pawnee Site.

One of the major differences in the two systems is the allocation of photosynthate to belowground parts. On the Pawnee Site 80% to 83% of net photosynthesis is channeled belowground (crowns + roots) while on Osage Site only 61% to 63% is allocated to belowground parts. This difference is still magnified when net belowground production is considered. Thus of the total net production (net photosynthesis - crown + root respiration) 64% to 74% is channeled belowground at Pawnee and only 36% to 43% at Osage. This increase in the magnitude of difference is due to a higher respiratory rate at Osage in response to higher temperatures and more moist conditions (root respiration at Pawnee is 63% of that at Osage). Thus in tallgrass prairies considerably more photosynthate stays aboveground. However, in response to greater precipitation at Osage, more roots grow in deeper layers on that site as compared to Pawnee.

The transfer of standing dead material into litter compartment is faster in the shortgrass prairie, where the dead compartment turns over every 9 months as compared to the tallgrass prairie where the turnover period is 20 months. Thus a greater proportion of dead shoots is maintained in the tallgrass prairie, a fact which is supported by time-series harvest data.

The peak decomposition rate (when there are no limiting water or temperature conditions) of litter and roots on Pawnee Site is 1.4 (juvenile roots), 6.3 (nonsuberized roots and litter), and 3 (suberized roots) times higher than at Osage Site. These differences resulted from tuning the model to the Osage Site. We are not aware of any study where these rates have been compared under optimal conditions. However, both litter and roots of the Pawnee Grassland are richer in nitrogen content. The nitrogen content in litter at Osage varied from 0.53% to 0.61%, in

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roots from 0.38% to 0.68%; the same at Pawnee were in the range of 0.74% to 1.25% and about 0.8% in litter and roots, respectively (Bokhari & Singh 1975). Nitrogen-rich material may be more conducive to decomposition (Hunt 1976) resulting into higher peak decomposition rate for Pawnee material.

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APPENDIX

SUMMARY OF SYMBOLS USED

- $A_c$  is a control constant for the translocation to the crowns (NOD).
- $A_{ij}$  is the fraction of photosynthate sent to the  $i^{\text{th}}$  layer that is allocated to the  $j$  root type (NOD).
- $A_i^T$  is the fraction of total photosynthate sent the  $i^{\text{th}}$  soil layer (NOD).
- $A_r$  is the control constant for translocation to the roots (NOD).
- $B$  is the biomass of either crowns, live nonsuberized roots, or live suberized roots ( $\text{g} \cdot \text{m}^{-2}$ ).
- $B_a$  is the photosynthetically active biomass ( $\text{g} \cdot \text{m}^{-2}$ ).
- $B_d$  is the biomass of old standing dead ( $\text{g} \cdot \text{m}^{-2}$ ).
- $B_l$  is the live shoot biomass ( $\text{g} \cdot \text{m}^{-2}$ ).
- $B_s$  is either the recent or old standing dead biomass ( $\text{g} \cdot \text{m}^{-2}$ ).
- $B_t$  is the sum of crown biomass and the live suberized and nonsuberized root biomass in the top two soil layers ( $\text{g} \cdot \text{m}^{-2}$ ).
- $C$  is the combined water tension and air temperature control parameter for photosynthesis (NOD).
- $C_b$  is the crown biomass ( $\text{g} \cdot \text{m}^{-2}$ ).
- $C_d^L$  is the average yearly turnover rate for the transfer of standing dead to litter ( $\text{yr}^{-1}$ ).
- $C_m$  is the maximum shoot turnover rate produced by soil water stress ( $\text{day}^{-1}$ ).
- $C_p$  is the shoot turnover rate without soil water stress ( $\text{day}^{-1}$ ).
- $C_t$  is the minimum air temperature that will cause frost damage ( $^{\circ}\text{C}$ ).
- $C_t^P$  is the cumulative sum of the product of the temperature and soil water control parameters for photosynthesis (NOD) at time  $t$ .

- $D_i^D$  is the depth control parameter for decomposition in the  $i^{\text{th}}$  layer (NOD).
- $D_{ij}$  is the biomass of dead roots of the  $j^{\text{th}}$  type in the  $i^{\text{th}}$  layer ( $\text{g} \cdot \text{m}^{-2}$ ).
- $D_{ij}^L$  is the death rate of live roots of the  $j^{\text{th}}$  type in the  $i^{\text{th}}$  layer ( $\text{g} \cdot \text{m}^{-2}$ ).
- $D_j$  is the maximum turnover rate for dead roots of the  $j^{\text{th}}$  type ( $\text{day}^{-1}$ ).
- $D_j^T$  is the total additional death rate of live roots of the  $j^{\text{th}}$  type in the bottom four layers ( $\text{g} \cdot \text{m}^{-2} \cdot \text{day}^{-1}$ ).
- $D_m$  is the maximum fraction of live roots of the  $j^{\text{th}}$  type that will die per day.
- $D_s$  is the death rate of live shoot biomass ( $\text{g} \cdot \text{m}^{-2} \cdot \text{day}^{-1}$ ).
- $E_{ij}$  is the additional death rate of live roots of the  $j^{\text{th}}$  type in the  $i^{\text{th}}$  soil layer ( $\text{g} \cdot \text{m}^{-2} \cdot \text{day}^{-1}$ ).
- $F_1$  is the fractional leaf area of the old standing dead biomass above  $H_1$  (NOD).
- $H_1$  is the average height of the live shoot biomass (cm).
- $H_0$  is the average height of the old standing dead biomass (cm).
- $J_a$  is the turnover rate of juvenile roots to suberized roots ( $\text{day}^{-1}$ ).
- $J_i^A$  is the rate of transfer from juvenile roots to nonsuberized roots ( $\text{g} \cdot \text{m}^{-2} \cdot \text{day}^{-1}$ ).
- $L_a$  is the leaf area of old standing dead biomass (NOD) that is above the average height of the live biomass (NOD).
- $L_b$  is the litter biomass ( $\text{g} \cdot \text{m}^{-2}$ ).
- $L_d$  is the leaching rate of recent or old standing dead ( $\text{g} \cdot \text{m}^{-2} \cdot \text{day}^{-1}$ ).
- $L_l$  is the leaching rate of litter biomass ( $\text{g} \cdot \text{m}^{-2} \cdot \text{day}^{-1}$ ).

- $M$  is the soil water tension control parameter for translocation to the shoots (NOD).
- $M_d$  is the water tension control parameter for root death (NOD).
- $M_g$  is the rate which litter is mechanically mixed into the top soil layer ( $g \cdot m^{-2} \cdot day^{-1}$ ).
- $M_i^D$  is the soil water control parameter for decomposition in the  $i^{th}$  layer (NOD).
- $M_i^1$  is the soil water control parameter for the allocation of photosynthate to the  $i^{th}$  layer (NOD).
- $M_i^2$  is the fraction of photosynthate in the  $i^{th}$  layer allocated to the juvenile roots type (NOD).
- $M_p$  is the maximum photosynthesis rate ( $g \cdot g^{-1} \cdot day^{-1}$ ).
- $M_r$  is the soil water tension control parameter for respiration (NOD).
- $M_s$  is the soil water tension control parameter for shoot death (NOD).
- $N_a$  is the maximum turnover rate of nonsuberized roots to suberized roots ( $day^{-1}$ ).
- $N_i^A$  is the rate of transfer from nonsuberized roots to suberized roots ( $g \cdot m^{-2} \cdot day^{-1}$ ).
- $P$  is the phenological stage of the plant (NOD).
- $P_a$  is the phenology control parameter for the aging of nonsuberized roots (NOD).
- $P_c$  is the fraction of net photosynthate translocated to the crowns (NOD).
- $P_d$  is the leaf area index of old standing dead (NOD).
- $P_i^C$  is the value of the cumulative sum of the product of the soil water control parameter for phenological progression times the temperature control parameter for photosynthesis at the beginning of the  $i^{th}$  phenological stage (NOD).

- $P_m$  is the peak net photosynthesis rate per calorie of solar energy ( $g \cdot g^{-1} \cdot day^{-1} \cdot cal^{-1}$ ).
- $P_m^H$  is the soil water control parameter for phenological progression (NOD).
- $P_m^1$  is the soil water control parameter for phenological progression during phenological stage less than 3 (NOD).
- $P_m^2$  is the soil water control parameter for phenological progression during phenological stage greater than or equal to 3 (NOD).
- $P_n$  is the net photosynthesis rate ( $g \cdot m^{-2} \cdot day^{-1}$ ).
- $P_p$  is the phenology control parameter for photosynthesis (NOD).
- $P_r$  is the fraction of net photosynthate translocated to the roots (NOD).
- $Q$  is the fraction of standing dead biomass transferred to litter by daily rainfall ( $day^{-1}$ ).
- $Q_j$  is the ratio of the biomass of live roots of the  $j^{th}$  type in the bottom four layers to the total biomass of roots of the  $j^{th}$  type (NOD).
- $Q_1$  is the maximum possible fraction of standing dead leached by the rainfall ( $day^{-1}$ ).
- $R_b$  is the recent standing dead biomass ( $g \cdot m^{-2}$ ).
- $R_c$  is the ratio of shoot biomass to crown biomass (NOD).
- $R_d$  is the daily rainfall ( $cm \cdot day^{-1}$ ).
- $R_{ij}$  is the biomass of live roots in the  $i^{th}$  layer that are of the  $j^{th}$  type ( $j = 1$  - juvenile roots,  $j = 2$  - nonsuberized roots, and  $j = 3$  - suberized roots) ( $g \cdot m^{-2}$ ).
- $R_{ij}^D$  is the decomposition rate of dead roots of the  $j$  type on the  $i^{th}$  layer ( $g \cdot m^{-2} \cdot day^{-1}$ ).

- $R_j$  is the fraction of root biomass of the  $j^{\text{th}}$  type that is respired per day at  $40^\circ\text{C}$  with flow soil water tension ( $\text{day}^{-1}$ ).
- $R_r$  is the ratio of shoot biomass to the total live root biomass (NOD).
- $R_s$  is the respiration rate of the  $j$  root type ( $\text{g} \cdot \text{m}^{-2} \cdot \text{day}^{-1}$ ).
- $R_y$  is the long-term yearly average rainfall ( $\text{cm} \cdot \text{yr}^{-1}$ ).
- $S_d^L$  is the transfer of both recent and old standing dead at the end of each year ( $\text{g} \cdot \text{m}^{-2} \cdot \text{day}^{-1}$ ).
- $S_i$  is the soil water tension in the  $i^{\text{th}}$  layer (-bars).
- $S_l$  is the solar radiation incident upon the top of the live plant canopy ( $\text{langley} \cdot \text{day}^{-1}$ ).
- $S_r$  is the solar radiation above the plant canopy ( $\text{langley} \cdot \text{day}^{-1}$ ).
- $S_s$  is the shortwave solar radiation without any cloud cover ( $\text{langley} \cdot \text{day}^{-1}$ ).
- $S_s^6$  is the value of shortwave solar radiation without any cloud cover when plant dormancy starts ( $\text{langley} \cdot \text{day}^{-1}$ ).
- $S_t$  is the 14-day average soil temperature from 0 to 15 cm ( $^\circ\text{C}$ ).
- $S_w$  is the soil water tension at the appropriate soil layer (-bars).
- $S_5^P$  is the value of the shortwave solar radiation without any cloud cover on the first day that  $C_t^P$  is greater than or equal to  $P_5^C$  ( $\text{langley} \cdot \text{day}^{-1}$ ).
- $T_b$  is the amount of photosynthate translocated to the live root biomass ( $\text{g} \cdot \text{m}^{-2} \cdot \text{day}^{-1}$ ).
- $T_c$  is the translocation from live shoots to crowns ( $\text{g} \cdot \text{m}^{-2} \cdot \text{day}^{-1}$ ).
- $T_d$  is the temperature control parameter for root death (NOD).
- $T_i$  is the average daily soil temperature in the  $i^{\text{th}}$  layer ( $^\circ\text{C}$ ).
- $T_i^D$  is the temperature control parameter for decomposition on the  $i^{\text{th}}$  layer (NOD).

- $T_{ij}$  is the rate of transfer of photosynthate to the live roots of the  $j^{\text{th}}$  type in the  $i^{\text{th}}$  soil layer ( $\text{g} \cdot \text{m}^{-2} \cdot \text{day}^{-1}$ ).
- $T_m$  is the minimum air temperature ( $^{\circ}\text{C}$ ).
- $T_m^C$  is the air temperature at which live shoots will freeze ( $^{\circ}\text{C}$ ).
- $T_m^5$  is the 5-day moving average of minimum air temperature at 2 meters ( $^{\circ}\text{C}$ ).
- $T_p$  is the temperature control parameter for photosynthesis (NOD).
- $T_r$  is the temperature control parameter for respiration (NOD).
- $T_s$  is the rate of transfer of stored carbohydrate to the live shoots from the crowns, suberized roots, or nonsuberized roots ( $\text{g} \cdot \text{m}^{-2} \cdot \text{day}^{-1}$ ).
- $W$  is the daily average wind speed ( $\text{km} \cdot \text{hour}^{-1}$ ).
- $W_i^A$  is the constant weight factor for the allocation of photosynthate to the  $i^{\text{th}}$  layer (NOD).
- $Z_q$  is the parameter that controls the extinction of light in the plant canopy (NOD).