Defoliation Effects on Carbohydrate Reserves of Desert Species[1]

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Highlight

Representative plants of eight desert species were defoliated at four phenological stages. These species used varying amounts of carbohydrate for regrowth; however, carbohydrate use and storage varied widely among phenological stages within species. There was a direct relationship between average total carbohydrate levels in the autumn and the amount of regrowth after defoliation. The carbohydrate reserve level in the autumn appears to be a good indicator of defoliation effects during the preceding growing season.

Efectos de Defoliacion (Pastoreo) sobre las Reservas de Carbohidratos en Algunas Especies Deserticas.

Resumen[3]

El manejo de pastizales requiere mas conocimientos sobre las respuestas fisiológicas dc las plantas después del pastoreo. El estudio se llevó a cabo para determinar la influencia de la defoliación sobre las reservas de carbohidratos en las yemas basales y las raíces. Se incluyeron cinco plantas arbustivas y dos gramíneas defoliadas durante las épocas de primavera temprana, primavera tarde, floración y antes del letargo. Había diferentes respuestas entre especies y épocas de defoliación. Sin embargo, había una relación directa entre la cantidad de carbohidratos almacenados en otoño y la cantidad de recrecimiento después de la defoliación. Plantas defoliadas durante las épocas de primavera temprana y floración tuvieron menos carbohidratos debido al menor tiempo para recrecer entre la defoliación y letargo. La cantidad de carbohidratos cn reserva influye en la producción de forraje en el segundo año.

Future rangeland management will require more basic knowledge about the physiological responses of plants to foliage removal. A thorough knowledge of carbohydrate synthesis, translocation, utilization, and storage as influenced by various ecological parameters is valuable in determining when and to what extent plants may be utilized for optimum productivity with minimum damage to the plant resource. The depletion of carbohydrate reserves is believed to be a primary factor for loss in plant vigor and subsequent range deterioration.

Since plant vigor may be closely associated with carbohydrate reserves, it is worthwhile to determine the phenological growth stage in which forage species can withstand defoliation without severe reserve depletion. Therefore, this study was conducted on typical salt-desert shrub species to determine carbohydrate reserve depletion and storage after defoliation at four phenological growth stages. The species studied were: big sagebrush (*Artemisia tridentata*), black sagebrush (*Artemisia arbuscula* var. *nova*), shadscale (*Atriplex confertifolia*), Nuttall saltbush (*Atriplex falcata*), winterfat (*Eurotia lanata*), Indian ricegrass (*Oryzopsis hymenoides*), needle-and-thread (*Stipa comata*), and squirreltail (*Sitanion hystrix*).

Experimental Area and Procedure

Plant samples were collected from three locations in northwestern Utah from 1967 to 1969. The climate in the study areas is semi-arid with warm, dry summers and cold winters. Average yearly precipitation at the study areas was slightly greater during 1967 and 1968 and slightly less than the 10-year average of 21 cm in 1969. Site descriptions were given by Coyne and Cook (1970). Defoliated and control plants were located within the same exclosures as those utilized by Coyne (1969), except that a third replication in Rush Valley, Utah was added.

Defoliations were made by clipping 90% of the plant's current photosynthetic tissue. The first clipping was done during early spring, about April 1. Most desert species had produced only about 10 percent of their anticipated annual growth based on weight. Squirreltail was somewhat more advanced and was in the second or third leaf stage.

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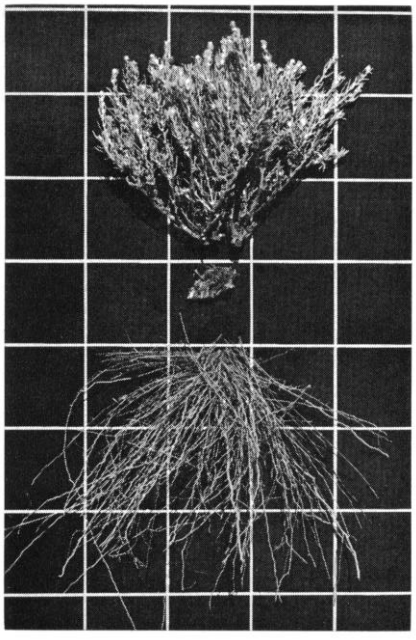

FIG. 1. Winterfat separated into roots, crowns and tops. Each square is equivalent to 1-dm².

The second defoliation treatment occurred during late spring, about May 10, when plant twigs and grass culms were rapidly elongating, but before the flowering stage. The flower heads of squirreltail, however, were in the boot stage at this time. It was estimated that about 40 to 50% of anticipated total annual growth of woody species and 60 to 70% of anticipated total annual growth of the grasses had been produced. The third clipping was made about July 1 when most twig and culm elongation had ceased. Indian ricegrass, needle-and-thread, Nuttall saltbush, and winterfat were in the fruit development stage. Seeds of squirreltail were disseminating and plants were becoming semiquiescent during this period. The two sagebrush species were in the flower-bud stage. Approximately 85 to 95% of anticipated total annual growth of all species had been produced. The last defoliation treatment was made about November 12 when all plants were quiescent.

Total available carbohydrates (TAC) were determined from root and crown samples of defoliated plants that had regrown about 20% of mature size. Root and crown samples from control plants were also taken at the same time. Still other defoliated and control plants were sampled in the autumn at quiescence. Plants which were defoliated during quiescence in 1967 and 1968 were not sampled until the following growing season and fall of 1968 and 1969, respectively.

Root samples from woody species included those roots with diameters less than or equal to 8 mm. This excluded only the taproots and the larger lateral roots. Crown tissue of woody species was defined as the tissue between the first stem branches and the first concentration of roots (Fig. 1). All the fibrous root systems of grasses (to a 30 cm depth) were collected and the lower three to four cm of the culms were designated as crown tissue (Fig. 2). No attempt was made to separate live tissue from dead unless decay was obvious.

Plant parts were briefly washed with water, placed into labeled pint jars, covered with 95% ethanol to reduce enzyme activity, and sealed tightly. Later in the laboratory, lids were removed from the jars and the samples were placed in a forced-draft, steam-heated dryer at 70 C. Approximately 1-week was required to evaporate the ethanol and an additional week to dry the samples.

After drying, the samples were ground to pass through a 40-mesh screen. Laboratory analyses were conducted to determine TAC as milligrams of available carbohydrates per gram of dry plant matter. TAC as defined by Weinmann (1947) and Smith et al. (1964) include sugars, dextrins, starches and fructosans. Structural carbohydrates such as pentosans, hemicellulose, and cellulose were not included in the TAC fraction. No allowance was made for the water of hydrolysis from polysaccharides in the calculations (Grotelueschen and Smith, 1967).

Extraction of TAC from ½-gram samples of plant material was accomplished by using 0.2 N sulfuric acid as described by Smith et al. (1964). These extracts were analyzed

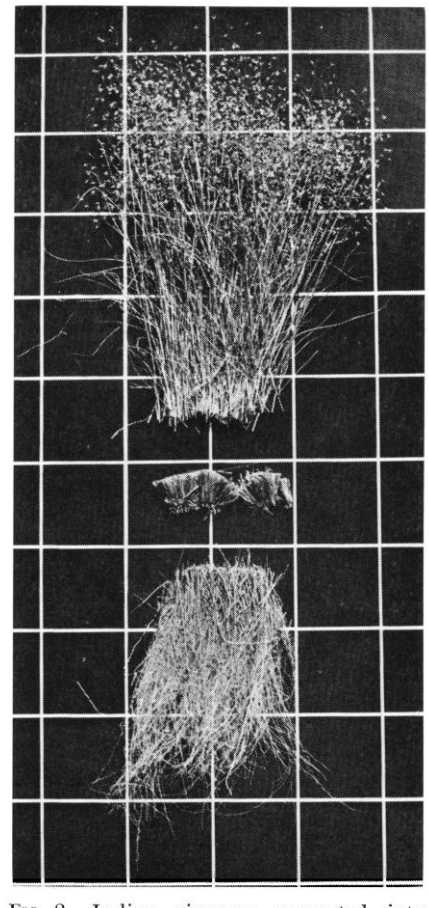

FIG. 2. Indian ricegrass separated into roots, crowns and tops. Each square is equivalent to 1-dm².

on a glucose equivalent basis by using an iodometric titration developed by Heinze and Murneck (1940) with modifications of reagents as suggested by the Association of Official Agriculture Chemists (1965). Standard curves were determined for each stock solution.

Results and Discussion

With the diversity of annual growing conditions during this study, yearly differences and differences among species in the amount of regrowth after defoliation until autumn frosts were significant ($P < .05$). Plants which were clipped when near maturity (about July 1) usually did not attain 20% regrowth before autumn collections were taken. The two sagebrush species usually had less regrowth after defoliation than the other species. Nuttall saltbush and

squirreltail produced more regrowth after defoliation than did the other species.

Total Available Carbohydrates at the Time of Defoliation Treatments

Numerous researchers have reported the annual cycling of carbohydrate reserves in perennial plants and found that they followed somewhat similar patterns (McCarty, 1935; Throughton, 1957; Weinmann, 1961; Priestly, 1962; Cook, 1966; McConnell and Garrison, 1966; Donart, 1968; and Coyne and Cook, 1970). The low point in the reserve cycle normally occurs after initial spring growth and the maximum occurs at or near maturity.

Significant differences ($P < .05$) in TAC concentrations between roots and crowns were evident for all species except squirreltail which had similar TAC concentrations in both roots and crowns. Carbohydrate reserves in roots of all browse and suffrutescent species exceeded crown reserves; but crowns of Indian ricegrass and needle-and-thread contained larger TAC concentrations than roots. The roots of all sampled species usually had a larger increase than crowns in TAC storage following initial draw-down during early spring growth.

In a previous study by Coyne and Cook (1970), carbohydrate reserves from all plants studied were generally lowest during the spring when plants were making most rapid growth (about May 10) and were highest during quiescence in the fall. In general, most species had about 60% as much TAC concentration in the storage organs during early maturity (about July 1) as at quiescence in the autumn. Squirreltail was the exception and had stored considerable reserves during semiquiescence in July.

Total Available Carbohydrates Utilized in Producing Regrowth after Defoliation

Several researchers have found carbohydrate reserves were lower in plants after defoliation as compared to control plants (Weinmann, 1943; Sprague and Sullivan, 1950; Reynolds and Smith, 1962; Smith, 1962; Wolf et al., 1962; Jameson, 1963; Everson, 1966; Donart and Cook, 1970). In the present study, reduced carbohydrate reserve levels in defoliated plants were assumed to be the result of continued respiration, reduction in photosynthesis, and the use of reserves in producing regrowth (Table 1). Negative values in Table 1 indicate that the control plants utilized more TAC in growth and respiration than the defoliated plants used in respiration and production of 20% regrowth.

Since defoliation treatments were not initiated until the spring of 1967, only data for 2-years are available for plants defoliated during quiescence in the autumn of 1967 and 1968. Since plants clipped when near maturity (about July 1) during any year seldom attained 20% regrowth before fall quiescence, data from this treatment

Table 1. Average difference in total available carbohydrates (TAC) when content in defoliated plants was subtracted from the controls. These figures represent TAC in milligrams per gram of sample utilized in attaining 20 percent of mature size following defoliation of eight species during 1967, 1968, and 1969.

		Quiescence[1]		Early growth		Rapid growth[2]	
Species	Year	Roots	Crowns	Roots	Crowns	Roots	Crowns
Big sagebrush	1967	—	—	16	−3	20	3
	1968	32	6	24	−1	8	−3
	1969	4	1	17	3	—	—
	Avg	18	4	19	0	14	0
Black sagebrush	1967	—	—	20	7	20	8
	1968	18	2	16	0	26	4
	1969	8	0	2	3	—	—
	Avg	13	1	13	3	23	6
Shadscale	1967	—	—	−1	0	16	15
	1968	21	4	15	5	30	16
	1969	10	8	4	11	—	—
	Avg	16	6	6	5	23	16
Nuttall saltbush	1967	—	—	−2	−3	20	8
	1968	−26	−13	−14	−10	13	0
	1969	14	8	28	15	—	—
	Avg	−6	−2	4	1	16	4
Winterfat	1967	—	—	14	5	16	5
	1968	26	6	22	3	18	4
	1969	14	−1	1	8	—	—
	Avg	20	2	12	5	17	4
Indian ricegrass	1967	—	—	5	3	0	−1
	1968	1	3	−1	8	10	22
	1969	0	8	−7	29	—	—
	Avg	0	6	−1	13	5	10
Needle-and-thread	1967	—	—	1	−6	7	14
	1968	0	8	2	16	4	21
	1969	−10	−5	−3	9	—	—
	Avg	−5	1	0	6	6	18
Squirreltail	1967	—	—	24	17	34	41
	1968	−6	8	14	26	26	41
	1969	12	27	43	72	—	—
	Avg	3	18	27	38	30	42

[1] Only two years of data were available for the quiescence defoliation treatment.
[2] Plants defoliated during rapid growth in the dry summer of 1969 seldom attained 20 percent regrowth before fall quiescence.

were not considered in any of the analyses.

Shadscale, Nuttall saltbush, and squirreltail utilized differing amounts ($P < .05$) of TAC for regrowth during the 3-years of study (Table 1). Nuttall saltbush and squirreltail utilized significantly more ($P < .05$) TAC in producing regrowth in 1969 than in 1968. Yearly differences in the amounts of TAC reserves utilized by the other five species were not statistically significant.

There were marked differences ($P < .05$) among the eight clipped species in the amounts of TAC reserves used to produce 20% regrowth. Squirreltail utilized significantly more ($P < .05$) TAC reserves for regrowth than did the other seven species. Squirreltail utilized approximately 28 mg TAC/g of sample for regrowth; whereas, all other species except Nuttall saltbush utilized from 0 to 23 mg TAC/g of sample in producing regrowth after defoliation (Table 1). Control plants of Nuttall saltbush often used more reserves for growth than defoliated plants used for regrowth.

There were small differences in amounts of TAC utilized in producing regrowth after any one defoliation (Table 1). Nuttall saltbush, needle-and-thread and squirreltail appeared to use more reserves when plants were defoliated during the early spring. Growth rates for spring-clipped plants were generally high during the favorable spring months. Higher respiration rates also could have contributed to greater reductions in TAC reserves during this period.

Shadscale withdrew more TAC for regrowth in 1967 and 1968 when defoliated during late spring growth in May than when defoliated during early growth in April (Table 1). Squirreltail had greater TAC drawdown after being defoliated during early spring growth than during quiescence in 1968 and 1969. These and other observed differences contributed to the significant ($P < .05$) year by species and treatment by species interactions.

Significant differences ($P < .05$) were evident in the amount of TAC reserves utilized from roots or crowns of the eight species. Root TAC reserves were utilized more ($P < .05$) than crown reserves for regrowth after defoliation treatments in big sagebrush, black sagebrush, and winterfat (Table 1). Crown TAC reserves, however, were utilized more ($P < .05$) than root reserves for regrowth in Indian ricegrass and squirreltail.

The use of reserves from various storage organs among years did not appear to be consistent. Shadscale root reserves were utilized about three times as heavily as crown reserves in producing regrowth after defoliation treatments in 1968 (Table 1). More use was made of crown TAC reserves than root reserves for regrowth in 1969. The reason for this differential usage from reserve organs is not known unless TAC was translocated from one storage area to another.

Carbohydrate Reserves in the Autumn as Affected by Earlier Defoliation Treatments

As stated previously, defoliation during various phenological stages causes the use of varying amounts of carbohydrate reserves for regrowth and respiration. The reserves used, however, may not be replenished unless the plant has an opportunity to regrow and mature after defoliation. Thus, insufficient carbohydrate reserves in the autumn may become a critical factor in the over-wintering of plants and subsequent growth the next spring. Therefore, critical stages in the annual developmental cycle and carbohydrate reserve cycle in the eight desert species studied may be delineated by determining carbohydrate reserve levels in both defoliated and control plants during autumn quiescence.

Both root and crown samples from plants from each defoliation treatment and from control plants were collected during the autumn of each year for TAC analyses (Table 2). The carbohydrate reserve storage in the autumn after defoliation treatments was significantly ($P < .01$) different among the eight species. In general, the more regrowth attained in the current growing season by a species after defoliation, the greater was the carbohydrate reserve storage by fall.

Autumn reserve storage usually decreased as the time between defoliation treatment and normal quiescence lessened. Plants which were defoliated during rapid growth (about May 10) or near maturity (about July 1) had little regrowth and consequently had little photosynthetic tissue present for carbohydrate synthesis during late summer; whereas plants which were defoliated during quiescence (about November 12) the previous year, or during early growth (about April 1) had more regrowth and greater carbohydrate storage by quiescence. Several researchers reported similar findings for other species (Sampson and McCarty, 1930; Laycock and Conrad, 1968; Robison and Massengale, 1968).

The analyses of data for individual species indicated significant ($P < .05$) yearly differences in autumn TAC reserve storage for big sagebrush, black sagebrush, needle-and-thread, and squirreltail. Reserve storage in big sagebrush and black sagebrush was greatest following the unusually wet, late growing season in 1968. This indicated that dry growing conditions experienced in 1969 reduced reserve storage in the two sagebrush species. This differs from research findings of Brown and Blaser (1970). They found soluble carbohydrate concentrations to be greater in orchardgrass (*Dactylis glomerata*) crowns when plants were grown under conditions of moisture stress.

Although the same TAC storage trend in roots and crowns of both sagebrush species was evident, roots were considered to be better indicators of defoliation effects than crowns (Table 2). The significant differences ($P < .05$) between autumn reserves in plant parts among defoliation treatments for big sagebrush was probably caused by a larger decrease of TAC in the roots

Table 2. Average total available carbohydrates (TAC) (mg/g) reserves stored at the time of fall quiescence in the roots and crowns of eight desert species from five defoliation treatments. Samples were taken in the autumn of each year during 1967, 1968, and 1969.

