MONTANA STATE UNIVERSITY

The in vitro digestibility and utilization of Big Sagebrush and Black Sagebrush
by Karl David Striby

A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science in Range Science
Montana State University
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Abstract:
The relative forage quality of 4 Artemisia taxa was evaluated as reflected by in vitro organic matter digestibility (IVOMD), crude terpenoid content, and forage utilization. Taxa included A. nova, A. tridentata vaseyana, A._t. wyomingensis, and A.jt. tridentata.

Current years growth was collected from each taxon on January I, February 15, and April 1, 1981. Collections from A.t. vaseyana and A._t. wyomingensis were segregated into lightly and heavily grazed plants. Crude terpenoids on the foliage epidermis were extracted with chloroform and quantified. Extracted and intact (fresh) foliage were ground in liquid nitrogen and frozen until in vitro digestion. IVOMD was determined using mule deer, sheep, and steer rumen inocula. A total of 1569 plants from the 4 taxa were examined for degree of hedging from combined deer and elk utilization in the spring of 1981. Utilization assessment indicated big game preference for the taxa.

Order of increasing digestibilty among intact taxa was A. nova A._t. vaseyana, A._t. wyomingensis and A._t. tridentata. IVOMD generally increased from January to February to April. Fewer and contrasting differences in IVOMD were evident for extracted foliage among taxa and dates. A._t. vaseyana was consistently less digestible than A. nova which was generally less digestible than A._t. wyomingensis and A.Jt. tridentata. Extracted foliage was an average 13.2% more digestible than intact foliage. All inocula had similar digestive efficiency.

A._t. vaseyana contained the lowest crude terpenoid level, A. nova and A._t. wyomingensis contained intermediate levels, and A._t. tridentata contained the highest level. Crude terpenoid concentrations were greater on January 1 and February 15 than on April 1. Non-volatile crude terpenoids decreased IVOMD through microbial inhibition and/or resistance to digestion. The crude terpenoid concentration was negatively associated with IVOMD within each taxon, however, compositional differences might account for the variability in IVOMD among the taxa. Even though non-volatile crude terpenoids decreased IVOMD, digestibility remained high relative to other forages. Variation in IVOMD and crude terpenoid concentration was not related to utilization differences. Increasing order of preference appeared to be A._t. tridentata, A. nova, A._t. yas-¦eyana, and Ar_t. wyomingensis. Lightly and heavily grazed plants of either A._t. vaseyana or A._t. wyomingensis were digested equally well and contained similar crude terpenoid levels. Therefore, apparent animal grazing preference was not influenced by either digestibility or crude terpenoid concentration.

THE IN VITRO DIGESTIBILITY AND UTILIZATION

OF BIG SAGEBRUSH AND BLACK SAGEBRUSH

by

Karl David Striby

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Karl David Striby

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November 27, 1985
Date

Carl L. Hambolt
Chairperson, Graduate Committee

Approval for the Major Department

November 27, 1985
Date

Arthur E. Linto
Head, Major Department

Approval for the College of Graduate Studies

_12-3-85_
Date

M. Malone
Graduate Dean

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ABSTRACT

The relative forage quality of 4 Artemisia taxa was evaluated as reflected by in vitro organic matter digestibility (IVOMD), crude terpenoid content, and forage utilization. Taxa included A. nova, A. tridentata vaseyana, A.t. wyomingensis, and A.t. tridentata. Current years growth was collected from each taxon on January 1, February 15, and April 1, 1981. Collections from A.t. vaseyana and A.t. wyomingensis were segregated into lightly and heavily grazed plants. Crude terpenoids on the foliage epidermis were extracted with chloroform and quantified. Extracted and intact (fresh) foliage were ground in liquid nitrogen and frozen until in vitro digestion. IVOMD was determined using mule deer, sheep, and steer rumen inocula. A total of 1569 plants from the 4 taxa were examined for degree of hedging from combined deer and elk utilization in the spring of 1981. Utilization assessment indicated big game preference for the taxa. Order of increasing digestibilty among intact taxa was A. nova A.t. vaseyana, A.t. wyomingensis and A.t. tridentata. IVOMD generally increased from January to February to April. Fewer and contrasting differences in IVOMD were evident for extracted foliage among taxa and dates. A.t. vaseyana was consistently less digestible than A. nova which was generally less digestible than A.t. wyomingensis and A.t. tridentata. Extracted foliage was an average 13.2% more digestible than intact foliage. All inocula had similar digestive efficiency. A.t. vaseyana contained the lowest crude terpenoid level, A. nova and A.t. wyomingensis contained intermediate levels, and A.t. tridentata contained the highest level. Crude terpenoid concentrations were greater on January 1 and February 15 than on April 1. Non-volatile crude terpenoids decreased IVOMD through microbial inhibition and/or resistance to digestion. The crude terpenoid concentration was negatively associated with IVOMD within each taxon, however, compositional differences might account for the variability in IVOMD among the taxa. Even though non-volatile crude terpenoids decreased IVOMD, digestibility remained high relative to other forages. Variation in IVOMD and crude terpenoid concentration was not related to utilization differences. Increasing order of preference appeared to be A.t. tridentata, A. nova, A.t. vaseyana, and A.t. wyomingensis. Lightly and heavily grazed plants of either A.t. vaseyana or A.t. wyomingensis were digested equally well and contained similar crude terpenoid levels. Therefore, apparent animal grazing preference was not influenced by either digestibility or crude terpenoid concentration.

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INTRODUCTION

The widespread existence of the woody sagebrushes (subgenus Tri-
tatae of the genus Artemisia) in western North America has a signifi-
cant impact on the ecology and economics of rangeland resources
(Beetle 1960, Gifford et al. 1979, Blaisdell et al. 1982). In recent
years many investigators have agreed that members of this group cannot
be placed into uniform taxonomic and management categories. The
assorted taxa are valuable or undesirable in different degrees and have
important site and management implications (Beetle 1970, Morris et al.
1976, McArthur 1979). The need to more accurately categorize sagebrush
taxa for the purpose of improving resource management was summarized by
A. A. Beetle who said in 1977,

> "It is no longer fashionable to refer in a general way to sage-
> brush....This wide variety in ecological adaptation, distri-
> bution and significance reflects important differences in site
> potential and consequently in management technique. Knowledge
> of the ecological characteristics of the species, and in many
> instances the subspecies of sagebrush will be an important tool
> to the range manager."

The great diversity of the sagebrushes, their vast distribution and the
dichotomous nature of their value, justifies intense efforts to
understand their beneficial uses.

Shrubs are indispensable in the diets of many wild and domestic
herbivores (Dietz 1972). Yet, less is known about the forage quality
of shrubs than other forage classes occurring on rangelands (Ritten-
house and Vavra 1979).

The relative acceptability and nutritive value of the various
sagebrush taxa are major components of their diverse ecological profiles

(Beetle and Johnson 1982). The utilization of sagebrush in the diets
of livestock and big game animals varies from no use to heavy use on
winter ranges, where other forage species may be limited (Urness 1979).
During the winter when range animals may be under considerable nutri-
tional stress, the nutritive value of available forages is of critical
importance (Ward 1971, Wallmo et al. 1977). Sagebrush is relatively
high in digestible protein, phosphorous and carotene when compared to
alternate forage species during the winter (Cook et al. 1954). How-
ever, the essential oils and other secondary metabolic products of
sagebrush are suspected to influence the preference, digestibility and
intake of these shrubs by browsing animals (Nagy 1979, Kelsey et al.
1983).

Knowledge of the factors affecting the forage quality of the
sagebrushes can influence management decisions on sagebrush ranges.
Range management practices such as grazing systems, sagebrush control
techniques and reseeding on big game ranges warrant site specific
decisions that may benefit by considering the forage value of the
particular sagebrush species or subspecies at hand (Beetle and Johnson
1982, Morris et al. 1976, Blaisdell et al. 1982).

Big sagebrush (Artemisia tridentata Nutt.) and black sagebrush
(Artemisia nova Nelson) are two species that are widely distributed on
western rangelands. Relative to other sagebrush species, big sage-
brush ranks first in total acreage covered, being a dominant or
subdominant on approximately 58,632,000 ha (226,374 square miles)
(Beetle 1960). It is represented by three subspecies; basin (ssp.
tridentata), mountain (ssp. vaseyana (Rydb.) Beetle), and Wyoming

(ssp. <u>wyomingensis</u> Beetle and Young) big sagebrushes. Black sagebrush

ranks third in total acreage, occupying approximately 11,215,000 ha

(43,300 square miles) (Beetle 1960). Together, these 4 taxa comprise

over 70 percent of the total sagebrush acreage in the 11 western states

(Beetle 1960, Beetle and Young 1965). Their significance to the

environment and to range managers matches their extensive distribution.

This study was initiated in order to further the understanding of

the forage quality and the unique chemistry of black sagebrush and the

3 subspecies of big sagebrush. Objectives were as follows:

1. Compare in vitro organic matter digestibility (IVOMD) of 4 sagebrush taxa during winter as an indication of relative nutritive value.

2. Distinguish forage utilization differences among sagebrush taxa on big game winter range as an indication of animal grazing preference.

3. Determine the concentration of crude terpenoids in the sagebrush taxa during winter.

4. Evaluate the influence of crude terpenoid concentration on the IVOMD of sagebrush.

5. Investigate the influence of digestibility and crude terpenoid concentration on the relative forage utilization of the sagebrush taxa.

LITERATURE REVIEW

Factors of Forage Quality

Range research techniques which measure the quantity and quality of vegetation draw from several fields of specialization. Disciplines such as agronomy, ecology and animal husbandry are often utilized, while highly specialized fields such as plant physiology and animal physiology have made major contributions (Subcommittee on Range Research Methods 1962). Each science helps unravel the many interrelationships found in biological systems.

Mott (1973) identified 2 biological systems basic to the evaluation of forages. The environment-plant system and the plant-animal system were used to describe the quantity and quality of forages produced per unit of land, labor and capital. Both systems determined the total yield of animal products (meat, milk, wool, etc.) per unit area. Forage quality, in toto, could be measured by animal production response, providing animal potential was held constant and forage was the sole source of food.

Animal and range scientists agree that the quality of a forage depends on its nutrient content, the digestibility of the nutrients, the metabolizability of the digested nutrients and the amount the animal will consume (Cook and Harris 1968, Dietz 1970, Barnes 1973, Church 1977, Kothmann 1980). The 2 basic components of forage quality as described by Mott (1973) are "forage nutritive value" and "forage consumed" (Figure 1). According to Mott, forage nutritive value is determined by the following 3 factors: (1) nutrient composition, (2)
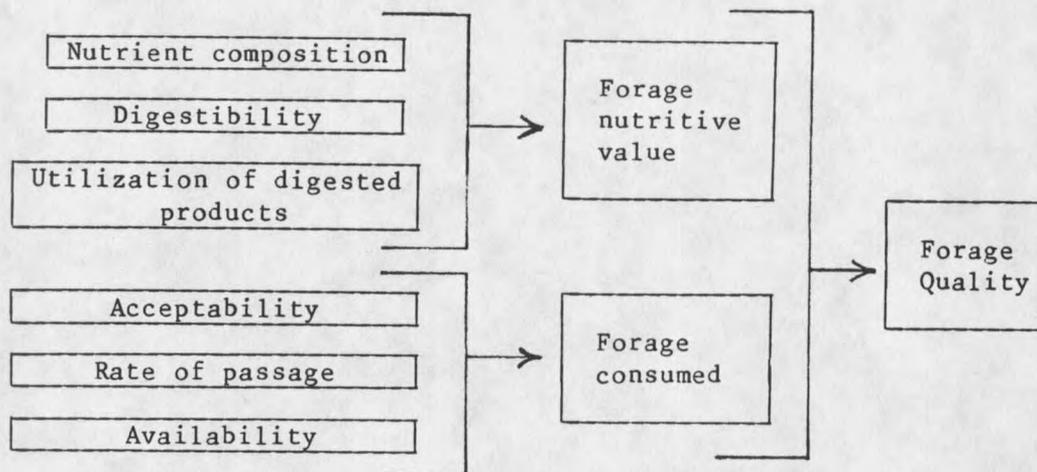
Figure 1. Diagramatic representation of the factors of forage quality
(adapted from Mott, 1973).

digestibility, and (3) utilization of digested products. Nutrient com-
position is dependent only on the plant and its environment. Digest-
ibility and the efficiency of utilization of digested products are
associated with both the plant and animal. When animal production
potential and environmental effects are constant, forage consumed (also
referred to as "voluntary intake") is determined by 3 factors as
follows: (1) acceptability, (2) rate of passage, and (3) availability.
Acceptability is described by the readiness with which a forage is
selected and eaten. Rate of passage through the digestive tract is a
function of forage fiber mass and rate of digestion. Availability
refers to the amount of forage available for consumption. Each factor
of forage consumption depends on the characteristics of both plant and
animal.

Mott's (1973) description of forage quality considers environment
and plant and animal parameters which are fundamental to optimum output
of domestic livestock products. Terms commonly used to express overall

forage quality, such as "digestible energy consumption" or "rate of consumption of digestible dry matter" or "digestible organic matter intake", encompass the concepts of both forage nutritive value and forage consumed. These terms are recognized to be of prime importance in determining animal performance on pasture and range settings (Cramption 1957, Mott and Moore 1970, Rittenhouse and Vavra 1979). Currently, voluntary intake is considered as the more critical of the 2 components of forage quality in determining animal production potential (Ingalls et al. 1965, Mott and Moore 1970, Rittenhouse and Vavra 1979). While these principles are directly applicable to maximizing agricultural production, they are also relevant to the maintenance of healthy, productive wildlife populations (Dietz 1970, Wallmo et al. 1977).

The factors of forage quality pertinent to this study included digestibility and acceptability. A brief description of these factors and their importance follows.

Digestibility

The performance of all ruminant species utilizing range forage is, to a great extent, determined by the ability of the rumen microbes to efficiently utilize the nutrients in the forage consumed (Dietz 1970). Determination of forage digestibility has long been recognized as necessary to the assessment of forage nutritive value. In discussing nutrition of wild ruminants, Atwood (1948) stated that the gross composition of a forage alone was not capable of preventing starvation. Routine feed analyses were not always reliable as positive indicators

of nutritive value and such analyses must be supplemented by digestibi-
lity data. Blaxter et al. (1961) recorded a 100% increase in sheep
weight gain when digestible dry matter of sheep diets increased from 50
to 55%. Digestibility is the most commonly used measure of forage
nutritive value (Van Soest 1973). It is unlikely that a technique to
assess nutritive value could be developed that did not take digestibi-
lity into account (Riewe and Lippke 1970).

An important nutritive element provided by forages in the diet of
ruminants is energy (Reid et al. 1959, Cook 1970). Feeding standards
for all animals are based, in part, on energy requirements (Church
1977). Total digestible nutrients (TDN) and digestible energy (DE) are
measures commonly used to express energy needs. Digestible dry matter
(DDM), digestible organic matter (DOM), TDN, and DE are highly corre-
lated and these are often regarded as comparable measures of forage
nutritive value (Swift 1957, Heaney and Pigden 1963, Reid et al. 1959,
Rittenhouse et al. 1971, Van Soest 1973).

Acceptability

Arnold (1964) asserted that an understanding of the mechanisms
involved in forage selection and ingestion by ruminants are basic to
our knowledge of their nutritional needs and productivity. Yet, the
principles underlying forage acceptability are very complex and have
long been in need of further clarification (Cook 1953, Hanley 1982).
The foraging animal experiences a stimulus-response chain of events in
food selection as follows: recognition of the food; movement to the
food; appraisal; initial eating; cessation of eating. Food selection

may occur anywhere along the above chain and is controlled by a number

of complex mechanisms (Heady 1975).

Palatability and preference are 2 different concepts that are

inseparable in food selectivity (Heady 1975, Kothmann 1980). Heady

(1964, 1975) defined palatability as plant characteristics which stimu-

late a selective grazing response by animals, and preference as animal

reactions that facilitate food selection. Although neither forages nor

plants, per se, exhibit preference, "forage preference" indicates a

proportional choice among 2 or more forages by the grazing animal

(Heady 1964). Forage palatibility and animal preference are important

factors governing range utilization and they represent valuable tools

in formulating grazing management practices, stocking rates and pasture

mixes (Subcommittee on Range Research Methods 1962, Malechek and

Leinweber 1972).

There seems to be no universally accepted, specific definition for

the term "palatability" since in the past it has been variously used to

describe forage and animal attributes ranging from tastiness to volun-

tary intake (Martin 1970, 1978). In contrast to Heady's definition,

the Range Term Glossary Committee (1974) defined palatability as "the

relish with which a particular species or plant part is consumed by an

animal." To further confound the subject, palatability and preference

are some times used interchangeably (Heady 1964, 1975). Since it has

been subjected to such wide interpretation, some authors have reported

that the use of the term "palatability" in the discussion of the con-

cepts operating in forage selectivity tends to embrace some degree of

ambiquity (Mott 1959, McClymont 1967, Van Soest 1973, Stoddart, Smith

and Box 1975). In this thesis, the terms palatability and preference
follow Heady's definitions.

According to Heady (1975), palatability factors are those charac-
teristics of plants that are recognized by the animal senses of touch,
smell and taste. They may stimulate a selective response of either
acceptance or rejection. Major palatability factors are nutrient com-
position, growth stage, external plant form, associated feed elements
and possibly digestibility. These, in turn, can be affected by season
of use, weather patterns, soils and topography (Heady 1975).

In the past, palatability studies have placed much emphasis on
nutritive values rather than the research of palatability, per se,
resulting in a disproportionate concentration on composition of nutri-
tive elements (proximate analysis, NDF, ADF, etc) (Heady 1964). Other
palatability factors such as plant parts, plant growth stages, past
grazing use, climate, topography, soil moisture and fertility have been
examined mainly through their influence on nutrient composition (Heady
1964). No completely consistent relationship between any of the men-
tioned palatability factors and animal preference has been found, as
many observations are the result of association rather than cause and
effect (Martin 1970, Heady 1975). Many of the nutritive components
that have been extensively researched, such as crude protein, crude
fiber and lignin, etc., are hardly recognized by their smell or taste,
while other compounds not measured by the usual nutritional analyses
are responsible for stimulating these senses (Heady 1975). Within
plant species similar in gross physical form and chemical

characteristics, selection may be based on subtle chemical differences affecting smell and taste (McClymont 1967).

While the extent of palatability influence on voluntary intake is not completely understood, many researchers agree that these factors are related (Van Soest 1973, Milchunas et al. 1978, Martin 1978). Some authors contend that forage palatability directly governs rate and total intake of forage (Jones 1952, Tribe 1952, Hurd and Blaser 1962, Dietz 1970). Others have reported that there is no evidence to indicate that highly preferred forages increase total intake, yet provision of unpalatable forages may reduce it (Van Soest 1965, McClymont 1967). Arnold (1964) maintained that animals can adapt to different grazing situations and consume as much of an unpalatable forage as a highly preferred one. A major question to answer when considering the extent to which palatability influences intake is whether the animal will consume enough of an unpalatable forage to reach either rumen capacity or energy balance (Martin 1970).

Many factors besides palatability affect food selection. Physiological and psycological conditions internal to the animal such as perception through the 5 senses, breeding, pregnancy, lactation, growth, fear, excitement, rumen fill and hunger influence animal behavior and thus preference (Heady 1975). Environmental factors such as climate, soil, topography and vegetation have a direct bearing on animal behavior and therefore influence food preference (Heady 1975). Evolutionary factors such as kind of animal and innate instincts differ markedly between animal species thereby altering diet selection. Learned behavior such as previous grazing experience can affect animal

food preferences (Heady 1975). This complex of stimulus-response
mechanisms is not well understood for grazing ruminant animals (Heady
1975).

The In Vitro Rumen Fermentation Procedure

The in vivo digestibility trial is a time consuming and expensive
procedure for estimating forage nutritive value (Barnes 1965). At
least 3 animals and large amounts of forage are required to attain pre-
cise results (Heaney 1970). With unpalatable feeds or wild animals,
feed intake can be a problem (Smith 1950, Bissel et al. 1955, Dietz et
al. 1962, Milchunas et al. 1978, Striby et al. 1983). When a food item
must be mixed with an acceptable base feed, the resultant digestibility
by difference of the food item is sometimes confounded by interaction
with the base feed (Dietz et al. 1962, Schneider and Flatt 1975,
Milchunas et al. 1978, Striby et al. 1983).

The in vitro rumen fermentation procedure was designed to circum-
vent these difficulties. Because of its simplicity, speed, precision
and economy, this procedure is widely used to estimate the digestibi-
lity of forages by wild and domestic ruminants (Pearson 1970).
Numerous in vitro digestion techniques have been developed since its
first recorded use by Pigden and Bell in 1955 (Barnes 1966). Of these,
the two-stage technique of Tilley and Terry (1963) has the highest
correlation and lowest standard error of the estimate for prediction of
in vivo dry matter digestibility (Barnes 1965, 1966). Therefore, it is
the method of choice used by many researchers for assessment of forage
nutritive value (Oh et al. 1966, Van Soest 1967, Mott and Moore 1970,

Harris 1970, Pearson 1970, Urness et al. 1977, Milchunas and Baker 1982).

In vitro digestibility has been mainly reported as digestible cellulose or digestible dry matter (Pearson 1970). Cellulose digestibility, alone, is not necessarily a good predictor of forage nutritive value because cellulose is not characteristic of the whole forage dry matter (Barnes 1965, Van Soest 1967). In vitro dry matter digestibility is more often used because it is simpler to determine analytically and subject to less variability than in vitro cellulose digestibility (Johnson 1970). In vitro organic matter digestion is sometimes used to exclude error associated with indigestible ash which is principally composed of silica (Jones and Handreck 1967, Van Soest 1968, Milchunas et al. 1978).

In vitro digestion procedures have limited application in that results are not absolute measurements of in vivo parameters such as DDM, DE and TDN (Johnson 1966). Also, procedures are subject to significant variation inherent in biological systems and resulting from inconsistent laboratory methods (Johnson 1966). These limitations should be recognized before interpreting and applying in vitro results to the animal, across laboratories and across some localities (Johnson 1966).

Generally, in vitro digestibility data has 2 applications in the assessment of forage nutritive value. In unaltered form, it can be used as a relative ranking of forage digestibility (Johnson 1966). If in vitro data is to be used in establishing animal feeding practices or

nutritional requirements on the range, in vitro digestibility must
first be correlated to in vivo digestibility (Johnson 1966). This is
accomplished by determining the in vivo digestibility of standard fora-
ges by the ruminant species being studied. Standard forage samples,
chosen to represent foods having a wide range of digestibility, are
then included in subsequent in vitro digestion trials. Once uniform
regression lines have been established between the in vivo and in vitro
digestibilities of the standards, the in vitro technique can be used to
predict the in vivo nutritive values of other forages (Johnson 1966).
This is not necessary when only the relative ranking of forages is
desired (Barnes 1965) which was an objective of this study.

Barnes (1967) found that the average in vitro digestible dry
matter for 3 forages ranged from 38.7 to 53.3% among 5 laboratories
using different methods. This variation was approximately reduced by
half after employing identical methods (Barnes 1968). Barnes concluded
that a standard procedure and consistent handling of inocula and each
substrate reduces variation among laboratories and among runs and
within runs.

The rumen fluid inoculum is the major source of variation in the
in vitro system (Johnson 1966). Diet quality affects the abundance,
diversity and activity of the microbial population in the rumen (Van
Soest 1983), however there are conflicting reports regarding the effect
of the diet of the inoculum donor on in vitro digestion. Differences
in the precision and accuracy of in vitro digestion due to the diet
donor have been demonstrated thereby implying that the inoculum donor
should be fed the same forage to be evaluated, or a standard forage of

known in vivo digestibility (Warner 1956, Asplund et al. 1958, Church
and Peterson 1960, Hungate 1960, Taylor et al. 1960, Van Dyne 1962,
Bezeau 1965, Pearson 1970, Ward 1971, Nelson et al. 1972, Robbins et
al. 1975, Horton et al. 1980). Yet some researchers have reported
little or no variability in in vitro digestion due to the diet of rumen
inocula donors (Quicke et al. 1959, Scales et al. 1974, NikKhah and
Tribe 1977, Pederson and Welch 1982, Welch et al. 1983b). Different
ruminant species do not digest all forages with equal efficiency (Van
Soest 1983). This leads to the assumption that rumen inocula donor
species might affect in vitro digestion thus requiring species-specific
evaluations (Milchunas et al. 1978). As with the influence of diet,
reports concerning effects of animal species on the precision and
accuracy of in vitro digestion are inconsistent. Significant differen-
ces in extent and variability of in vitro digestion of some foods have
been observed when inocula donors of different species were maintained
on similar diets (Warner 1956, Asplund et al. 1958, Hungate et al.
1960, Ward 1971, Scales et al. 1974, Robbins et al. 1975, Palmer et al.
1976, Horton et al. 1980, Blankenship et al. 1982). Conversely, others
have reported no significant in vitro digestion differences attribu-
table to inoculum donor species (Van Dyne 1964, Le Fevre and Kamstra
1960, Welch 1983b). Other confounding evidence is that supplied by
Troelsen and Hanel (1966), Rueggiero and Whelan (1976) and Milchunas et
al. (1982), who found that the digestive capacity of rumen inoculum
from the same animal, on the same feed can vary from one day to the
next. Palmer et al. (1976) and Palmer and Cowan (1980) successfully
predicted in vivo digestion by white-tailed deer with in vitro

estimates using rumen fluid inocula from Jersey cows maintained on

forages other than those being evaluated. Troelson and Hanel (1966),

Bryant and Robinson (1968) and Milchunas et al. (1982) conclude dif-

ferences in the digestive capacities of rumen inocula are the result of

sampling time after feeding and diet composition. Milchunas (1982)

further suggests that it does not matter what species of rumen inoculum

donor is used as long as it correlates well with the in vivo digestion

of the particular animal species being studied.

The Forage Quality of Sagebrush

The food value of sagebrush, like other forage species, is

influenced by the factors of forage quality as outlined by Mott (1973).

However, unlike many forage species, the sagebrushes produce secondary

metabolic compounds including the so-called "essential" or "volatile

oils" that are believed to affect such factors as acceptability,

digestibility and metabolizability (Cook et al. 1954, Nagy 1979, Kelsey

et al. 1983). A review of the availability, acceptability and nutrient

composition of sagebrush is followed by descriptions of its secondary

metabolic products, and digestibility.

Availability and Acceptability to Ruminants

Because of its vast distribution and abundance, sagebrush is

highly available for consumption by wildlife and domestic range animals

(McArthur et al. 1979, Beetle and Johnson 1982). Sagebrush-grass vege-

tation is one of the largest, if not the largest, range ecosystem in

the western United States (Blaisdell et al. 1982). The 20 or so sage-

brush taxa comprising the subgenus _Tridentatae_ inhabit approximately

108,782,000 ha (420,000 square miles) in 11 western states (McArthur et al. 1981, Beetle and Johnson 1982). Sagebrush species occur as climax shrubs in a variety of biomes (Gifford et al. 1979). The range of big sagebrush alone extends from near sea level to near tree line on approximately 58,632,000 ha (226,374 square miles) (Beetle 1960). It is the most common and widespread shrub in western North America (McArthur et al. 1979). Black sagebrush is the third most common sage-brush species being distributed over approximately 11,215,000 ha (43,000 square miles) in 10 western states (Beetle 1960).

Elk, domestic sheep, mule deer and pronghorn antelope, respect-ively, have been shown to be moderate to heavy consumers of sagebrush. Whereas pronghorn eat considerable amounts of sagebrush on a year-round basis (Sundstrom et al. 1973), sagebrush use by most ruminants occurs mainly during winter when herbaceous forage species are dormant and in limited supply or are covered by snow (Laycock 1967, Carpenter et al. 1979, Houston 1982). Kufeld et al. (1973) evaluated 99 food habits studies of the Rocky Mountain mule deer to determine the relative importance of forage plants as reflected by their consumption. Studies that referred to combined deer and elk use, or "game use" were excluded. In reference to big sagebrush, they listed 47 studies reporting heavy consumption during winter, 30 studies reporting heavy consumption during spring and 17 studies that cited moderate consump-tion during fall. In a similar evaluation of 60 food habits studies of the Rocky Mountain elk, Nelson and Leege (1982) listed 9 studies that reported moderate use of big sagebrush during winter and 4 studies that reported moderate use of big sagebrush during fall. Cook and Harris

(1954) reported that the diets of domestic sheep grazing Utah desert winter ranges of mixed flora contained 17% black sagebrush and 5% big sagebrush over a 5-year period. Laycock (1967) concluded that three-tip sagebrush (Artemisia tripartita Rydb.) and other sbrubs constitute an important part of sheep diets and heavy late fall grazing is a practical method to control sagebrush. Similarly, Frischknecht and Harris (1973) concluded that sheep eat large amounts of big sagebrush in late fall and can control it on seeded cattle range. Narjisse (1981) reported that experienced sheep ate substantial quantities of basin big sagebrush during June and moderate amounts during August and November, while goats refused to eat it at these times. Generally, sagebrush consumption by cattle is low (Frischknecht and Harris 1973, Cook and Harris 1968, Blaisdell et al. 1982).

Nutrient Composition

During winter, sagebrush is relatively high in essential nutrients when compared to other forages. Grasses, forbs and deciduous shrubs become tough and dry, loosing their nutritive value with advancing maturity, while sagebrush remains comparatively green and succulent (Dietz et al. 1958, Cook 1972). In assessing the nutrient content of important deer browse plants in southwestern Colorado, Dietz (1958) found that big sagebrush contained the highest levels of protein, phosphorous and carotene, and the lowest levels of crude fiber of the 5 species analyzed during late winter. Dietz concluded that big sage-brush is of outstanding significance in the management of deer winter range since it was the only browse species that substantially exceeded

minimum amounts of nutrients required by deer. Cook et al. (1954) eva-
luated the nutritive value of winter forage plants on ranges of western
Utah and reported that black sagebrush and big sagebrush were decidedly
higher in protein, phosphorous and carotene than grasses, which were
superior only in energy. Cook concluded that black sagebrush and big
sagebrush are valuable forage plants for domestic sheep on winter
ranges and furnish adequate amounts of the important nutrients for
pregnant ewes except in the case of energy.

Secondary Metabolic Products

The aromatic and bitter qualities of sagebrush have long been
suspected to influence its forage value. Early records suggest that,
because of its pungent nature, sagebrush was not relished by some ani-
mals and was possibly toxic (Bailey 1869, Pammel 1911). In reference
to Artemisia tridentata, McCreary (1927) stated "Unfortunately the
palatability of the leaves is lowered by the presence of a bitter prin-
ciple and of nearly 3% volatile oil which gives them a bitter pungent
taste." In 1931 McCreary further reported that there was little fat in
the exceptionally high ether extract of big sagebrush, most of which
was probably terpene-like compounds of low digestibility.

Sagebrush foliage is rich with a wide variety of secondary
metabolic products having aromatic and bitter properties. As McCreary
surmised in 1931, terpenoids are present in high concentrations. Sub-
stantial quantities of both monoterpenes and sesquiterpene lactones
are present (Kelsey and Shafizadeh 1980, Welch and McArthur 1981), as
well as lower concentrations of 2 classes of phenolics, the coumarins

(Shafizadeh and Melnikoff 1970) and flavonoids (Rodriguez et al. 1972).
Highly volatile, non-terpenoid hydrocarbons such as acetone and
methacrolein are also present (Scholl et al. 1977, Kelsey et al. 1983).
In addition to these secondary products, cuticular waxes cover leaf
surfaces (Thomas 1976, Kelsey et al. 1982). Each class of compounds
has unique physical, chemical and biological properties that govern its
isolation and analysis and may influence the forage quality of sage-
brush (Kelsey et al. 1983). A brief description of these properties
follow in Table 1.

Numerous studies have been conducted in an effort to clarify the
relationships between the unique chemistry of sagebrush and its forage
value. Most investigations have concentrated on the influence of the
essential oils on digestibility and palatability. Conclusions drawn
from these studies have been in some cases inconclusive and con-
flicting. Reports indicate that the essential oils of sagebrush kill
rumen microorganisms, reduce microbial digestion of forage (Nagy et al.
1964, Nagy and Tengerdy 1968), reduce appetite (Nagy et al. 1964) and
reduce palatability (Cook et al. 1954, Nagy and Tengerdy 1968, Sheehy
1975, Narjisse 1981), and increase both plant toxicity (Cook et al.
1954, Johnson et al. 1976) and non-metabolizable energy content (Cook
et al. 1952). Conversely, others have found little or no net effect of
the essential oils on sagebrush digestibility (Welch and Pederson 1981,
White et al. 1982b, Cluff et al. 1982) or palatability (Scholl et al.
1977, Welch et al. 1983, White et al. 1982a).

Technically the essential oils are the volatile steam distillable
components that give plants their characteristic odor (Harborne 1973).

Table 1. Properties of secondary metabolic products of sagebrush.

Class of compound	Percent foliage dry wgt	Physical state	Volatility	Sensory perception	Biological activity	References[1]
Monoterpenes	0.5-9.0	liquid	high	aromatic pungent	Antimicrobial Animal toxin Feeding deterrent Phytotoxic	1,2,3,4,5,6, 7,8,9,13
Sesquiterpene lactones	2.3-3.5	solid	low	bitter	Alergenic Antimicrobial Animal toxin Antifungal Cytotoxic Feeding deterrent[2] Phytotoxic	6,7,10,11 12,13,14,15 16,17,18,19 20,21
Phenolics (coumarins & flavinoids)	0.01-2.1	solid	low	astringent bitter sweet	Animal toxin[2] Cytotoxic[2] Feeding attractant Feeding deterrent[2] Phytotoxic	22,23,24,25, 26,27,28,29 30
Cuticular waxes & misc. compounds	3.8-10.2[3]	solid	low	----	Limited digestibility	31
Highly volatile non-terpenoids (i.e. acetone, methacrolein)	unknown	liquid	very high	pungent	Possible feeding deterrent Mucosa irritant	1,32

20

Table 1. (continued)

[1]References:

1. Kelsey et al. (1983)
2. Sneva et al. (1983)
3. Guenther (1948)
4. Buttkus et al. (1977)
5. Nagy and Tengerdy (1968)
6. Mabry and Gill (1979)
7. Kelsey et al. (1984)
8. Narjisse (1981)
9. Asplund (1968)
10. Kelsey and Shafizadeh (1980)
11. Shafizadeh et al. (1971)
12. Kelsey (1974)
13. Rodriguez et al. (1976)
14. Mitchell et al. (1970)
15. Mitchell and Dupuis (1971)
16. Mitchell and Epstein (1974)

17. Picman and Towers (1983)
18. Wisdom et al. (1983)
19. Picman (1984)
20. McCahon et al. (1973)
21. Amo and Anaya (1978)
22. Harborne (1979)
23. Harborne (1982)
24. Hanks et al. (1973)
25. Stevens and McArthur (1974)
26. Francis (1973)
27. Rice (1974)
28. Shafizadeh and Melnikoff (1970)
29. Rodriguez et al. (1972)
30. Brown (1973)
31. Martin and Juniper (1970)
32. Lewis and Tatken (1980)

[2]The biological activities of many of the sesquiterpene lactones and phenolics specific to sagebrush species have yet to be tested. Activities cited here apply to related compounds isolated from other plant species.

[3]The range of values for percent cuticular waxes and miscellaneous compounds was approximated by subtracting minimum and maximum amounts of other secondary products from the respective minimum and maximum amounts of crude terpenoids cited in Kelsey et al. (1982) (ie. min. crude terpenoids-6.6% for vaseyana, max. crude terpenoids-24.8% for tridentata).

Many essential oils, including those of sagebrush, consist largely of liquid terpenoids (Guenther 1948, Nagy 1966). The monoterpenes are the most volatile and most abundant terpenoids found in many plant species, along with lesser amounts of sesquiterpenes and diterpenes (Guenther 1948, Tyler et al. 1981). For the purpose of this discussion, "sesquiterpenes" refers to the non-lactonized hydrocarbons ($C_{15}H_{24}$-$C_{15}H_{18}$) and related alcohols, aldehydes and ketones (Sutherland and Park 1967). Like other plant species, the terpenoid fraction of sagebrush essential oils is largely composed of monoterpenes (Scholl et al. 1977, Kelsey and Shafizadeh 1980, Welch and McArthur 1981); the literature suggests that sagebrush volatile oils do not contain significant amounts of sesquiterpenes or diterpenes. This author found only 1 reference to sesquiterpenes or diterpenes that have been isolated and positively identified from sagebrush volatile oils. Buttkus et al. (1977) reported that 2 sesquiterpenes and 4 diterpenes together comprises less than 1% of the steam distillable terpenoids in big sagebrush. The chemical and physical properties of the sesquiterpene lactones categorically separate them from the sesquiterpenes. Because they are crystalline solids with high melting points, the sesquiterpene lactones do not readily volatilize and generally are seldom found in steam distilled essential oils (Sutherland and Park 1967). Sagebrush foliage contains substantial quantities of sesquiterpene lactones (Kelsey and Shafizadeh 1980, Kelsey et al. 1982). However, none are found in the steam distilled essential oils of sagebrush. Likewise, the crystalline phenolics and cuticular waxes are absent from sagebrush volatile oils (Kelsey 1984, personal communication). At the other end of the

volatility scale are the non-terpenoid organic compounds such as ace-
tone and methacrolein. Because of their extreme volatility, these com-
pounds are lost during steam distillation and are absent in steam
distilled essential oils (Kelsey et al. 1983).

The substitution of solvent extraction in place of steam distilla-
tion as the extracting process has in recent years revealed an array
of secondary compounds in sagebrush tissues. The coumarins and sesqui-
terpene lactones were isolated, identified and recognized as taxonomic
markers for shrubby Artemisia species (Young 1965, Winward and Tisdale
1969, Shafizadeh and Melnikoff 1970, