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CARBOHYDRATE TRANSLOCATION IN BLUE GRAMA, BUFFALO GRASS, AND WESTERN WHEATGRASS AS INFLUENCED BY TEMPERATURE AND GROWTH STAGE

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ABSTRACT

A study was undertaken to examine the effects of temperature and stage of growth on the translocation of $^{14}\mathrm{C}$ to blue grama, buffalo grass, and western wheatgrass roots. Accumulation of $^{14}\mathrm{C}$ in blue grama and western wheatgrass roots was significantly affected by temperature and growth stage, respectively. Temperature and growth stage did not significantly influence $^{14}\mathrm{C}$ accumulation in buffalo grass roots.

INTRODUCTION

Over the past 15 years studies on the movement and distribution of organic solutes within plants has drawn the interest of many investigators and given this field considerable impetus, especially with the advent of radioactive tracers. The long-lived radioisotope of carbon (14°C) has been particularly helpful in following the path of carbon through the plant after assimilation. With the results of these tracer studies a consistent pattern of translocation is being derived which will help clarify some growth analysis observations. These studies are essential to the understanding of how climate and agricultural practices affect plant growth. With this knowledge it should be possible to select plants capable of producing the highest yields possible under the existing environmental conditions.

The purpose of this study was to examine the effects of temperature and growth stage on translocation of carbon in blue grama (Bouteloua gracilis H.B.K.), buffalo grass (Buchloe dactyloides Nutt.), and western wheatgrass (Agropyron smithii Rydb.). The study was divided into three separate experiments. Experiment 1 was conducted: (i) to determine the necessary amount of radioactive ¹⁴C needed for adequate plant labeling, (ii) to test the apparatus designed for use in labeling plants, and (iii) to determine some translocation characteristics of each grass. Experiment 2 was designed to determine the time course of sucrose labeling for the three grasses. The effect of temperature and growth stage on carbon translocation and photosynthate distribution in each grass was determined by Experiment 3.

REVIEW OF LITERATURE

Carbohydrate Movement From the Leaf

Following a buildup of assimilates in the photosynthetic tissue of a leaf, there seems to be a movement of only a certain amount and kind of substances into the conducting phloem tissue. Sugars, usually sucrose, but in some plants stachyose or other carbohydrates, generally constitute the bulk of organic material moving through the phloem. A considerable number of nitrogenous compounds and steroids are also known to be translocated (Biddulph and Cory, 1965; Clauss, Mortimer, and Gorham, 1964; Mittler, 1953; Mortimer, 1965; Trip, Nelson, and Krotkow, 1965; Webb and Burley, 1962, 1964; Zimmermann, 1958). Generally, this movement of assimilates into the conducting tissue occurs against a concentration gradient (Bieleski, 1966; Phillis and Mason, 1933; Roeckl, 1949). Also, energy is required for the transfer of assimilates from photosynthetic to conducting tissue (Ullrich, 1962; Ziegler, 1956). A reason for a reduction in light intensity reducing not only the photosynthetic rate but also the proportion of assimilates moved from leaves (Hartt, Kortschak, and Burr, 1964; Hartt and Kortschak, 1967) may be related to an alteration in the products of photosynthesis, but part of the effect may be that the energy required to transfer the assimilates from leaf to conducting tissue may have also dropped. Limiting the rate of photosynthesis by reducing the carbon dioxide concentration, however, has been shown to increase the transfer of assimilates to conducting tissue (Nelson, 1963). Although this effect may be related to a failure to divert carbon into leaf storage products during low rates of carbon dioxide fixation, there is also the possibility that because less energy is used for carbon dioxide fixation, more energy is available for transfer.

Pristupa (1964) demonstrated the movement of assimilates from the photosynthetic tissue into the conducting vessels of small vascular bundles and within 3 hr into the phloem of large bundles with a series of microautoradiographs of cereal leaves treated with 14CO2. The rate of movement of assimilates out of the leaf can vary. For example, in tobacco 46% of the carbon assimilated at any one time may have left the leaf in 3 hr (Clauss et al., 1964) and 68% in 96 hr. Porter and Bird (1962) found a much slower initial loss of assimilates from a tobacco leaf that had been kept in darkness for 48 hr prior to the assimilation of 14 CO $_{2}$. Joy (1964) found that about 50% of the carbon assimilated was translocated from the leaf of a sugar beet within 24 hr and about 70% in 3 days; however, Mortimer (1965) showed that up to 60% of the assimilated carbon could be exported within 4 hr. The movement from the leaf of labeled carbon assimilated during grain development in wheat may be almost complete in 24 hr, or it may take several days (Lupton, 1966). It has been reported that only 20% of the assimilated carbon was exported from a tomato leaf 24 hr after assimilation (Khan and Sagar, 1966). Less than 30% of the assimilates moved out of a pine seedling branch in 3 days (Balatinecz, Forward, and Bidwell, 1966); however, there probably was actively growing tissue within the branch itself which could explain the slow movement.

Although a general translocation pattern seems to exist with an initial rapid transfer of assimilates from the leaf which is followed by a slower movement (Clauss et al., 1964), it is not always clear from published data as to the cause of the great variations of assimilate transfer from a fully grown leaf. It is dependent not only upon factors within the leaf but also upon the ability of other parts of the plant to use or store the available

assimilates (Hansen, 1967; Hew, Nelson, and Krotkov, 1967; King, Wardlaw, and Evans, 1967). Where leaf area is large relative to the growth requirements for carbohydrates, the demand for assimilates per unit leaf area will be small. Removal of the upper part of a leaf in Lolium temulentum L., thus reducing leaf area relative to growth, stimulated the transfer of carbohydrates from the remaining basal area (Evans and Wardlaw, 1964). However, in sugarcane the opposite effect was obtained from removal of the upper part of a leaf blade. A reduction in flow of assimilates from the remainder of the leaf was incurred (Hartt, et al., 1964). Another factor in the modification of carbohydrate movement from the leaf may be the ability of a leaf to temporarily store excess carbohydrates (Mortimer, 1965).

Very young leaves obtain their carbohydrates as exports from older leaves. Not until they reach one-third to one-half of the maximum leaf area is their assimilation of carbohydrates high enough to meet the growth requirements and is the export of assimilates started (Forde, 1965; Webb and Gorham, 1964). Leaves have been shown to be most active in exporting assimilates soon after reaching their maximum size, and the rate of export declines steadily with age (Clauss et al., 1964; Vyvyan, 1924).

Assimilate Distribution in Relation to Leaf Position

There is a pattern of assimilate distribution in most plants that shows a relation to leaf position. The lower leaves act as the main source of assimilates for the shoot apex. The intermediate leaves may transport assimilates in either direction. This pattern has been shown to occur in many plants, and even grasses and cereals (Evans and Wardlaw, 1964; Williams, 1964). When considering the direction of movement of assimilates, it must be

remembered that a living plant is not a static organism and that the position of the leaf relative to the shoot is forever changing. Thus, a typical pattern of distribution of assimilates has been shown for wheat (Doodson, Manners, and Myers, 1964) and the perennial grass, timothy (Williams, 1964). This pattern indicates that initially a young leaf exports to the adjacent shoot apex; but as development advances and more leaves separate this leaf from the shoot apex, an increasingly greater proportion of the assimilates move to the roots. One exception to this general pattern is the observation by Khan and Sagar (1966) that in tomato plants 14 C assimilated by the lower leaves moved upward to the shoot apex, while assimilates from the upper leaves moved downward. The upward movement from the lower leaves might be explained by a redistribution of assimilates that first moved downward and then subsequently moved back to the shoot apex through the xylem (Winter and Mortimer, 1967). Also, Bonnemain (1965) has demonstrated that the vascular traces of a tomato leaf unite with the other vascular traces only at the node below the point of insertion of the leaf. Therefore, the assimilates have to travel through one internode downward before moving up to the shoot apex. In the work by Khan and Sagar (1966) the flow of assimilates from the upper leaves was very slow so that, at the time of harvest, it would have appeared that many of the assimilates were still traveling that passage through the internode and actually appeared to be moving downward.

Assimilate Demand

During early growth a leaf will require carbohydrates from other parts of the plant. Once the leaf is fully developed, it is no longer capable of importing assimilates, even when placed in darkness (Aronoff, 1955; Doodson

et al., 1964; Rabideau and Burr, 1945; Williams, 1964). Some exceptions occur and appear to involve the redistribution of leaf assimilates back through the xylem (Eschrich, 1966; Williams, 1964) or occur when movement into the leaf has been stimulated by the addition of growth substances (Booth et al., 1962).

Movement of assimilates away from the site of assimilation may continue even when the leaves are detached or isolated by ringing. However, this movement is greatly enhanced by growing tissues and storage organs (Aronoff, 1955; Hartt, 1962; Hartt and Kortschak, 1964; Humphries, 1963). Tissues differ in their demand for assimilates, and there are a number of mechanisms that can cause these differences. First, there is the ability to deplete the supply of carbohydrates and, thus, create a concentration gradient in favor of movement to the certain organ. Consequently, either the intensity of metabolism and the active unloading of the vein system (Geiger, 1966), or the number of sites of utilization and the size of a growing organ may be important. Distance from the site of assimilation to the organ may be important in developing and maintaining a concentration gradient. growth substances, moving out from the organ, may either suppress the development of alternate sites of assimilate utilization or alternately stimulate translocation of assimilates through the vascular system to the sites of utilization (Booth et al., 1962; Davies and Wareing, 1965; Hew et al., 1967; Muller and Leopold, 1966; Seth and Wareing, 1967).

It has been suggested (Wardlaw, 1968) that flowers are a weak sink and fruits a strong sink in grapes. Regrowth of corn following removal of the cob (Loomis, 1945) suggests that fruits develop at the expense of vegetative growth (Lenoard, 1962). Dominance of reproductive over vegetative organs

has been illustrated several times by the pattern of assimilate distribution or changes in pattern following leaf or fruit removal (Bonnemain, 1965; Hansen, 1967; Khan and Sagar, 1966; Wardlaw, 1965), whereas in trees, heavy seed production may be associated with decreased secondary thickening (Kozlowski and Keller, 1966). Although in cereals there may be some movement of assimilates from the ear to the developing stem during the initial stages of grain development, this movement seems to stop as stem development stops, and an increased movement of assimilates to the grain is noticed (Buttrose and May, 1965). This same restriction in movement is evident in pods of bean plants; however, up to half of the assimilates could be exported from a green pod if this was the only portion of the plant illuminated (Wanner and Bachofen, 1961). The exported assimilates are then moved to other pods of the plant. The sugar beet (Geiger, 1966) also appears to dominate vegetative growth in a manner similar to fruits.

Growth of established shoots appears to have priority over root and bud growth where conditions simulate assimilate deficiency (Evans and Wardlaw, 1963). In *Pinus*, Nelson (1964) observed that translocation of assimilates to the roots under low light intensities was less than under high light intensities. Roots and buds appear to be parts of the plants that are low in priority for assimilates compared to other organs in a plant and only receive assimilates in excess of the requirements of other parts.

The relative abilities of roots and buds to obtain assimilates depend on many conditions. Roots on intact shoots growing under low light conditions will continue to grow slowly, although bud development is almost totally inhibited. However, if the shoot apex is removed, as often occurs with

severe defoliation of pasture species, the buds are released from apical dominance and then grow at the expense of the root system (Milthorpe and Davidson, 1966).

Within the shoot there may be competition for assimilates between the shoot apex, leaves at different stages of development, and expanding stem tissue. The apex, because of its small size, will not have a large demand for assimilates, but the intensity of this demand may be high. The actual apex, if relatively inactive, might be expected to show retarded development during periods of general assimilate deficiency. Friend, Helson, and Fisher (1962) working with wheat found that differences in light intensity had only slight effects on the development of the apex.

A leaf at the stage of most rapid development seems to retard the growth of the next youngest leaf above it (Vyvyan, 1924). Stem expansion could occur at the same time leaf expansion is occurring and may compete with young leaves for assimilates. However, studies of this phenomenon have not been undertaken to show its importance. Competition between the stem and developing ear for assimilates in cereals has been shown by Friend (1965), when he found that both stem height an ear length increased with increasing light intensity up to 2,500 footcandles.

Although storage organs actively accumulate assimilates, the leaves, stem, and roots have some capabilities for holding excess carbohydrates such as starch, oligosaccharides, or simple sugars. Temporary storage of assimilates in the stem of cereals, at the time of anthesis, is followed by a redistribution of these materials to the ear and new shoots (Stoy, 1965).

Environmental Factors Affecting Carbohydrate Distribution

After considering the previous factors, it should be evident that the environment can control the distribution of assimilates in one or more ways. Environmental factors may affect assimilate distribution by causing changes in the rate of growth of developing organs (which also may be influenced by hormonal levels, by alterations in photosynthetic levels, and by outflow of assimilates from leaves) or by directly affecting movement of assimilates. Also, changes in plant development, e.g., from leaf production to flower and fruit formation, will add to the above effects.

Temperature. With shifts in temperature there is often a marked change in the development pattern of plants, much of which is presumably caused by direct growth rate change of the developing organs. The accumulation of soluble carbohydrates at low temperatures suggests that growth rates are affected more by temperature than are photosynthetic rates (Evans and Wardlaw, 1964): however, the differences in response may be due somewhat to a limitation of photosynthesis at higher temperatures through an inadequate supply of carbon dioxide (Gaastra, 1963). Reduced growth due to low temperatures has been shown to reduce the rate of assimilate translocation (Hartt, 1965a: Vernon and Aronoff, 1952; Whittle, 1964); however, since translocation itself is a metabolic process, it may be directly affected by temperature. For example, where the photosynthetic rate does not fail with low temperatures, but shoot growth declines, more assimilates will become available for the growth of roots and buds. Therefore, the change in distribution of assimilates with falling temperature is not necessarily associated with differences in the optimum temperature for growth of different plant organs. Friend (1966) found the optimum temperature for growth of attached roots in wheat

Translocation of assimilates from the leaves of sugarcane was found to be more dependent on root than shoot temperature (Burr et al., 1958). Part of this effect could be related to the production of tillers from the base of the sugarcane plant where temperatures will be close to those of the root system. Also, any change in temperature may affect nutrient uptake.

Although there is evidence to infer that movement of assimilates through conducting tissue is associated with metabolically active cells and may be dependent upon temperature, there is no conclusive evidence that reduced translocation is ever the primary cause of limiting growth under conditions of low temperatures. There is little indication from most work that the optimum temperature for translocation differs from that for growth. Hsia, Waon, and Wang (1963) concluded from their work on wheat. in which they lowered the temperature on the ear, stem, and flag leaf separately, that the effect of temperature on the distribution of assimilates from the flag leaf was primarily dependent on the growth of the ear and to a lesser extent on the function of the leaf. Lowering the temperature of the stem from 20°C down to 8°C had no observable effect on assimilate distribution. The effect of temperature on the regions of growth and assimilate movement out of the leaf was assumed to be related to the energy requirements of these processes (Geiger, 1966; Ullrich, 1962). The failure of Hsia et al. (1963) to find any direct effect of temperature on translocation is not in accordance with the results of several other workers who have shown that local stem or petiole temperatures from 0°C to 5°C inhibited the movement of applied ^{32}P

and of 14 C assimilates (Swanson and Whitney, 1953; Webb, 1967; Webb and Gorham, 1965).

The effect of temperature on translocation may be transient as shown by the work of Swanson and Geiger (1967) on sugar beets. Whittle (1964) has suggested that the recovery of translocation under low temperatures could be related to a buildup of sugars in the supply regions of the plant, and hence, the development of a steeper sugar concentration gradient through the cooled zone. However, Ford and Peel (1966) concluded, from their work on the relation between temperature and movement of $^{14}\mathrm{C}$ through a willow stem to an aphid colony, that lateral movement out of the sieve tubes is metabolic and dependent on temperature, whereas longitudinal movement down the length of the sieve tubes is independent of temperature. Perhaps temperature effects on cell-membrane permeability and lateral release of assimilates could explain some of the effects of temperature on translocation. It is apparent that this aspect still needs clarification not only in relation to the effects of temperature on the pattern of assimilate distribution but also in relation to the mechanism of translocation. However, it seems likely that the primary effect of temperature on assimilate distribution is associated with growth rather than sugar conduction, as the shifts in distribution of assimilates with reduced temperature are the reverse of the changes normally associated with a decrease in assimilate supply.

Light. Even though the pattern of assimilate movement is influenced by the relative ability of different organs to "attract" the available carbohydrate, it is also influenced by the rate of assimilate production in photosynthesis, which is regulated by the duration of intensity of light.

Root and bud growth are inhibited to a greater extent than shoot growth by

a reduction in light. Nelson et al. (1961) observed reduced movement of $^{14}\mathrm{C}$ assimilates from the needles to roots in conifers grown under low light.

Although root growth is more restricted than shoot growth under low light, there are some instances where it has been shown that, of the assimilates leaving a leaf, the proportion moving to the root system is greater in the dark than in the light (Nelson, 1964; Nelson and Gorham, 1957). Thrower (1964) has shown that a reduction in the rate of photosynthesis of an expanding soybean leaf, due either to darkening or a reduction in the supply of carbon dioxide, results in a smaller demand and reduced import of assimilates into the growing leaf. Such an effect could explain the observed differences in assimilate distribution pattern between light and dark. Translocation of assimilates to the growing organs throughout a normal 24-hr cycle may occur largely in the dark period or largely in the light period (Mason and Maskell, 1928). However, under low light conditions with less accumulation of carbohydrates in leaves and stems, translocation during the dark period is likely to become far less important than during the light period. Therefore, by reducing movement of assimilates during darkness, the over all effect would be to increase the relative proportion of assimilates reaching the shoot.

Movement of assimilates out of a leaf, as mentioned earlier, is influenced by light energy. Therefore, not only is the rate of photosynthesis reduced under low light but also the proportion of assimilated carbon leaving the leaf. Hartt and Kortschak (1964) and Hartt (1965b) have suggested that there is a light process involved in translocation in a sugarcane leaf, with a maximum response at low intensities (approximately 100 footcandles). However, Shanigina (1965), working with tomatoes, has found that a decrease

in light intensity from about 3,600 down to 900 footcandles, which has only a small effect on leaf photosynthetic rate, results in a slower outflow of assimilates and an increase in leaf polysaccharides. This response of translocation to decreasing light intensities, at higher levels than those reported by Hartt (1956b), suggests that either sugarcane leaves respond in a different manner than leaves of other species or the response may have been affected by detaching the sugarcane leaves.

Day length, through changes in plant development, will have a considerable indirect effect on the distribution of assimilates. Nelson (1963) noted that movement of assimilates in larch was affected by day length through effects on root and shoot development. Perhaps the more conspicuous effects of day length are related to the change from vegetative to floral development, and probably the greater translocation of assimilates in long-day plants under long days and short-day plants under short days is the result of this developmental process.

water. Gates (1955a) has already pointed out that the effect of water stress on growth and therefore on the distribution of photosynthetic assimilates is not fully understood. Elongation growth commonly shows an early response to water stress, whereas photosynthesis and the accumulation of assimilates continues for some time after stress is evident in the elongation of the plant (Iljin, 1957). The observation by Slayter (1957) that dry weight accumulation ceased earlier than stem elongation in tomato plants is an exception. Other forms of growth are not so easily altered by stress as is elongation. For example, grain development in cereals may be unaffected by a stress that causes wilting of the leaves (Asana, Saini, and Ray, 1958). The response to water stress depends on the organs involved.

Iljin (1957) suggested that cells, such as those found in seeds, buds, and storage organs, which generally lack vacuoles and are filled with food reserves will be the most resistant to desiccation. It is resistance to desiccation rather than the ability of an organ to function with a low water content that appears to give an organ the ability to withstand water stress.

There are often marked alterations in the pattern of assimilate distribution when plants are subject to water stress. These alterations may be the direct result of reduced growth rates or of reduced photosynthetic rates, although there is some evidence for a more direct effect of stress on the conduction of assimilates.

The observation by Hartt (1967) of an increase in the sugar content of the stem when sugarcane plants are under water stress seems to fit Iljin's (1957) theory, i.e., "reduced growth under stress results in the accumulation of sugars." Hartt favors a direct cause-and-effect explanation in which sugar accumulation is the result of a reduced velocity of movement through the conducting system. This is somewhat similar to a view expressed earlier by Gates (1955a,b) who suggested that changes in the weight ratios of different plant organs when under stress were due to a modification of translocation. Roberts (1964) observed that water stress increased the upward movement of assimilates in yellow poplar. Also, during grain development of wheat, a water stress that caused reduced photosynthetic activity in the leaves resulted in an increased movement of assimilates from the lower leaves to the ear (Wardlaw, 1967). This is similar to translocation that occurs when assimilation is reduced under low light intensities.

The work of Plaut and Reinhold (1965) on the movement of applied sucrose in bean plants under water stress has been interpreted as showing that water stress directly alters translocation. Certainly, changes in xylem tension affect pressures within the sieve tubes of the phloem, as Peel and Weatherley (1962, 1963) demonstrated by measuring the exudation of phloem sap through aphid stylets. However, where growing organs are not subject to the same stress as the rest of the plant, as with the ear of wheat during grain development, velocity of movement of labeled assimilates through the conducting tissue was found to be relatively insensitive to stress (Webb and Burley, 1964). This is evidence, in part, for the suggestion by Nelson (1963) that water stress affects the movement of assimilates into but not through the conducting tissue. There is ample evidence that there is a reduction in the rate of movement of assimilates out of the photosynthetic tissue during water stress (Hartt, 1967; Plaut and Reinhold, 1965; Roberts, 1964; Wardlaw, 1967; Wiebe and Wihrheim, 1962). The close interaction between growth and translocation makes it difficult to assess the relative importance of these processes in determining the pattern of distribution of assimilates in plants under water stress. In the few instances where growth has been eliminated as a factor it appears that translocation is relatively insensitive to stress. Also, the observation by McWilliam (1968) of a significant movement of assimilates from stem to roots and buds in the perennial grass (Phalaris tuberosa L.O.) when the plants are dormant due to a restricted water supply, suggests that the transport system is insensitive to desiccation.

METHODS AND MATERIALS

Experiment 1

Blue grama, buffalo grass, and western wheatgrass seed harvested at Eads, Colorado; Lubbock, Texas; and Newell, South Dakota, respectively, was obtained from the Longmont Seed Co., Longmont, Colorado. Seedlings were started in flats of sand and then transplanted, one plant per pot, into plastic pots (12 cm in diameter by 13 cm in depth with drainage holes) containing sand when the plants were 5 to 10 cm in height. Plants were watered daily and given one-fifth strength Hoagland's solution (Hoagland and Arnon, 1950) once a week. The plants were maintained in a growth chamber with a 26.7°C day/21.1°C night temperature regime and an 18-hr photoperiod from cool-white fluorescent lamps and incandescent bulbs. The light source produced about 23,680 lux over the visible spectrum as measured with a Weston light meter.

Plants were labeled with 14 C, 8 to 9 weeks after transplanting by exposing two plants in a 6" \times 12" \times 18" plexiglass chamber to 40 μ C 14 CO $_2$ /plant for 10 min. The 14 CO $_2$ was released by dripping Na 14 CO $_3$ solution into 2 N H $_2$ SO $_4$ and then circulating it through the plexiglass chamber with an air pump. After 10 min the remaining 14 CO $_2$ was trapped by circulating the gas stream through a 1 N NaOH solution. The plexiglass chamber was removed and the plants remained in the growth chamber until harvest.

Two plants of each species were harvested 3, 9, and 24 hr after labeling. They were then washed and blue grama and buffalo grass were sectioned into upper and lower roots, crown (2-cm section above the roots), and herbage. Western wheatgrass was additionally sectioned into upper and lower rhizomes. Plant parts were immediately frozen with dry ice, freeze-dried, weighed, and

ground with a ball mill grinder. Samples of the plant material were then assayed for ¹⁴C activity by a modified Schoniger combustion technique (Schoniger, 1955) (Fig. 1). A weighed plant sample (10 to 25 mg) was wrapped in black weighing paper and placed within a nichrome wire coil suspended from the rubber stopper of a 250-ml Erlenmeyer flask. Ethanolamine (1 ml) was placed in the flask which was then purged with pure oxygen and tightly stoppered. The sample was ignited with an infrared light source, and the flask was allowed to set overnight to allow complete carbon dioxide diffusion to the trapping reagent. Ethylene glycol monomethyl ether (1 ml) was added to the flask and mixed. A 1-ml aliquot was added to 15 ml of a 1.3:1.9 (v/v) ethylene glycol monomethyl ether:toluene cocktail solution (Jeffay and Alvarez, 1961) and counted on a Beckman LS-150 liquid scintillation counter. The toluene cocktail was made by dissolving 5.5 g of 2,5-diphenyl-oxazole (PPO) and 0.3 g of 1,4-bis(2-(4-methyl-5-phenyloxazolyl))-benzene (dimethyl-POPOP) in one liter of toluene.

Results of radioactivity in each section are presented as percent of total plant activity.

Experiment 2

A sod of blue grama, buffalo grass, and western wheatgrass was obtained from the Pawnee Site north of Nunn, Colorado, and maintained in the greenhouse. Tillers of blue grama and western wheatgrass and stolons of buffalo grass were obtained from the sod and started in flats of sand on a rooting bench. Plants 5 to 10 cm tall were transplanted (one plant per pot) into plastic pots (12 cm in diameter by 13 cm in depth with drainage holes) containing sand. They were watered daily and given one-fifth strength Hoagland's solution (Hoagland and Arnon, 1950) once every week. Growth conditions were the same as in Experiment 1.

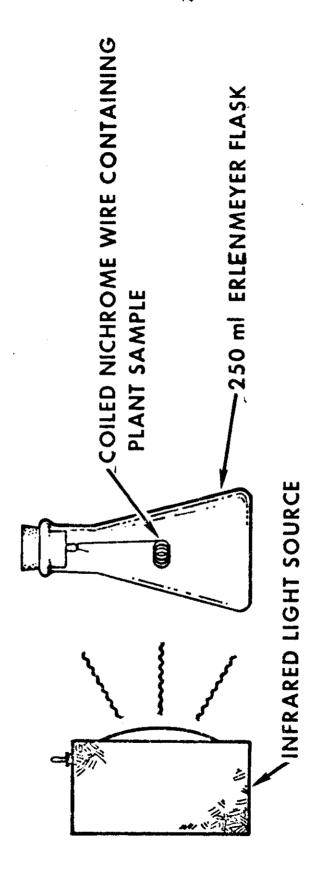


Fig. 1. Diagram of combustion apparatus.

Plants were labeled with ^{14}C at the vegetative growth stage by exposing 21 plants to 8.5 μc $^{14}\text{CO}_2/\text{plant}$ for 5 min in a plastic tent. A small fan inside the tent facilitated air movement. Method of ^{14}C exposure was as described in Experiment 1.

Plants were harvested 0.5, 1, 2, 3, 4, 5, and 6 hr after labeling; washed; and sectioned into herbage, crown (2 cm above the roots), and root tissue. The sectioned material was then treated as previously described in Experiment 1 except the dried tissue was ground to 40 mesh with a Wiley mill.

Sugars were extracted from the root tissue with 85% ethanol (v/v), filtered through Whatman no. 1 filter paper, and concentrated to approximately 3 ml in a rotary-evaporator with reduced pressure at 45°C. The extract was transferred to 13 imes 100 mm test tubes, taken to dryness, and re-extracted with ethylacetate:water (1:1 v/v) to remove nonpolar constituents. The upper phase containing much of the pigmentation in the sample was discarded. The lower phase was redried and taken up in 100 μ liter of 85% ethanol. Sugars were separated by thin-layer chromatography on cellulose precoated plastic sheets obtained from Brinkman Instruments, Inc. Six samples containing 10 to 50 μg sucrose in 20 $\mu liter$ were spotted on each plate with two standards and one blank spot. Sugars were separated according to a procedure described by Vomhoff and Tucker (1965). After separation the two outer strips containing the sugar standard markers were cut from the plate, sprayed with 0.1 g of p-anisidine HCl in 10 ml of 95% ethanol, and placed in a 110°C oven for development. The separated sucrose spots were located with the standard markers, scraped into a 15-ml centrifuge tube, and eluted with 2 ml of distilled water. The solution was mixed and

centrifuged at 1,000 rpm for 10 min. Two 0.5-ml aliquots were taken for sucrose analysis, and one 0.5-ml aliquot was taken for determination of radioactivity. The latter aliquot was added to toluene cocktail containing 9% (v/v) Biosolve- $3\frac{1}{2}$ and counted in a Beckman LS-150 liquid scintillation counter. Sucrose was determined by a ferricyanide technique (Furuholmen et al, 1964; Ting, 1956) modified to determine micro-quantities of sugar. The samples were hydrolyzed with 0.2 N $\rm H_2SO_4$ for 15 min in a boiling water bath, cooled, and heated again under the same conditions after addition of 5 ml of ferricyanide reagent (see Appendix I). After cooling, 3 ml of 7 N $\mathrm{H}_{2}\mathrm{SO}_{4}$ were slowly added, and the samples were mixed thoroughly to remove all gas. Finally, 4 ml of arsenomolybdate reagent (see Appendix II) were added and mixed immediately. Percent transmission of each sample was then read on a Bausch and Lomb Spectronic 20 spectrometer at $745~\mathrm{nm}$. A standard curve containing 0, 12.5, 25.0, 37.5, and 50.0 μg sucrose was determined with each set of samples and was used to obtain the μg of sucrose in each sample. The sucrose and radioactive data were used to calculate sucrose specific activity (dpm/µg sucrose).

Experiment 3

Blue grama, buffalo grass, and western wheatgrass plants were started as described in Experiment 2. Plants were grown on a greenhouse bench, grouped according to stage of growth, and then transferred to growth chambers with 32.2/26.7°C, 26.7/21.1°C, and 21.1/15.6°C day/night temperature regimes 1 week before labeling. All other growth conditions were the same as described for Experiment 2. Growth stages were selected as described in Table 1.

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Table 1. Criteria for selection of growth stages.

Species	Growth Stage Number	Plant Description		
Blue grama	1	Less than 50% of the heads at anthesis		
	2	50% or more of the heads at anthesis		
Buffalo grass	1	Two stolons or less per plant		
	2	Three stolons or more per plant		
Western wheatgrass	1	Less than 50 cm in height		
	2	Greater than 50 cm in height		

Plants were labeled as described in Experiment 2 except the tent was enlarged to facilitate 24 plants instead of 21.

Harvesting was carried out as described in Experiment 2 at 2 and 6 hr after labeling. Plants were divided into shoot and root sections, frozen, freeze-dried, weighed, and ground. Samples were combusted in duplicate as previously described to determine the radioactivity in each section. Results are presented as percent of total plant activity.

Statistical Analysis

All results were analyzed statistically with standard procedures, and Duncan's Multiple Range Test (Steel and Torrie, 1960) was used to compare treatment means. The experimental design for Experiment 1 was a split plot, and Experiments 2 and 3 were completely randomized.

The percentage data from Experiments 1 and 3 had to be transformed so that the linear additive models for standard statistical procedures would apply. Root and crown data were transformed with square roots. Shoot and herbage data were transformed by determining the square root of the difference between the total plant activity (100%) and the percent of total plant activity in the shoots or herbage. Therefore, in Experiment 3 the transformed values from roots and shoots are the same.

RESULTS AND DISCUSSION

Experiment 1

Distribution of ^{14}C among plant parts at three time periods after exposing each of the entire plant growing vegetatively to 40 μC $^{14}\text{CO}_2/\text{plant}$ for 10 min is shown in Table 2. It appeared that each grass translocated labeled carbon at different rates. Buffalo grass retained nearly all of the ^{14}C in the herbage while only 80% of the plant activity in blue grama

Table 2. Distribution of ^{14}C within plant parts at three time periods after exposing entire plants growing vegetatively at 26.7/21.1°C to 40 μc CO $_2/\text{plant}$ for 10 min.

Spe cie s	Plant Part	Percent Total Plant Activity		
		3 hr	9 hr	24 hr
Blue grama	Herbage	79.5	81.0	80.5
	Crown	13.1	10.5	12.4
	Upper roots	4.8	4.2	3.3
	Lower roots	2.6	4.2	3.8
Buffalo grass	Herbage	99.3	98.8	95.2
	Crown	0.3	0.4	1.7
	Upper roots	0.2	0.3	0.9
	Lower roots	0.1	0.5	2.2
Western wheatgrass	Herbage	81.0	72.6	64.9
	Crown	5.4	3.5	7.8
	Upper roots	10.4	12.7	17.6
	Lower roots	3.2	11.2	9.7

and western wheatgrass remained in the herbage after 3 hr. Translocation of $^{14}\mathrm{C}$ from herbage continued up to 24 hr (the last sample period) in western wheatgrass. In contrast movement of $^{14}\mathrm{C}$ activity out of blue grama herbage was nearly complete after 3 hr, and it only continued at a slow rate in buffalo grass. Western wheatgrass moved more $^{14}\mathrm{C}$ from herbage to crown and root plant parts than the other two grasses. Blue grama accumulated more of the translocated $^{14}\mathrm{C}$ in crown that root section while western wheatgrass accumulated more translocated $^{14}\mathrm{C}$ in the root sections. Translocation of $^{14}\mathrm{C}$ in buffalo grass was too small to establish a partitioning trend between crown and root sections. Except for western wheatgrass, distribution of $^{14}\mathrm{C}$ activity between upper and lower roots within grasses was nearly equal after 9 hr. The higher percentage of total plant activity in upper roots as compared to lower roots of western wheatgrass was probably due to the presence of more rhizomes in the upper root section.

Continued loss of ¹⁴C activity from the herbage of western wheatgrass indicates that this grass was still transporting carbon to the roots after 24 hr. Since these grasses were in early vegetative growth, the extra partitioning of radioactive photosynthate in western wheatgrass as compared to the other grasses was probably used for root and rhizome growth rather than for energy storage. Similarly, the lack of ¹⁴C accumulation in roots of buffalo grass probably reflects partitioning of photosynthate to rapidly growing stolons.

It was concluded from these results that partitioning of photosynthate within the three grasses at early vegetative growth stages was basically different. It was also found that it was not necessary to use 40 uc of $^{14}\text{CO}_2$ to label each plant as the method of analysis could detect lesser

quantities of radioactivity. The chamber used to label the plants was expanded to facilitate more plants and reduce the time involved in labeling.

Experiment 2

This study was designed to learn how rapidly and to what extent labeled sucrose entered the roots of buffalo grass, blue grama, and western wheatgrass and equilibrated with root sucrose pools. Fig. 2 shows the time course of root sucrose labeling in each grass after exposing entire plants to 8.5 µc $^{14}\text{CO}_2/\text{plant}$ for 5 min. Radioactive sucrose entering the roots of blue grama and western wheatgrass caused a rapid increase in the specific activity of the root sucrose pool for 2 to 3 hr after labeling. The decline in the specific activity of root sucrose after 3 hr indicated that some of the soluble sucrose pool was being used to form other types of carbon compounds. Therefore, the root sucrose pool appeared to be in dynamic exchange with the translocation stream.

The root sucrose labeling pattern of buffalo grass differed from the other two grasses in that two peaks in sucrose specific activity were observed. Furthermore, the specific activity of sucrose was not as high as in the other two grasses. However, buffalo grass did have the same characteristic rapid increase in sucrose specific activity from the 0.5- to 2-hr translocation period.

Further study and analysis of radioactivity within plant root carbohydrate fractions might better explain carbohydrate transformations in blue grama and western wheatgrass after the 3-hr translocation period and in buffalo grass after the 2-hr translocation period. Also, longer translocation periods should be used to determine how much of the labeled sucrose remains in the soluble sucrose pool. The results of this experiment

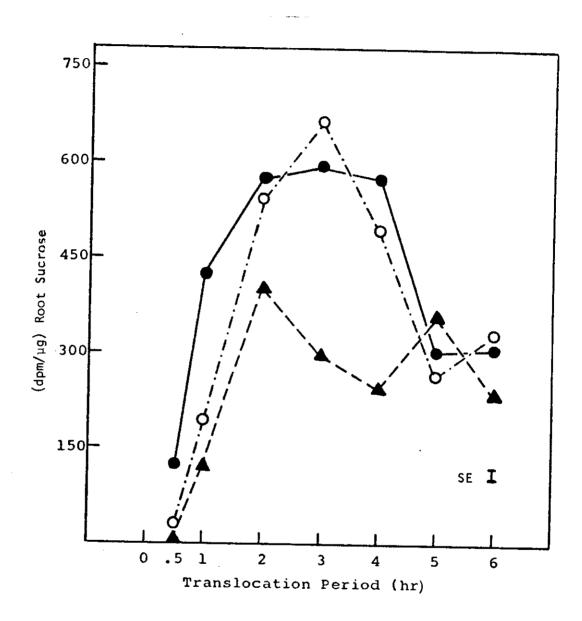


Fig. 2. Time course of root sucrose labeling in blue grama (---), buffalo grass (---), and western wheatgrass (---) after exposing entire plants to 8.5 μc ¹⁴CO₂ for 5 min.

3,"

indicated that the root sucrose pool was in equilibrium with the translocation stream.

Experiment 3

As indicated in the literature review, many environmental and plant morphological factors can affect carbon translocation. Studies were conducted to characterize the effect temperature and plant growth stage have on carbon translocation of blue grama, buffalo grass, and western wheatgrass.

Analysis of variance results are summarized in Appendix Table 3. Carbon partitioning between tops and roots, as indicated by ¹⁴C distribution, was affected by temperature in blue grama only when averaged over both translocation periods and growth stages. The significant time and temperature interaction (Appendix Table 3a) and the nonsignificant temperature effect at the 6-hr translocation period (Appendix Table 3g) indicated that the temperatures used influenced ¹⁴C distribution in blue grama more at the 2-hr than the 6-hr translocation period. Therefore, it was concluded that temperature did not significantly affect final photosynthate partitioning in the three grasses in the temperature regimes used in the study. It must be remembered, however, that all plants used in each temperature regime were grown on a greenhouse bench and were acclimated at the treatment temperature for only 1 week before beginning the translocation experiment. Therefore, these results do not reflect long-term growing conditions at the temperatures used in the experiments.

Plant growth stage significantly influenced partitioning of ^{14}C in western wheatgrass but not in blue grama or buffalo grass (Appendix Table 3). More of the total ^{14}C activity in western wheatgrass was found in roots at the earlier, as compared to the latter, growth stage (Appendix Table 5).

These significant differences may, however, be due to sampling before $^{14}\mathrm{C}$ partitioning was complete.

Fig. 3 graphically represents the interaction of temperature and translocation period on the percent total plant ¹⁴C activity in the roots. Accumulation of ¹⁴C in the roots of blue grama significantly increased with an increase in temperature (Appendix Table 5). As the temperature increased from 21.1/15.6°C to 26.7/21.1°C the rate at which ¹⁴C was partitioned to the roots more than doubled. Nearly all of the ¹⁴C activity observed in blue grama roots at 6 hr after labeling in the 26.7/21.1°C temperature regime was already present 2 hr after labeling. As the temperature increased to 32.2/26.7°C rate of ¹⁴C translocation declined again, but it was higher than at 21.1/15.6°C.

Accumulation of ¹⁴C in the roots of buffalo grass and western wheatgrass was not significantly affected by temperature (Appendix Table 3). However, an increase in temperature resulted in less transport of ¹⁴C to the roots of buffalo grass. Temperature did not influence the rate at which ¹⁴C was moved to roots of buffalo grass as indicated by the parallel lines representing root ¹⁴C activity at 2 and 6 hr after labeling (Fig. 3). Most of the ¹⁴C activity observed in the roots at 6 hr was already present 2 hr after labeling. Although not statistically significant, distribution of ¹⁴C to the roots of western wheatgrass was the highest at the 26.7/21.1°C temperature regime 6 hr after labeling. Initial rate of ¹⁴C translocation was lowest in western wheatgrass compared to the other grasses as shown by the low activity at the 2-hr sample period. Translocation rate increased slightly with temperature.

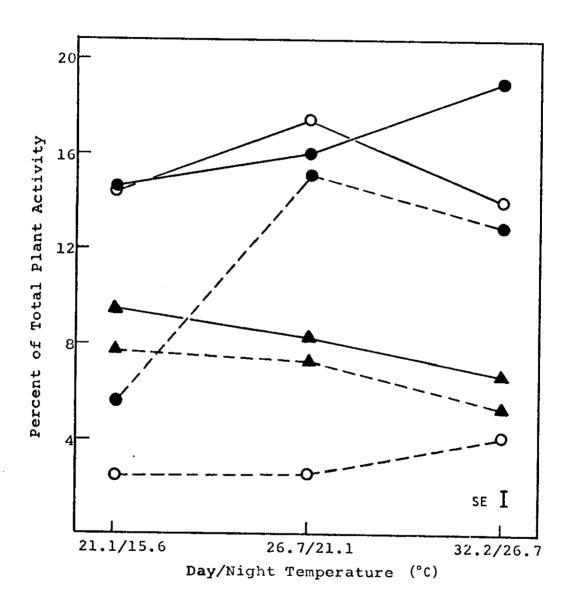


Fig. 3. Comparison of the percent total plant ¹⁴C activity in roots of blue grama (), buffalo grass (), and western wheatgrass (). The interaction of the three temperature regimes and the 2-hr () and 6-hr () translocation periods averaged over two growth stages is shown.

These results indicated that temperature influenced the accumulation of $^{14}\mathrm{C}$ in the roots of the three grasses although final partitioning of $^{14}\mathrm{C}$ between shoots and roots was not significantly affected by temperature.

Fig. 4 presents the interaction of total $^{14}\mathrm{C}$ activity in roots of the three grasses among temperatures and species averaged over time. Nonsignificant time imes temperature and time imes species imes temperature interactions at growth stages 1 and 2 (Appendix Table 3d and Table 3e, respectively) indicated that these interaction relationships were similar at both the 2- and 6-hr sample periods. At growth stage 1, partitioning of 14°C to roots of blue grama increased as the temperature changed from 21.1/15.6°C to 26.7/21.1°C and then declined somewhat. In contrast, ¹⁴C partitioning in buffalo grass and western wheatgrass was similar over the temperature range studied. At growth stage 2, $^{14}\mathrm{C}$ accumulation in the roots of blue grama increased from the coolest to the warmest temperature regime. However, 14C activity in growth stage 2 roots at 32.2/26.7°C was slightly lower than roots of growth stage 1 at the 26.7/21.1°C temperature regime. Buffalo grass responded to increasing temperature with a slight but steady decline in accumulation of 14 C in the roots. At growth stage 2 western wheatgrass accumulated more $^{14}\mathrm{C}$ in roots at 26.7/21.1°C than at either higher or lower temperatures. Differences in partitioning of $^{14}\mathrm{C}$ between tops and roots may reflect differences in root growth or reserve energy storage.

It must be remembered that data in Fig. 4 reflect the temperature and species interaction averaged over time. Consequently, temperature and growth stage effects on ^{14}C distribution to roots of each grass are not demonstrated for each translocation period. However, it was evident that ^{14}C distribution averaged over time was affected by temperature and growth stage.

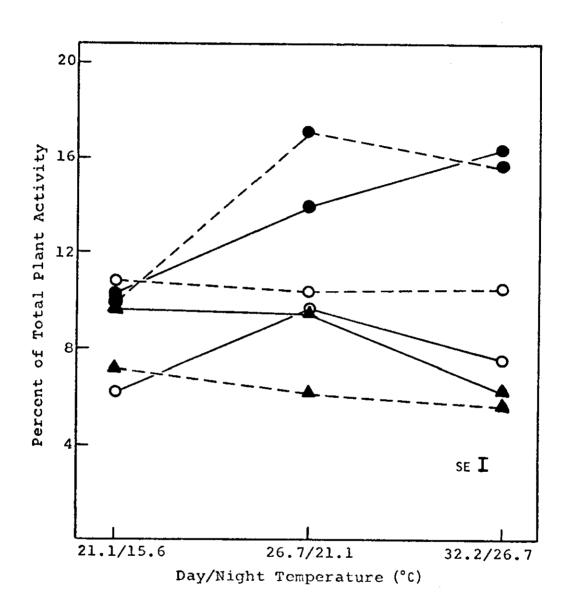


Fig. 4. Percent total plant C activity in roots of blue grama (●), buffalo grass (♠), and western wheatgrass (●). Comparison of growth stages 1 (———) and 2 (———) for an interaction of temperature and species averaged over time.

Interaction of species and time on ¹⁴C partitioning between tops and roots averaged over temperature is shown in Fig. 5. Although slope of the lines for each species was slightly different between growth stages, the growth stage × time interaction of ¹⁴C partitioning for each species was not significant (Appendix Tables 3a, 3b, and 3c). Buffalo grass and blue grama accumulated at least half of the total ¹⁴C detected in their roots by the 2-hr sample period. In contrast, western wheatgrass accumulated most of the total ¹⁴C observed in the roots between the 2- and 6-hr translocation period. Since the final distribution of ¹⁴C between tops and roots of blue grama and western wheatgrass was similar at growth stage 1, the rate of distribution apparently was higher in blue grama than western wheatgrass.

The literature was inconclusive as to whether carbon translocation is affected directly by temperature (Burr et al., 1958; Ford and Peel, 1966; Friend, 1966; Swanson and Geiger, 1967; Wardlaw, 1968; Webb, 1967) or through the growth rates of various organs as influenced by temperature (Ford and Peel, 1966; Hartt, 1965 α ; Hsia et al., 1963; Ullrich, 1962; Webb and Burley, 1964). The results from this study also seem inconclusive in this respect. However, they tend to show there is a distinct interaction between the effect of temperature and growth stage on the partitioning of $^{14}\mathrm{C}$ to the roots of blue grama, buffalo grass, and western wheatgrass. Western wheatgrass was the only grass in which stage of growth had a significant effect on $^{14}\mathrm{C}$ distribution (Appendix Table 3c). Distribution of $^{14}\mathrm{C}$ in buffalo grass was not significantly affected by temperature, translocation period, or growth stage (Appendix Table 3b). However, certain trends, such as a decrease in $^{14}\mathrm{C}$ accumulation with an increase in temperature at each growth stage, could be seen. Temperature and stage of growth influenced

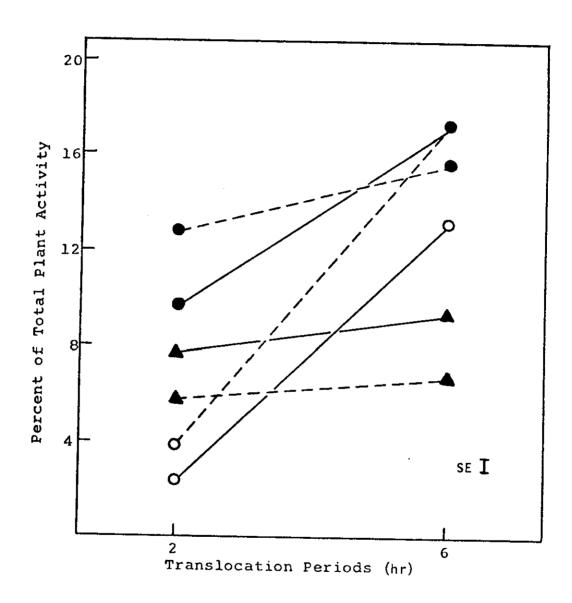


Fig. 5. Percent total plant ¹⁴C activity in roots of blue grama (♠), buffalo grass (♠), and western wheatgrass (♠). Comparison of growth stages 1 (← − −) and 2 (← −) for the interaction of species and time averaged over three temperatures.

translocation in blue grama quite differently than buffalo grass and western wheatgrass. Accumulation of $^{14}\mathrm{C}$ in the roots 6 hr after labeling appeared to increase as temperature increased. The variation in $^{14}\mathrm{C}$ accumulation in the roots due to growth stage could be an indication of the variation in assimilate demands as a result of differences in maturity.

This study attempted to demonstrate how temperature and growth stage affect translocation to the roots of blue grama, buffalo grass, and western wheatgrass. The results indicated that further study be conducted to obtain more information about the effect of growth stage on distribution of assimilates. The author contends there is a distinct interaction between these two parameters since roots at each growth stage of each grass accumulated ¹⁴C in varying amounts. Methods which should be considered in additional study include:

- 1. The use of a greater range of growth stages.
- 2. Analysis of sucrose specific activity as a measure of actual assimilate translocation.
- Temperature control on various plant parts to determine if temperature does affect translocation directly or through the growth rates of the various plant parts.

SUMMARY

The main objective of this study (Experiments 1, 2, and 3) was to determine the effect of temperature and stage of growth on the distribution of $^{14}\mathrm{C}$ to the roots of blue grama, buffalo grass, and western wheatgrass. The following conclusions were made from the results.

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Experiment 1

- The apparatus used to label the plants was adequate for this study;
 yet, the chamber could be enlarged to facilitate more plants and
 reduce time of labeling.
- 2. Labeling of plants with 40 μ c 14 CO $_2$ /plant was not necessary as the method of analysis used for plant analysis could detect lesser quantities of 14 C.
- 3. Blue grama accumulated the highest percentage of total plant ^{14}C activity in the roots 9 hr after labeling as compared to 3 and 24 hr after labeling.
- 4. Buffalo grass translocated the lease amount of 14 C to the roots as compared to blue grama and western wheatgrass, but it increased slightly in percent total plant activity as 14 C moved to roots up to 24 hr after labeling.
- 5. A loss in 14 C from the lower roots after the 9-hr translocation period and an increase in percentage 14 C in the crown tissue and upper roots of western wheatgrass 24 hr after labeling could indicate a slight upward movement of 14 C or a loss in the other plant parts due to respiration.

Experiment 2

 The rapid increase of sucrose specific activity in the roots of each grass from 0.5 to 2 hr after labeling indicates that a rapid interchange occurred between the translocation stream and the sucrose pool in the roots.

Experiment 3

- 1. All three grasses accumulated more total plant $^{14}\mathrm{C}$ activity in the roots at 6 hr than at 2 hr after labeling.
- 2. Temperature significantly affected translocation in blue grama with the highest percentage (16%) of ¹⁴C activity occurring in roots of the plants grown at the highest temperature (32.2/26.7°C). Buffalo grass roots decreased slightly in percent ¹⁴C activity with increasing temperatures. Accumulation of ¹⁴C in roots of western wheatgrass was highest at the 26.7/21.1°C temperature regime and declined at higher and lower temperature regimes.
- 3. Blue grama and western wheatgrass at growth stage 1 accumulated more ¹⁴C in 2 hr after labeling than plants of both grasses at growth stage 2. Buffalo grass reacted in the reverse of blue grama and western wheatgrass. Plants at growth stage 2 accumulated more ¹⁴C for both translocation periods than those at growth stage 1.

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APPENDIX I. ALKALINE FERRICYANIDE REAGENT

Dissolve 160 g anhydrous sodium carbonate and 150 g disodium phosphate hepta hydrate in 850 ml distilled water. Add 4.0 g potassium ferricyanide and dilute to 1 liter. Store in a brown bottle. Reagent is stable for 2 to 3 months.

APPENDIX II. ARSENOMOLYBDATE SOLUTION

Dissolve 25 g of ammonium molybdate tetrahydrate in 450 ml distilled water. Add 21 ml concentrated $\rm H_2SO_4$ followed by 3 g disodium arsenate in 25 ml distilled water. Heat to 55°C for 30 min with constant stirring in a water bath or in an incubator at 37°C for 24 to 48 hr. Store in a brown bottle. Reagent is stable for 2 to 3 months.

APPENDIX III APPENDIX TABLES

Appendix Table 1. Analysis of variance summary table of plant radioactivity from Experiment 1. The square root of the percent of total activity in various sections is given.

Source	df	Mean Square	F
	a. Herbaq	ge Section	
Species	2	23.890	22.072 *
Error (a)	3	1.083	
Time	2	1.555	2.436 NS
Species × time	4	0.387	0.608 NS
Error (b)	6	0.638	
	b. Crown	ı Section	
Species	2	9.835	15.598 *
Error (a)	3	0.630	
Time	2	0.620	1.028 NS
Species × time	4	0.082	0.139 NS
Error (b)	6	0.601	
	c. Upp	er Roots	,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,
Species	2	13.445	97.931 **
Error (a)	3	0.136	
Time	2	0.225	1.237 NS
Species × time	4	0.235	1.299 NS
Error (b)	6	0.181	

Appendix Table 1 (continued).

Source	df	df Mean Square	
	d. Lower	? Roots	
Species	2	5.170	13.518 *
Error (a)	3	0.383	~ _
Time	2	1.485	4.916 NS
Species × time	4	0.300	0.985 NS
Error (b)	6	0.301	

^{*} Significant F value at 0.5 level.

^{**} Significant F value at 0.1 level.

NS Non-significant.

Appendix Table 2. Analysis of variance summary table of plant radioactivity from Experiment 2. Root sucrose specific activity $(dpm/\mu g)$.

Source	df	Mean Square	F
Species	2	146,826.00	7.211 *
Error (a)	6	20,361.00	
Time	6	220,955.80	17.471 **
Species × time	12	30,789.70	2.435 *
Error (b)	33	12,647.10	- -

^{*} Significant F vlaue at 0.5 level.

^{**} Significant F value at 0.1 level.

Appendix Table 3. Analysis of variance summary table of plant radioactivity from Experiment 3. Square root of the percent of total activity in tops and roots of various species and various growth stages is given.

Source	df	Mean Square	F
	a. Blue	Grama	
Temperature (Te)	2	3.530	9.289 **
Error (a)	9	0.376	- -
Growth Stage (GS)	1	0.060	0.176 NS
GS × Te	2	0.345	1.015 NS
Error (b)	9	0.340	
Time (ti)	1	6.730	29.088 **
Ti × Te	2	1.555	6.721 **
Ti × GS	1	0.864	3.736 NS
$Ti \times Te \times GS$	2	0.300	1.298 NS
Error (c)	16	0.231	~
	b. Buffalo	Grass	
Temperature (Te)	2	1.365	3.262 NS
Error (a)	9	0.420	
Growth Stage (GS)	1	2.230	3.279 NS
GS × Te	2	0.105	0.147 NS
Error (b)	9	0.680	+-
Time (Ti)	. 1	0.490	0.643 NS
Ti × Te	2	0.012	0.015 NS
Ti × GS	1	0.013	0.017 NS
Ti × Te × GS	2	0.153	0.199 NS
Error (c)	17	0.769	

Appendix Table 3 (continued).

Source	df	Mean Square	F
	c.	Western Wheatgrass	
Temperature (Te)	2	0.380	1.086 NS
Error (a)	9	0.350	- -
Growth Stage (GS)	1	2.750	7.051 *
GS × Te	2	0.460	1.179 NS
Error (b)	9	0.390	- +
Time (Ti)	1	52.240	145.552 **
Ti × Te	2	0.558	1.550 NS
Ti × GS	1	0.072	0.199 NS
Ti × Te × GS	2	0.030	0.083 NS
Error (c)	17	0.360	***
	(d. Growth Stage 1	
Temperature (Te)	2	0.398	1.401 NS
Error (a)	9	0.284	
Species (Sp)	2	9.127	18.857 **
Sp × Te	4	1.244	2.570 NS
Error (b)	18	0.484	
Time (Ti)	1	15.753	26.812 **
Ti × Te	2	0.371	0.632 NS
Ti × Sp	2	6.737	11.466 **
Ti × Te × Sp	4	0.752	1.279 NS
Error (c)	25	0.588	

Appendix Table 3 (continued).

Source	df	Mean Square	F
		e. Growth Stage 2	
Temperature (Te)	2	0.924	2.119 NS
Error (a)	9	0.436	
Species (Sp)	2	6.848	17.469 **
Sp × Te	4	1.188	3.031 *
Error (b)	18	0.392	
Time (Ti)	1	21.308	64.941 **
Ti × Te	2	0.363	1.106 NS
Ti × Sp	2	4.772	14.543 **
Ti × Te × Sp	4	0.184	0.562 NS
Error (c)	25	0.328	
	f.	2 hr-Translocation Period	
Temperature (Te)	2	1.745	2.815 NS
Error (a)	9	0.620	
Growth Stage (GS)	1	0.260	1.036 NS
GS × Te	2	0.047	0.187 NS
Error (b)	9	0.251	
Species (Sp)	2	14.416	38.151 **
Sp × Te	4	2.272	6.011 **
Sp × GS	2	1.268	3.3 55 *
Sp × GS × Te	4	0.442	1.169 NS
Error (c)	36	0.378	

Appendix Table 3 (continued).

Source	df	Mean Square	F
	g.	6 hr-Translocation Period	
Temperature (Te)	2	0.074	0.463 NS
Error (a)	9	0.160	
Growth Stage (GS)	1	0.037	0.061 NS
GS × Te	2	0.225	0.369 NS
Error (b)	9	0.610	
Species (Sp)	2	9.914	18.619 **
Sp × Te	4	0.457	0.858 NS
Sp × GS	2	1.949	3.660 *
$Sp \times GS \times Te$	4	0.067	0.126 NS
Error (c)	32	0.532	

^{*} Significant F value at .05 level.

^{**} Significant F value at .01 level.

NS Non-significant.

Appendix Table 4. Percent of total plant 14C activity (radioactivity) in the roots of blue grama, buffalo grass, and western wheatgrass averaged over four replicates.

		Translocation Period					
Temperature (°C)	Growth	Stage 1	Growth Stage 2				
	2 hr (%)	6 hr (%)	2 hr (%)	6 hr (%)			
	В	lue grama					
21.1/15.6	5.94	14.07	5.31	15.24			
26.7/21.1	19.16	15.33	11.07	16.96			
32.2/26.7	13.29	17.81	12.92	20.08			
	Buf	falo grass					
21.1/15.6	7.10	7.52	8.39	11.44			
26.7/21.1	6.27	6.16	8.75	10.54			
32.2/26.7	4.42	7.12	6.43	6.30			
	Wes ter	n wheatgrass					
21.1/15.6	3.62	18.22	1.71	10.67			
26.7/21.1	2.75	18.04	2.64	16.77			
32.2/26.7	5.39	16.03	3.01	12.13			

Appendix Table 5. Influence of translocation period, temperature, and growth stage on percent of total $^{14}\mathrm{C}$ activity in roots of blue grama, buffalo grass, and western wheatgrass after exposing entire plants to 8.5 μc $^{14}\mathrm{Co}_2/\mathrm{plant}$ for 5 min. Values within each paramenter and species followed by the same letter are not significantly different at the 0.05 level.

		Species							
Parameter	Blue Grama	Buffalo Grass	Western Wheatgrass (%)						
	(%)	(%)							
Translocation Period									
2 hr	11.3 a	6.9 a	13.8 a						
6 hr	16.6 ь	8.2 a	15.3 b						
Temperature (°C)									
32.2/26.7	16.0 ь	6.1 a	9.1 a						
26.7/21.1	15.6 ь	7.9 a	10.0 a						
21.1/15.6	10.1 a	8.6 a	8.6 a						
Growth Stage									
1	14.3 a	6.4 a	10.7 Ь						
2	13.6 a	8.6 a	7.8 a						

APPENDIX IV

FIELD DATA

Translocation data collected by Daniel P. Knievel is found in data sets A2U00FO, A2U00GO, and A2U00HB. Field definitions and data listings follow.

A2U00F0

Data Field	Columns	Format
SAMPLID	1- 6	(46)
REDITORIE	선= 표	(A1)
SPECIES	10-10	(41)
TE MD	12- 12	(41)
GROWTHSTG	13- 13	- ·
TLOCPER	14+ 14	(A1)
PLANTPAPT	16+ 16	(Al)
PARTWT		(A)
• • •	18- 51	(F4.2)
SUMBLALI	24- 26	(F3.1)
DD+1]	2H- 34	(F7.0)
SAMPLWIZ	36- 38	(F3.1)
DEWS	40- 45	=
SUCRSAMP	48+ 50	(F7.0)
SHODOSE	· •	(F3,1)
	51- 55	(F5.1)
SUCRACTIV	57- 62	(F6.2)

Printed listing follows:

```
NOTES ON DATA FIELDS:
SPECIES
    1 BLUE GRAMA
    2 BUFFALO GRASS
    3 WESTERN WHEATGRASS
TEMP.
            DAY (18 HRS)
                            MIGHT (6 HRS)
                   70
                                60
    2
                   80
                                10
                   90
                                80
    3
GROWTHSTG
            GROWTH STAGE (SEE FORTHCOMING PAPER BY SCHMER AND KNIEVEL)
    1 EARLY (A)
    2 LATE (B)
TL OCPER
          TRANSLOCATION PERIOD
    1 2-HR
    2 6-HR
            PLANT PART
PLANTPART
    1 ROOTS
    2 STEM BASE
    3 HERRAGE
PARTWT
         WEIGHT (G) OF PLANT PAPT
           WEIGHT (MG) OF COMHUSTED SAMPLE. DUPLICATE 1
SAMPI WT1
       TOTAL DPM (DISINTEGRATIONS / MINUTE) OF COMBUSTED SAMPLE. DUPLICATE 1
DPM1
STW JAMP.
           WEIGHT (MG) OF COMBUSTED SAMPLE. DUPLICATE 2
DPM2
       TOTAL DPM OF COMBUSTED SAMPLE. DUPLICATE 2
SUCRSAMP
           WEIGHT (MG) OF PLANT-PART SAMPLE FOR SUCROSE EXTRACTION
          SUCROSE IN EXTRACT (MICROGRAMS)
SUCROSE
SUCRACTEV
            SPECIFIC ACTIVITY OF EXTRACTED SUCROSE (DPM / MICROGRAM)
717026 1 1 111 1
                    82
                         85
                              14918 113
                                          17480 253 8123
                                                            4566
717018 1 1 112 1
                         99
                    40
                             119150
                                    98
                                          117444 251 6538
                                                           18939
717082 1 1 121
                    53
                         90
                              19771 120
                                          35782 250 7427
                                                            5972
717090 1 1 122
                    61
                        113
                              49444 100
                                          60793 250 2358
                                                           16170
71T010 1
           211
         1
                   102
                        100
                              82317
                                          63924 258 2308
                                     93
                                                           26353
71T002 1 1 212
                    15
                        24
                             111154 107
                                         142985 246
                                                      305
                                                           27078
71T074 1 1 221
                    11
                        101
                              51788
                                     95
                                          53415 255 3135
                                                            7909
71T066 1
         1 222
                    77
                        100
                              45217 101
                                          38031 250 1860
                                                            5507
71T042 1
         1 311
                   47
                         91
                              53259
                                                252 2818
                                     96
                                          56717
                                                           33202
71T034
       1
         1
           312
                   132
                        123
                              57670
                                     99
                                          64266 250 1780
                                                           21959
717050
       1
         1
           321
                              55464 114
                   150
                        113
                                          53899 246 2923
                                                           37793
717058
      1
         1 322
                              95235
                    83
                        100
                                          85684 259 2645
                                     40
                                                           31468
717122 1 2 111
                    13
                         96
                             163643 105
                                         220193 259 8287
                                                           31048
71T114
       1 2 112 1
                    20
                         91
                              96466
                                     91
                                          80290 259 9592
                                                           16135
717178 1
         2 121
                    36
                        119
                              49462 114
                                          48448 244 8490
                                                            5098
71T186
       1
         2
           122
                    24
                        132
                              80957 117
                                          89464 255 7129
                                                            7362
71T106
      1
         2 211
                   29
                        103
                              44348 120
                                          46648 258 5456
                                                           17570
71T098
      1 2 212
                   14
                         32
                              73113 110
```

74195 247

41502 261

54955 247 1033

/17146 1 2 221

5 555

71T154 1

60

54

98

106

50113 101

47551 104

1206

501

18913

16741

945A

والمراجعين المعروب					
717130 1 2 311 1	24	98	111832 99	123063 252 4933	48689°
717138 1 2 312 1	14	95	28133 97	24326 258 2824	11362
717162 1 2 321 1	42	96	79099 103	71010 253 6961	12903
717170 1 2 322 1	47	163	142779 117	134719 251 5359	20737
717226 1 3 111 1	26	79	18202 108	34477 251 5051	4446
717234 1 3 112 1	41	વસ	136359 116	174496 262 2506	1430원
717250 1 3 121 1	34	93	1278 128	1438 254 8794	17
71T242 1 3 122 1	45	83	20998 111	25031 256 2050	4383
717210 1 3 211 1	83	105	9442 110	9044 250 522	3470
717218 1 3 212 1	59	91	131643 101	176043 257 579	19464
717258 1 3 221 1	224	132	3136 94	3549 255 709	2811
717266 1 3 222 1	163	105	30266 43	27038 251 2271	2819
717194 1 3 311 1	68	90	24753 91	20862 245 4724	8199
71T202 1 3 312 1	67	117	35275 102	31249 254 5248	6389
717274 1 3 321 1	66	99	7462 98	15533 248 4072	3575
717252 1 3 322 1	204	101	23686 127	30911 254 3583	4167
717028 2 1 111 1	90	93	43046 100	53739 250 6956	11551
71T020 2 1 112 1	<u>4 2</u>	110	159712 95	141263 246 5730	22578
717084 2 1 121 1	93	130	38517 97	29823 25110629	5499
717092 2 1 122 1	112	92	40182 150	56257 260 5372	10246
717012 2 1 211 1	69	179	153510 154	162412 257 1633	30985
717004 2 1 212 1	342	99	12040 101	24260 247 1432	
717076 2 1 221 1	144	111	26764 100	18684 247 65	3640
717068 2 1 222 1	87	99	39997 100	41686 256 1036	6025
717044 2 1 311 1	70	117	40040 116	45942 256 2039	43964
717036 2 1 312 1	73	95	78190 117	98115 260 2974	
717052 2 1 321 1	77	155	75221 116	102635 247 2782	15934
717060 2 1 322 1	91	115	148605 98	173075 244 3299	59425
717124 2 2 111 1	14	93	122279 100	142990 250 3474	31576
717116 2 2 112 1	18	86	83355 111	95651 259 8027	27692
717180 2 2 121 1	20	109	83615 114	84166 250 7843	9410
717188 2 2 122 1	48	98	93199 90	104857 24910276	13907
717108 2 2 211 1	32	85	43691 105	60451 258 901	11760
717100 2 2 212 1	23	99	61797 95	58571 256 1094	22122
717148 2 2 221 1	45	107	39344 97	44242 248 544	19588
71T156 2 2 222 1	21	89	62546 93	55035 250 1104	30107
717132 2 2 311 1	24	104	36937 103	23475 255 4767	16431
717140 2 2 312 1	38	98	83106 98		3567
71T164 2 2 321 1	14	90	46291 97	95970 255 6071 4 7 440 242 5001	18066
717172 2 2 322 1	33	106	129893 109		6963
71T228 2 3 111 1	26	107	53853 92		21865
717236 2 3 112 1	113	119	70704 90		13595
717252 2 3 121 1	239	100	9978 110		8026
717244 2 3 122 1	76	92	32406 44		2852
717212 2 3 2111	72	101	14633 116	25453 257 3423 13695 259 796	5002
717220 2 3 212 1	61	92	83975 167	82486 255 1422	4047
717260 2 3 221 1	147	123	3256 119	2502 254 1023	13428
717268 2 3 222 1	139	92	17402 72		934 2204
			<u> </u>	12811 247 968	229H

	4					
711196 2 3 311 1	147	100	98 73 8 7	S 2088	58 4 38 6	285)
717204 2 3 312 1	96	96	54173 121		53 4022	
717276 2 3 321 1	셔]	117	747 97	610 2	47 6042	
717284 2 3 322 1	93	94	23946 98	31815 2	43 3969	
717030 3 1 111 1	+1	95	31646 113		5510725	
717022 3 1 112 1	35	96	117414 107		5110428	20536
717086 3 1 121 1	64	<u> 89</u>	21504 100	-	45 7803	6571
717094 3 1 122 1	88	92	53748 114		52 5657	8057
717014 3 1 211 1	118	102	43424 106		53 4115	18887
717006 3 1 212 1	97	99	89581 101		7 1294	10829
717078 3 1 221 1	195	094	10169 92		55 898	5322
717070 3 1 222 1	89	90	38631 103		1 4002	9467
717046 3 1 311 1	43	91	111899 99	143305 29		113689
717038 3 1 312 1	119	102	74317 96	78619 24		15209
717054 3 1 321 1	43	100	88615 B2	75570 25		47083
717062 3 1 322 1	AK	109	104161 100	121310 29		31165
717126 3 2 111 1	26	96	104948 96	98515 24		20542
717118 3 2 112 1	30	133	123579 112	94675 25		11693
717182 3 2 121 1	34	94	64264 91		410421	9717
717190 3 2 122 1	28	114	86586 115	79033 24		8717
717110 3 2 211 1	38	116	94575 87	78726 29		22650
717102 3 2 212 1	21	A]	68557 104	93065 25		21798
717150 3 2 221 1	250	113	28406 99	21326 24		13687
71T158 3 2 222 1	44	101	65810 A6	55564 25		8593
717134 3 2 311 1	25	92	60099 98	57835 24		24766
717142 3 2 312 1	20	107	277891 108		5 4797	25816
717166 3 2 321 1	43	102	64904 116	87050 24		12853
71174 3 2 322 1	37	109	149465 113	167003 25		26450
717230 3 3 111 1	40	118	5575 91	4740 25		619
717238 3 3 112 1	31	110	99541 100	81521 25		11679
717254 3 3 121 1	79	89	5542 95	7798 25		1734
717246 3 3 122 1	104	109	72997 93	78070 25	"	7429
717214 3 3 211 1	141	114	12299 126	15498 24		7455
71T222 3 3 212TI	2.3	87	69533 97	102028 24		T4032
717262 3 3 221 1	101	92	4462 45	3500 24		580
717270 3 3 222 1	131	95	27078 113	32833 25		8813
717198 3 3 311 1	9.2	98	15398 117	13929 25		10327
717206 3 3 312 1	51	88	64557 104	80655 25		49632
717278 3 3 321 1	111	103	7024 99	9089 24		2113
717286 3 3 322 1	132	117	24146 97	22680 24		4520
717032 4 1 111 1	63	90	19442 192	21035 24		7772
77024 4 1 112 1	42	91	77826 91	66097 25		13704
71T088 4 1 121 1	82	107	28189 101		7.7183	5639
71T096 4 1 122 1	98	104	60275 92	56233 25		8023
71T016 4 1 211 1	140	107	92666 119	101090 24		55448
717008 4 1 212 1	55	91	61790 92	65628 249		14972
717080 4 1 221 1	44	111	51397 100	38329 25		14772
717072 4 1 222 1	114	111	51059 109	52557 25		9195
			-			27.43

711048	4	1	311	ī	196	80	106232	36	94555	255	1340	73923
71T040	4	ĩ	312	ī	83	99	129396	98	121181	255	2766	30215
71T056	4	i	321	i	105	115	65175	115	68815	243	2692	45158
71T064	4	1	322	ī	83	113	73644	113	105170	255	2447	30452
71T128	4	Ž	111	1	22	191	128396	103	103997	253	1284	23770
71T120	4	2	112	1	30	114	63755	191	81353	267	314	15250
711184	4	2	121	1	31	144	1 /9952	139	109874	248	6857	14011
71T192	4	2	122	1	43	103	33115	118	85850	255	7260	8782
717112	4	2	211	1	17	92	15649	113	20286	255	1139	11063
711104	4	2	212	1	24	89	46299	83	70784	250	1492	25729
717152	4	2	221	l	35	114	76143	112	68024	257	1253	10121
71 T160	4	2	223	1	34	105	104026	99	76195	241	3626	15776
71T136	4	5	311	1	50	102	38320	117	41946	256	3105	22643
71T144	4	2	312	1	1.0	101	46973	114	57675	259	4758	11616
71T168	4	2	321	1	42	93	90764	102	101741	251	5791	18908
71T176	4	2	355	1	16	105	97437	98	74013	255	3335	18408
717232	4	.3	111	1	34	90	A329	110	10335	256	3013	1560
71T240	4	3	115	1	52	199	102234	102	107791	257	1939	11338
71T256	4	3	121	1	80	85	3329	110	36 98	251	4487	492
71T248	4	3	122	1	141	86	25862	100	272 38	256	6734	3868
71T216	4	3	211	1	195	130	9707	124	9473	253	1709	3647
71T224	4	3	515	l	75	106	68104	94	74508	263	900	13594
717264	4	3	551	1	90	97	6527	117	11855	248	659	906
717272	4	3	555	1	184	123	12742	33	9635	249	416	1750
71T200	4	3	311	1	113	121	19842	49	137 31	255	1981	12550
71T208	4	3	312	1	5.8	94	82950	36	73464	254	2987	20919
717280	4	3	321	1	75	88	4565	95	9224	258	7331	S093
717288	4	3	323	1	111	91	17373	102	22404	259	5091	4670

A2U00G0

Data Field	Colum	ns	Format
	v	-	and the second of the second o
REPLICATE	1 -	ļ	(41)
TEMP	.3	3	(Al)
GROWTHSTG	۔ ت	ร	(A])
SPECIFS	7-	7	(Δ])
TLOOPER	9-	Q.	(41)
TOPSACTIV	11-	14	(F4.2)
POOTSACTIV	16-	19	(F4.2)

Printed listing follows:

```
NOTES ON DATA FIELDS:
                           MIGHT (6 HRS)
           DAY (18 HPS)
TEMP. (F)
                                HO
                   90
    1
                                70
                   80
    っ
                                ற்பி
                  79
    3
           GROWTH STAGE (SEE FORTHCOWING PAPER BY SCHMEP AND KNIFVEL)
GROWTHSTG
    1 EARLY (A)
    2 LATE (B)
SPECIES
    1 BLUF GRAMA
    2 BUFFALO GRASS
    3 WESTERN WHEATGRASS
TLOCPER TRANSLOCATION PERIOD
    1 2-HR
    2 6-HR
            PERCENT OF TOTAL PLANT C14 ACTIVITY CONTRIBUTED BY TOPS
TOPSACTIV
             PERCENT OF TOTAL PLANT CL4 ACTIVITY CONTRIBUTED BY ROOTS
ROOTSACTIV
1234567890123456789012345678901234567890123456789012345678901234567890
1 1 1 1 1 9155
                845
1 1 1 1 2 8007 1993
1 1 1 2 1 9036
                937
1 1 1 2 2 9863
                 137
      3 1 9106
                 894
    1
      3 2 8219 1781
    1
  1 2 1 1 8724 1276
    2 1 2 7844 2156
    2 2 1 9169 831
  1
1
      2 2 8981 1019
    2
    2 3 1 9628
                372
  1
  1 2 3 2 8874 1126
  2 1 1 1 8037 1963
1
  2 1 1 2 8777 1223
1
  2 1 2 1 9362
                 638
1
  2 1 2 2 9300
                 700
1
  2 1 3 1 9817
                 183
  2 1 3 2 7264 2736
  2 2 1 1 8719 1281
    2
       1 2 8713 1287
  2
  2 2 2 1 9229
                 771
1
  2 2 2 2 9201
                 799
                 295
  2 2 3 1 9705
 1
   2 2 3 2 7909 2091
   3 1 1 1 9625
                 374
   3 1 2 1 8843 1157
   3 1 2 2 8957 1043
   3 1 3 1 9615
                 385
       3 2 7425 2575
   3 1
         1 9540
   3 2 1
                 460
   3 2 1 2 8373 1627
   3 2 2 1 9372
                 628
                 893
   3 2 2 2 9107
```

3 1 9975

3 2 3 2 949A

3 2

1

25

502

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2 1 1 1 1 9132
               2 8543 1457
           1
                   9856
                              144
           2
              1
       1
                   8874
                            1126
           5
               2
       1
                   9670
                               330
            3
               1
2
       1
                   8418 1582
            3
              5
2
       1
                   8571 1429
               1
                   7470
                            2530
               2
            1
5
        2
            2
               1
                   9820
                               180
           3
        Š
                   9876
                               124
               1
    1
5
                   8868
                            1135
    1
        2
            3 2
   5
                   7762
                            223H
            1 1
                             2066
2
                2
                   7934
    2
            1
       1
    5
                               922
            2 1
                   9078
2 2 1 2 1 9078

2 2 1 2 2 9501

2 2 1 3 1 9698

2 2 1 3 2 8353

2 2 1 1 8730

2 2 2 1 2 8409

2 2 2 2 1 9506

2 2 2 2 2 9316

2 2 2 3 1 9796

2 2 3 3 2 9005

2 3 1 1 1 8884

2 3 1 2 1 9441

2 3 1 2 1 9441

2 3 1 2 2 9639

2 3 1 3 1 9234
        1
                               499
                               302
                    8353 1547
                    8730 1270
               2 8409 1591
1 9506 494
                               684
                                204
                                995
                              1116
                              1384
                                559
                                361
 2
     3
             3
                    9234
                                766
         1
                1
     3
             3
                2
                    8574
                              1426
         1
    3 3
                    9241
                                759
 5 5
         >
            1 1
         5
                    8357
                              1643
            1 2
            2 1
                                700
                     9300
     3 2 2 2 8450 1550
3 2 3 1 9553 447
3 2 3 2 8769 1231
  5
                                447
```

```
3 1 1 1 1 8809 1191
             1 2 8311 1689
             2 1
        1
                      9779
                                   221
3
         1
             2 2
                      8490 1510
3
             3 1
    1 1
                      9673
                                   327
3
    1 1 3 2 8512 1488
   T ? 1 1 8859 1141
3
   1 2 2 1 9335
3
   1 2 2 1 9335 664
1 2 2 2 9126 874
1 2 3 1 9543 457
1 2 3 2 9215 785
2 1 1 1 8869 1131
2 1 1 2 8348 1652
2 1 2 1 9154 846
                                   664
3
3
3
3
3
   2 1 2 2 9355
2 1 3 1 9671
3
                                   645
3
                                   324
   2 1 3 1 9671 329
2 1 3 2 8596 1404
2 2 1 1 9242 758
2 2 1 2 8664 1336
2 2 2 1 8325 1675
2 2 2 2 8867 1133
2 2 3 1 9796 2004
2 2 3 2 7491 2509
3 1 1 1 9515 485
3
3
3
3
3
3
3
3
    3 1
3
            1 2 8572 1428
    3 1 2 1 9276
3
                                  724
3
    3 1 3 1
            2 2 8989 1011
3 1 9904 96
   3 1 3 2 8374 1626
3 2 1 1 9559 441
3 2 1 2 8867 1133
3 2 2 1 8788 1212
3 2 2 2 9432 568
3
3
3
3
3
    3 2 3 1 9856
3
                                   144
    3 2 3 2 8450 1550
```

```
4 1 1 1 1 7588 2412
       1
          2 8017
                  1983
    1
       2
         1
             9560
                    440
            9925
4 1 1
       2 2
                     75
       3 1
            9397
     1
                    603
    1
       3 2 8438 1562
    2
  I
       1 1
            8679 1321
       1 2 8512 1488
  1
     5
       2 1
             9104
                    896
     2
       2 2 9541
  1
                    459
       3 1 9748
     2
                   252
  1
  1
    2 3 2 8192 1808
  2
    1 1 1
            7670 2330
  2 1
4
            8808 1192
       1
          2
  2
    1
       2 1
             9897
                    103
4
  2
    1 2 2 9380
                    620
  5
    1
       3 1
            9715
                    285
       3 2 8570 1430
    1
 2 1 1 8882 1118
2 2 1 2 7429 2571
2 2 2 1 9438 562
2 2 2 2 8399 1601
2 2 3 1 9648 352
4
  2
    2 3 2 8888
1 1 1 9598
4
                  1112
                   402
4
  3
       1 2 8872 1128
  3
       2 1
             9600
                    400
  3 1 2 2 9407
                    593
  3
    1
       3 1
            9798
                    202
  3 2
       1 1 9536
                   464
  3 2 1 2 8308 1692
  3 2 2 1 9183
3 2 2 2 8434
                    817
                   1566
 3 2 3 1
            9934
                     66
4 3 2 3 2 9017
                    983
```

A2U00HB

Data Field	Columns	Format
SAMPLIO	1- 5	(46)
REPLICATE	მ− ∺	(\(1 \)
SPECIES	16- 10	(A1)
TLOCOFP	12- 12	(A1)
SAMPLDATE	14- 15	(84)
PLANTPART	17- 17	(41)
LARLTIME	21- 24	(44)
। ४मा भर	21- 52	(12)
LARLMIN	23- 24	(12)
HARVTIME	26- 29	(44)
ндална	26- 27	(12)
ндримткј	28- 29	(5))
FROZITME	31- 34	(44)
FROZHR	31- 32	(12)
FROTMIN	33- 34	(12)
PARTHT	36- 3A	(F3.2)
SAMPI WT1	40- 42	(F3.1)
now]	44- 47	(F4.0)
SAMPI WITZ	49- 51	(F3,2)
5,000	53- 56	(F4.0)
SUCREAMP	58- 60	(F3.1)
SUCRASE	52- 66	(F5.2)
SUCPACTIV	68- 72	(FS.3)

Printed listing follows:

```
NOTES ON DATA FIELDS:
           SAMPLE IDENTIFICATION (71 = YEAR. K = KNIEVEL. 123 = SAMPLE NO.)
MAMPL ID
 PROTES
     1 BLUE GRAMA
     2 BUFFALO GRASS
     3 WESTERN WHEATGRASS
     4 SEDGE
 TLOCPER
           TRANSI OCATION PERIOD
     1 2-HP
     2 5-HP
 SAMPLDATE
              SAMPLE DATE
                       8 JUNE 24
     1 MAY
            4
     2 MAY 12
                        9 JULY
     3 MAY 19
                      10 JULY 15
                      11 JULY 29
     4 MAY 26
                      12 AUGUST 12
     5 JUNE
     6 JUNE
                      13 AUGUST 26
     7 JUNE 15
              PLANT PART
 PLANTPART
     1 ROOTS
     2 STEMBASE
     3 SHOOTS ABOVE STEM BASE
 (TIMES ARE MST, 24-HR CLOCK)
             TIME OF C14 LABELING
 I ABI TIME
             TIME OF PLANT HARVEST
 HARVTIME
             TIME FROZEN
 FROZTIME
           DRY WEIGHT (G) OF PLANT PART
 PARTHT
             WEIGHT (MG) OF COMPUSTED SAMPLE. HUPLICATE 1
  AMPLWT1
        DPM (DISINTEGRATIONS / MINUTE) OF COMBUSTED SAMPLE. DUPLICATE 1
 UPM1
             WEIGHT (MG) OF COMBUSTED SAMPLE. DUPLICATE 2
 SAMPI WT2
         DPM OF COMBUSTED SAMPLE. DUPLICATE ?
 DPM2
             WEIGHT (MG) OF ROOT SAMPLE FOR SUCROSE EXTRACTION
 SUCRSAMP
            SUCROSE (MICROGRAMS) IN EXTRACT
 SUCROSE
              SPECIFIC ACTIVITY (DPM / MICROGRAM) OF EXTRACTED SUCPOSE
 SUCRACTIV
 12345678901234567890123456789012345678901234567890123456789012345678901234567890123456789
                                                           361 256 12808
                                                                           4129
                                                 400 102
                        955 1203 1309 166 101
 71K050 1 1 1
                2 1
                                                                           4599
                                                      77
                                                          275 249 14323
                        955 1203 1309 119
                                            95
                                                 314
                2 1
 71K052 2 1 1
                                                          257 243 12748
                                                                           1874
                                                 220 110
                        955 1203 1309 197
                                            93
 71K054 3 1
                2 1
                                                               255
                                                 350
                                                      92
                                                           366
                                                                   14193
                                                                           6688
                        955 1203 1309 120
                                            73
                2 1
 71K056 4 1 1
                       1009 1203 1325
                                        26
                                            20
                                                  35
                                                      67
                                                           75
                                                               247
                                                                    2536
                                                                           4455
                3 1
 71K102 1 1 1
                                                          100 248
                       1009 1203 1325 137
                                                                    3988
                                                                           5614
                3 1
                                            ų, ų
                                                  39 113
 71K104 2 1
                                                           20 249
                                                                    9127
                                                                            608
                       1009 1213 1325 155
                                             78
                                                  21
                                                      76
                3 1
 71K106
                                                           67 246 11511
                                                                           2401
                       1009 1203 1325 142 128
                                                  77
                                                      83
 71K108 4 1 1
                3 1
                                                                           4271
                        930 1143 1230 121
                                                 398 107
                                                          540 250 32239
                                           114
                4 1
 71k158 1 1 1
                                                           394 247 14868
                                                                           8942
                                                 367 101
                        930 1143 1230 150 101
 71K160 2 1 1
                4 ]
                                                           172 246 25815
                        930 1143 1230
                                        36 102
                                                 142 107
                                                                           1461
                4 1
 71K162 3
          1
             1
                                                                           2525
                        930 1143 1230 135 102
                                                 425 104
                                                           582 249 22900
 71K164 4
                  1
                                                 307 103
                                                           440 247 26974
                                                                           6190
                        948 1153 1310 166 103
                5 1
 71K214 1
           1 1
                        948 1153 1310 213 102
                                                 154 104
                                                           215 258 27520
                                                                           3580
                5 1
 71K216 2 1 1
                                                 375 103
                                                           373 257 35563
                                                                           9040
                5 1
                        948 1153 1316 350 109
 71K218 3 1 1
                                                           162 253 18858
                                                                           7870
                                                 175 107
 ~1K220 4
             1
                5 1
                        948 1153 1310 116 106
           1
                                                                           1876
                                                 214 169
                                                           187 246 28655
```

942 1144 1242 189 103

98 116

40 106

942 1144 1242

547

222 246 38041

1K270 1

71K272 2 1 1

1 1 6 1

6 1

					-				30	376	36566	448
71K274 3 1 1	6 1	942	1148 1		3 5		42	_				403
71K276 4 1 1	6 1	942	114¤ 1	242		105		104	•	-	36998	
71K326 1 1 1	7 1	943	1150 1	230	144	107		104		-	30046	HA54
71K328 2 1 1	7 1	943	1150 1	230	131	102						12516
71k330 3 1 1	7 1	943	1150 1	230	224	103	251	103			38176	8305
71K330 3 1 1 71K332 4 1 1	7 1		1150 1		بت بنع	103	439	109	441	497	73511	7190
	81			256	ųμ	104	46	105	51	493	52515	271
71K382 1 1 1				256		103	48	194	141	4981	09719	151
71K384 2 1 1	8 1	1000		256		105		107	84	493	59772	754
71K386 3 1 1	8 1		1153		_	106	-	104			59091	180
71K388 4 1 1	8 1					100		100			22791	3827
71K438 T T T	9 1		1153			101		101	_		50943	2436
71K440 2 1 1	9 1		1153		-		_	194	144		8730	1954
71K442 3 1 1	9 1		1153.		-	102				49]	8237	1461
71K444 4 1 1	9 1		1153			101	_	100			10430	3106
71K066 1 2 1	2 l		1155		_	117	148	90	264			1915
71K068 2 2 1	2 1			1245	76	75	157	66		255	8948	3933
71K070 3 2 1	2 1	939	1155		73	121	385	74	282		18846	
71K072 4 2 1	2 1	939		1245	270	101		118	116		10438.	
71K118 1 2 1	3 1	941	1151	1245	101	100	240	142	270		13072	3691
71K120 2 2 1	3 1	941	1151	1245	170	116	804	117		241	7715	1133
71K122 3 2 1	3 1	941	1151	1245	96	114	628	115		257	7312	116
71K124 4 2 1	3 1	941		1245	132	140	1322	110	1226		6039	3145
71K174 1 2 1	4 î		1135		67	103	432	102	700		25610	9493
	4 1	958		1255	63	163	997	104	916	253	32912	12545
	4 1		1135		122	105	567	110	789	249	24209	11985
	4 1	958	1135		52		1351	102		247	30776	11071
71K180 4 2 1	5 1	,	1157		79	105	610	105	663	246	12930	14554
71K230 1 2 1		1000	1157		5 5	Sol	423	102	338		17121	17025
71K232 2 2 1	5 1		1157		56	103	930	103	740		27967	18943
71K234 3 2 1	5 1		1157		95	103	842	104				24110
71K236 4 2 1	5 1	1000				105	226	103			19280	7157
71K286 1 2 1	6 1	1003	1200		•			105	1341		52879	-
71K288 2 2 1	6 1	1003	1200		170		1544				24991	12248
71K290 3 2 1	6 l			1305	73	105	\$99	108	463			17290
71K292 4 2 1	6 l	1003	1500		дн		1154	106	693			
71K342 1 2 1	7 1	907	1158		142	103	509	103	-	_	46087	
71K344 2 2 1	7 1	917			۲H	103		102	869			10615
71K346 3 2 1	7 1	907	1158	1300		194		103	661		48003	
71K348 4 2 1	7 1	907	1158	1300	ध्य	102		102			38677	
71K398 1 2 1	8 1	950	1150	1245	133	105	52	102			23158	504
71K400 2 2 1	8 i		1150			105	381	106			18545	
71K402 3 2 1	8 i		1150			103	180	104			18201	1429
71K404 4 2 1	Ř 1	950				105	189	103			16046	
	9 1		1150			101	83	103	90	50 B	46994	1760
	$9\overset{1}{1}$		1150				93	102	92	505	78899	1146
71K456 2 2 1	9 1		1150				51	106	141	500	69525	1473
71K458 3 2 1			1150					103	256	494	86342	3101
71K460 4 2 1	91		1130				2324		2122			
71K082 1 3 1	2 1		1130				1052					17960
71k084 2 3 1	2 1		1139						1325			24194
71K086 3 3 1	2 1							117	2113	245		21013
71K088 4 3 1	2 1		1130					113		252	22055	11372
71K135 1 3 1	3 1		1157			119		101		249		
71K138 2 3 1	3 1		1157			112					22011	
71K141 3 3 1	3 1		1157					101			17449	
71×144 4 3 1	3 1	956	1157	1300	1 40	110	548	100	ת זיבי	503	I (444)	⁄ г.э .э~
									*			

71k191 1 3 1	4	1	943	1150	1240	21	110	2261	167	2191	242	20305	30309
71K194 2 3 1	4	-		1150		ς,	103	3339	103	3839	211	23083	15039
71k197 3 3 1	4			1150									19480
71k200 4 3 1	4			1150		_							32730
	5			1203								30882	17516
71K247 1 3 1		ı l	_	1203			. 08		102			24042	
71k250 2 3 1		-		1203									38809
71k253 3 3 1	_	1					106		106			27722	8554
71K256 4 3 1	5			1203			108		107			16928	2136
71K303 1 3 1		1		1153		ان الد از الد						32142	
71K306 2 3 1		1		1153						707	241 241	25363	780
71k309 3 3 1		1		1153			103		104				
71K312 4 3 1		1		1153		27	102	1436	110	2443	245 546	27329	26710
71k359 1 3 1		1		1155		51	105	2301	103	2134	500	42434	22/10
71K362 2 3 1	7			1155					102	3314	495	45921	3/83/
71K365 3 3 1	7			1155		90						40126	
71K368 4 3 1	7	l		1155								36697	
71K415 1 3 1	- 8	l		1147			103		103			60095	1824
71k418 2 3 1	8	1		1147	-		105		104			49829	
71K421 3 3 1	8	1	939	1147	1225		105					57133	1956
71K424 4 3-1	8	1	939	1147	1225	25	101	67	101			53649	2587
71K471 1 3 1	9	1	1007	1158	1257	11	161	2	-			43023	148
71K474 2 3 1	9	l	1007	115A	1257	14	105	163	101			55719	
71K477 3 3 1	9	1	1007	1158	1257	26	103	519	105	531		55677	6940
71K480 4 3 1	9	1	1007	1158	1257	97	$I\cup \Lambda$	207	103	265		58711	3800
71K494 1 1 1	10	1	933	1142	1217	128	103	5	104	1	491	34630	063
71K496 2 1 1		1	933	1142	1217	161	106	23	104	12	491	98411	163
71K498 3 1 1		1	933	1142	1217	108	105	ÿ	106	9	500	67863	317
71K500 4 1 1		1		1142		32	109	4	102	1	503	30708	233
71K550 1 1 1		ī	941	1129	1210	44	103	80	103	114	507	47716	762
71K552 2 1 1		ĩ	941	1129	1210	56	102	56	105	44	499	59940	261
71K554 3 1 1		ī	941	1129	1210	34	105	31	109	46	504	108926	066
71k556 4 1 1		ī		1129		51	107	96	106	6н	497	30967	1353
71k606 1 1 1		ī		1137		58	102	25	103	132	491	66742	249
71K608 2 1 1		-		1137		65	101	3	102	2	507	50307	096
71K610 3 1 1	12	ī		1137		152	103		102	13	490	26745	366
71K612 4 1 1				1137			105		102	11	495	39310	200
71K510 1 2 1				1142			103		104			73355	085
71K512 2 2 1				1142			106		101	8	506	96461	913
71K514 3 2 1				1142			104		105			087067	117
71K514 3 2 1				1142			104		108			58516	
71K566 1 2 1				1132			110		106			45175	
71k568 2 2 1				1132			107		109			43595	
		ì		1132			115		106			55251	
71K572 4 2 1		_		1132			119		108			38379	
	12			1140			105		102			75808	
71K624 2 2 1				1146			103		100			62264	
71K626 3 2 1				1140			104		104			91456	
71K628 4 2 1				1140			104		101			92918	
71K525 4 6 1 71K527 1 3 1		1		1150			105		107			60260	
71K530 2 3 1		1		1150			105		101			58237	
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	10			1150			103		109			60217	
71K536 4 3 1 71K583 1 3 1		1		1137			109		106			54916	
				1137			113		109			94520	
71K586 2 3 1	. 11	L	TOL	T T 17.7	17.13	, ,		e 1942		• '			

71K589 3 3 1 11 1	1004 1137 1218	28 111 93	111 16	508 57454	277
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	1004 1145 1241	52 104 10		490 51118	167
/1K639 1 3 1 12 1			102 10		182
71K642 2 3 1 12 1	1004 1145 1241			63 10744	299
71K645 3 3 1 12 1	1004 1145 1241	16 109 11	106 14	-	
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71K058 1 1 2 2 1	R15 1417 1450	170 78 243	91 295	256 7556	6795
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	815 1417 1450	155 133 743	77 516	255 14220	7466
		158 99 652	74 538	,	8008
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71k112 2 1 2 3 1	825 1429 1515		119 769	-	
71K114 3 1 2 3 1		Tal 115 PS8	-		11621
71K116 4 1 2 3 1	825 1428 1505	101 133 1325			20542
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	853 1447 1535	160 103 315	102 308	248 13041	4079
	853 1447 1535			256 27887	3543
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71k226 3 1 2 5 1	825 1425 1535		102 325		
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71K280 2 1 2 6 1	825 1413 1510	41 106 327	109 318	243 55386	3433
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71K340 4 1 2 7 1	815 1356 1450				
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71K396 4 1 2 8 1	749 1354 1435		105 511	503 35894	5860
71K446 1 1 2 9 1	869 1418 1501			÷ 502 11028	4483
	809 1418 1501	·	102 37		4563
	809 1418 1501		101 296	•	4717
71K450 3 1 2 9 1			- · · ·	5 501 23614	
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71K076 2 2 2 2 1	753 1410 1515				
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	848 1439 1539		124 23	9 256 6834	10198
	848 1439 1535			2 241 12570	9977
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71K242 3 2 2 5 1	812 1420 1516			1 247 16855	
71K244 4 2 2 5 1	812 1420 1510			1 248 28405	12053
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71K294 1	5 5	6	ì	757	1453	1451	43	197	263	106	2655	246	34212	3489
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	5 5		1	757	1403	1451		104	390	104	373	254	37490	6554
	5 5	6	î		- ,	1451		103		103	167		31400	3259
	5 5		1		1349	_		103		101	505	500	17486	6274
		7					_				621		35248	4820
	5 5		1		1349	1438		103		110				
	2 2	7	1		1349		170	103		198	815		56268	6413
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71K408 2	5 5	8	1	801		1505	1 33	102	249	101			23878	1758
71K410 3	2 2	В]	901	1357	1505	151	165	200	104	178	493	62771	1868
71K412 4	S S	8	1	801	1357	1505	128	104	334	103	364	497	69184	3447
71K462 1	2 2	9	1	819	142]	1517	131	106	141	102	179	490	32757	2184
	2 2	9	1	919	1421	1517	46	103	432	101	307	491	55255	3963
	2 5	9	1	819	1421	1517	ឧធ	100	234	105	261	492	50766	3767
	5 5	9	ì	· · · · · · · · · · · · · · · · · · ·	1421	1517		102	130	102	166		37223	4368
	3 5	ź	ì	-		1545	64		1238	76	1206		20170	
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	3 2	3				1520		101		113			22570	10204
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71K206 2	3 2	4	-		1443	_	46						21661	19400
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- 71K212 4	3 2	4	1	840	1443	1523	132	106	783	102	760	251	26439	11160
71K259 1	3 5	5	1	757	1415	1453	25	104	624	103	770	252	38462	7636
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	3 2		ì			1433		103	186	104			41117	2908
	3 2	6	i		1410	1433		109	1406	102	1315		39088	12386
	3 2	6	ì	=		1433		-	917	105			50064	8167
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71K380 4														
	3 2				1412				1258				49366	
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71K433 3			1		1402			101		101			60684	4764
71K436 4					1402			102		102			53411	4193
71K483 1	3 2				1416	-		105		105			68593	7083
71K486 2					1416			162		101			68371	5766
71K489 3	3 2				1416			101		105			29565	11970
	3 2		ì		1416			105		100			32705	
71K502 1			1		1420			102		104			108526	674
71K504 2	1 2	10	1	822.	1420	1459	103	105		103			77731	483
71K506 3	1 5	10	1	822	1420	1459	148	102	9	100	33	502	35128	205
71K508 4		10	1	822	1420	1459	55	101	24	103	49	495	65507	542
71K558 1	1 2	11	1	836	1425	1514	126	103	102	105	67	502	36632	1006
71K560 2				835	1425	1514	23	105	373	104	542	498	58241	3487

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71K562 3 1 2 11 1	836 1425 1514	91 705	103 111	196 491 36274	988
71K564 4 1 2 11 1	836 1425 1514	67 103	176 106	191 494 40399	2724
71K614 1 1 2 12 1	822 1407 1457	62 100	39 101	56 497 37319	342
71K616 2 1 2 12 1	822 1407 1457	48 104	1 100	2 507 57514	074
71K618 3 1 2 12 1	822 1407 1457	52 104	21 103	19 494 63304	055
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71K620 4 1 2 12 1	822 1407 1457	55 163	3 101	9 495 66465	035
71K518 1 2 2 10 1	809 1417 1525	139 103	11 107	10 493 75926	083
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71K5A0 4 2 2 11 1	824 1422 1500	13 112	197 70	8 493 83070	857
71K630 1 2 2 12 1	809 1494 1445	35 104	40 105	119 497 77577	135
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71K636 4 2 2 12 1	809 1404 1445	33 192	6 104	19 497 99301	059
71K539 1 3 2 10 1	757 1412 1506		57 109	73 494 71291	506
71K542 2 3 2 10 1	757 1412 1506		286 108	327 494 67979	1777
71K545 3 3 2 10 1	757 1412 1506		89 103	84 492 61318	589
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71K657 3 3 2 12 1	756 1401 1428		25 109	16 491 36964	150
71K660 4 3 2 12 1	756 1401 1428		5 102	13 498 69907	089
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71K044 2 4 2 1 1	815 1415 1440	145 76	218 87	207 253 38232	951
71K046 3 4 2 1 1	815 1415 1440		223 83	150 244 22889	1109
71KQ48 4 4 2 1 1	815 1415 1440	86 101	186 99	175 246 4633	1750
71K010 1 1 2 1 1	715 1315 1330	115 133	224 144	273 246 18168	117
71K012 2 1 2 1 1	715 1315 1330	141 91	153 120	158 252 14858	429
71K014 3 1 2 1 1	715 1315 1330		198 75	156 252 6704	413
71K016 4 1 2 1 L	715 1315 1330		331 86	280 256 9711	285
71K026 1 3 2 1 1	745 1345 1410		114 73	77 256 8491	2033
71K028 2 3 2 1 1	745 1345 1410		107 75	139 255 9804	1501
71K030 3 3 2 1 1	745 1345 1410		352 97	350 251 9112	1732
71K032 4 3 2 1 1	745, 1345, 1410	47 88	625 110	752 246 23699	1495
71K034 1 4 1 1 1	930 1130 1155		95 132	125 247 13473	1235
71K036 2 4 1 1 1	930 1130 1155	135 66	179 100	182 252 19528	2097
71K038 3 4 1 1 1	930 1130 1155	217 140	105 95	105 250 6906	9252
71K040 4 4 1 1 1	930 1130 1155		93 130	100 251 12672	1196
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71K020 2 3 1 1 1	915 1115 1140	57 115	293 100	236 251 2 1489	1713
71K022 3 3 1 1 1	915 1115 1140	96 97	427 90	520 253 15092	3484
71K024 4 3 1 1 1	915 1115 1140	45 R5	400 136	513 257 8592	3726