Species	Year	Control		Quiescence[1]		Early growth		Rapid growth		Near maturity	
		Roots	Crowns	Roots	Crowns	Roots	Crowns	Roots	Crowns	Roots	Crowns
Big sagebrush	1967	65	38	—	—	52	29	45	28	26	18
	1968	63	30	47	28	47	30	44	26	47	30
	1969	53	29	39	22	48	26	38	25	35	20
	Avg	60	32	43	25	49	28	42	26	36	23
Black sagebrush	1967	47	26	—	—	41	25	36	26	23	20
	1968	50	29	49	25	45	26	43	28	48	26
	1969	42	26	48	23	43	27	30	22	40	25
	Avg	46	27	48	24	43	26	36	25	37	24
Shadscale	1967	118	70	—	—	91	58	77	51	48	48
	1968	112	58	74	62	86	47	92	59	63	41
	1969	103	57	98	49	100	58	61	44	72	55
	Avg	111	62	86	56	92	54	77	52	61	48
Nuttall saltbush	1967	174	91	—	—	163	107	180	112	139	97
	1968	173	109	165	86	163	90	160	92	119	80
	1969	155	94	152	88	158	89	150	84	122	83
	Avg	168	98	158	87	161	95	165	96	126	86
Winterfat	1967	72	56	—	—	77	55	68	51	49	50
	1968	77	56	66	50	60	46	66	57	53	49
	1969	88	60	66	53	62	53	56	51	60	50
	Avg	79	57	66	52	66	51	63	53	54	50
Indian ricegrass	1967	44	80	—	—	41	67	41	52	28	39
	1968	38	74	34	59	39	80	28	40	24	32
	1969	47	78	50	68	44	62	28	45	25	46
	Avg	43	77	42	64	42	70	32	46	26	39
Needle-and-thread	1967	52	62	—	—	46	64	47	57	33	42
	1968	44	68	40	45	38	49	35	50	31	32
	1969	39	58	45	50	38	37	30	36	27	40
	Avg	45	63	42	47	40	50	37	48	30	38
Squirreltail	1967	131	109	—	—	123	115	126	84	104	76
	1968	112	102	103	84	102	97	93	84	114	98
	1969	116	80	84	88	61	59	84	62	90	60
	Avg	120	97	94	86	95	90	101	77	103	78

[1] Defoliation treatments were not initiated until the spring of 1967; therefore, no data were available for the quiescence defoliation treatment the first year of the study.

than in the crowns after clipping (Fig. 3). Coyne (1969) believed that roots were more important storage organs than crowns in both big sagebrush and black sagebrush.

Big sagebrush and black sagebrush had the lowest TAC reserve storage levels of any species studied (Table 2). These two species also had less regrowth following defoliation than did most other species studied. Therefore, sagebrush vigor may be related to the small concentration of TAC reserves that are available for regrowth following defoliations.

Significant differences among autumn TAC levels for plants from the various defoliation treatments could not be demonstrated for Nuttall saltbush and squirreltail. However, carbohydrate levels in control plants were usually slightly higher than TAC levels in defoliated plants (Table 2). Both Nuttall saltbush and squirreltail had larger TAC reserves in the autumn after defoliation treatment than other species studied and usually had greater regrowth after defoliation treatments than did any of the other species. These two species had two growth cycles during the wet late-summer and early-fall of 1968. Therefore, this study indicates that there may be a relationship between the level of TAC reserves stored by a plant species and the ability of the species to withstand defoliation or clipping treatments. Cook (1971) indicated that these two species withstood clipping treatments at different seasons and intensities better than many desert species.

Winterfat usually did not make good growth recovery following any defoliation treatment. Therefore,

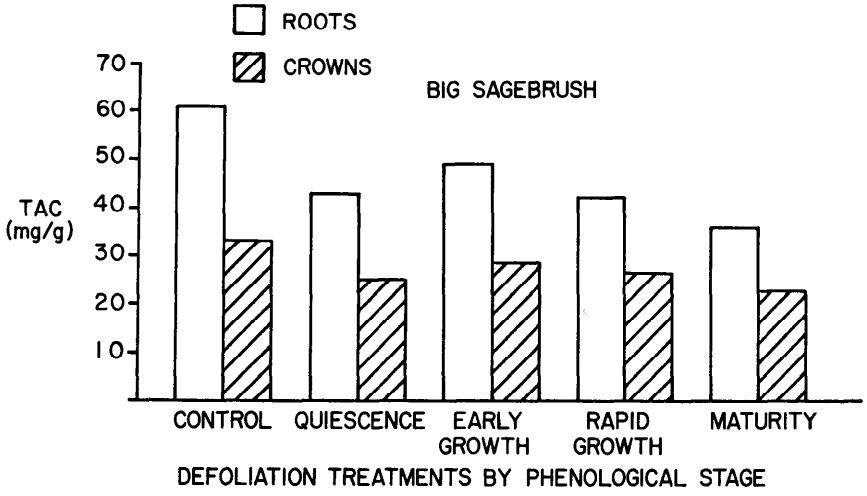

FIG. 3. Average total available carbohydrates (TAC) from the roots and crowns of big sagebrush in the fall from five defoliation treatments. The TAC levels represent an average for all locations for 1967, 1968, and 1969 in all treatments except the quiescence defoliations which were made only in 1968 and 1969.

the inadequate quantity of photosynthetic tissue produced by defoliated plants apparently limited carbohydrate synthesis and storage in this species (Fig. 4). The TAC concentrations among all defoliated plants were significantly ($P < .05$) lower than controls.

Defoliation effects on carbohydrate reserve storage in shadscale were greater for plants which had been defoliated during rapid spring growth or near maturity. Autumn reserve storage was not significantly different from the control, quiescence, and early spring growth defoliation treatments. However, TAC levels for shadscale were significantly higher ($P < .05$) in control plants than in plants that were defoliated during late spring growth and near maturity (Table 2). These differences were greater in TAC storage in roots than in the crowns.

Autumn TAC reserve stores in both roots and crowns of Indian ricegrass (Fig. 5) and needle-and-thread were usually somewhat higher among control plants compared with defoliated plants. However, TAC reserve storage in both species was significantly less ($P < .05$) when defoliations occurred during late spring growth or near maturity. Little regrowth was made in these grasses when they were defoliated during late spring growth or near maturity during flowering and seed development. Several researchers have reported that carbohydrate reserve storage in grass species was not significantly affected by defoliation or grazing treatments if the defoliation or grazing treatment were discontinued in time for substantial regrowth before fall quiescence (Sampson and McCarty, 1930; McCarty and Price, 1942; Hyder and Sneva, 1963; Paulsen and Smith, 1968). Such conclusions appeared to apply to Indian ricegrass and needle-and-thread in the present study, but not to squirreltail.

In the case of Indian ricegrass, TAC reserve storage in crowns was more affected by defoliation treatments than reserve storage in roots (Fig. 5). Coyne (1969) believed crowns to be more important than roots for TAC reserve storage in Indian ricegrass and needle-and-thread. Needle-and-thread crowns also contained the larger stores of carbohydrates than roots in the fall, but defoliation treatments affected both root and crown TAC reserve stores about the same (Table 2).

Summary and Conclusions

A study was conducted during 1967, 1968, and 1969 in northwestern Utah to determine the effects of defoliations during four phenological growth stages on carbohydrate reserve utilization and storage in desert plants. Carbohydrate levels were determined from root and crown samples for eight species: big sagebrush, black sagebrush, shadscale, Nuttall saltbush, winterfat, Indian ricegrass, needle-and-thread, and squirreltail.

Ninety percent of the plant's current photosynthetic tissue was removed by clippings during initial spring growth, late spring growth, near maturity, and fall quiescent

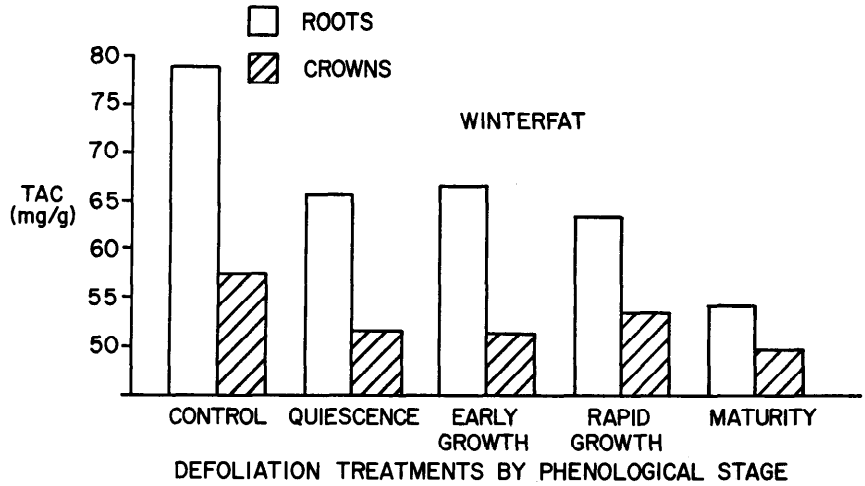

FIG. 4. Average total available carbohydrates (TAC) from the roots and crowns of winterfat in the fall from five defoliation treatments. The TAC levels represent an average for all locations for 1967, 1968, and 1969 in all treatments except the quiescence defoliations which were made only in 1968 and 1969.

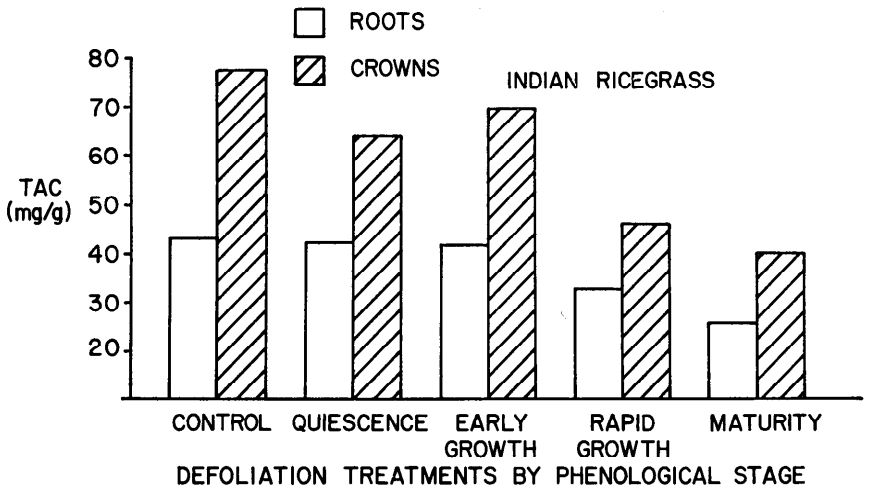

FIG. 5. Average total available carbohydrates (TAC) from the roots and crowns of Indian ricegrass in the fall from five defoliation treatments. The TAC levels represent an average for all locations for 1967, 1968, and 1969 in all treatments except the quiescence defoliations which were made only in 1968 and 1969.

phenological stages. Defoliated and control plants were excavated to a 30 cm depth and root and crown samples were taken for total available carbohydrate (TAC) analysis. Carbohydrate samples were taken during each of the three years at four harvesting periods; when defoliated plants had attained about 20% regrowth, and during the autumn when plants were quiescent.

Carbohydrate utilization to produce approximately 20% regrowth following defoliation was measured by comparing control and defoliated plants. The quantity of reserve depletion varied widely among treatments and among species. Squirreltail showed marked depletion in TAC in nearly all treatments. Most species which had been defoliated during late spring growth and when plants approached maturity had significantly smaller reserve stores than controls by fall quiescence. Species which made little regrowth after defoliation treatments had low fall TAC storage.

Root TAC concentrations were usually more affected than crown TAC concentrations by defoliation treatments. This was true for all species studied except Indian ricegrass and needle-and-thread, in which crown TAC levels were usually more affected than root TAC levels.

Both Nuttall saltbush and squirreltail had larger TAC reserves and usually had greater regrowth after defoliation treatments than did any of the other species studied. This indicated that a relationship may exist between the level of TAC reserves stored by a species and it's ability to withstand grazing or defoliation treatments.

Little relationship existed between the TAC level of a plant at the time of defoliation and the amount of carbohydrates used for regrowth. However, the concentration of carbohydrates stored by fall quiescence following defoliation was markedly affected by the ability of the plant to regrow and complete its annual life cycle. There was a direct relationship between average TAC levels in the autumn and the amount of regrowth made after defoliations. The TAC level of a species in the autumn appears to be a good indicator of treatment effects during the preceding growing season.

Literature Cited

ASSOCIATION OF OFFICIAL AGRICULTURAL CHEMISTS. 1965. Official methods of analysis of the Association of Official Agriculture Chemists. 10th ed. Washington, D. C. p. 498–499.

BROWN, R. H., AND R. E. BLASER. 1970. Soil moisture and temperature effects on growth and soluble carbohydrates of orchardgrass (*Dactylis glomerata*). Crop Sci. 10:213–216.

COOK, C. W. 1966. The role of carbohydrate reserves in managing range plants. Utah Arg. Exp. Sta. Mimeo Series 499. 11 p.

COOK, C. W. 1971. Effects of season and intensity of use on desert vegetation. Utah Agr. Exp. Sta. Bull. 483. 57 p.

COYNE, P. I. 1969. Seasonal trend in total available carbohydrates with respect to phenological stage of development in eight desert range species. Unpublished Ph.D. dissertation. Utah State University, Logan, Utah. 164 p.

COYNE, P. I., AND C. W. COOK. 1970. Seasonal carbohydrate reserve cycles in eight desert range species. J. Range Manage. 23:438–444.

DONART, G. B. 1968. Carbohydrate reserves in mountain range plants with respect to phenological stage of development and artificial defoliation. Unpublished Ph.D. dissertation. Utah State University, Logan, Utah. 70 p.

DONART, G. B., AND C. W. COOK. 1970. Carbohydrate reserve content of mountain range plants following defoliation and regrowth. J. Range Manage. 23:15–19.

Everson, A. C. 1966. Effects of frequent clipping at different stubble heights on western wheatgrass (*Agropyron smithii*, Rydb.). Agron. J. 58: 33–35.

GROTELUESCHEN, R. D., AND D. SMITH. 1967. Determination and identification of nonstructural carbohydrates removed from grass and legume tissue by various sulfuric acid concentrations, takadiastase and water. Agr. and Food Chem. 15:1048–1051.

HEINZE, P. H., AND A. E. MURNEEK. 1940. Comparative accuracy and efficiency in determination of carbohydrates in plant material. Mo. Agr. Exp. Sta. Res. Bull. 314. 23 p.

HYDER, D. N., AND F. A. SNEVA. 1963. Morphological and physiological factors affecting the grazing management of crested wheatgrass. Crop Sci. 3:267–271.

JAMESON, D. A. 1963. Responses of individual plants to harvesting. Bot. Rev. 29:532–594.

LAYCOCK, W. A., AND P. W. CONRAD. 1969. How time and intensities of clipping affect tall bluebell. J. Range Manage. 22:299–303.

MCCARTY, E. C. 1935. Seasonal march of carbohydrates in *Elymus ambiguous* and *Muhlenbergia gracilis* and

their reaction under moderate grazing use. Plant Physiol. 10:727–738.

McCarty, E. C., and R. Price. 1942. Growth and carbohydrate content of important mountain forage plants in central Utah as affected by clipping and grazing. U. S. Dep. Agr. Tech. Bull. 818. 51 p.

McConnell, B. R., and G. A. Garrison. 1966. Seasonal variation of available carbohydrates in bitterbrush. J. Wildlife Manage. 30:168–172.

Paulsen, G. M., and D. Smith. 1968. Influence of several management practices on growth characteristics and available carbohydrate content on smooth bromegrass. Agron. J. 60:375–379.

Priestly, C. A. 1962. Carbohydrate resources within the perennial plant. Commonwealth Bureau of Hort. and Plantation Crops Tech. Communication 27. 116 p.

Reynolds, J. H., and D. Smith. 1962. Trend of carbohydrate reserves in alfalfa, smooth bromegrass, and timothy grown under various cutting schedules. Crop Sci. 2:333–336.

Robison, G. D., and M. A. Massengale. 1968. Effect of harvest management and temperature on forage yield, root carbohydrates, plant density and leaf area relationships in alfalfa (*Medicago sativa* L. cultiver "moapa"). Crop Sci. 8:147–151.

Sampson, A. W., and E. C. McCarty. 1930. The carbohydrate metabolism of *Stipa pulchra*. Hilgardia 5: 61–100.

Smith, D. 1962. Carbohydrate root reserves in alfalfa, red clover, and birdsfoot trefoil under several management schedules. Crop Sci. 2:75–78.

Smith, D., G. M. Paulsen, and C. A. Raguse. 1964. Extraction of total available carbohydrates from grass and legume tissue. Plant Physiol. 39: 960–962.

Sprague, V. G., and J. T. Sullivan. 1950. Reserve carbohydrates in orchard grass clipped periodically. Plant Physiol. 25:92–102.

Troughton, A. 1957. The underground organs of herbage grasses. Commonwealth Bur. Pastures and Field Crops Bull. 44. 163 p.

Weinmann, H. 1943. Root reserves of South African highveld grasses in relation to fertilizing and frequency of clipping. J. South African Bot. 10: 37–54.

Weinmann, H. 1947. Determination of total available carbohydrates in plants. Plant Physiol. 22:279–290.

Weinmann, H. 1961. Total available carbohydrates in grasses and legumes. Herbage Abst. 31:255–261.

Wolf, D. D., K. L. Larson, and D. Smith. 1962. Grass-alfalfa yields and food storage of associated alfalfa as influenced by height and frequency of cutting. Crop Sci. 2:363–364.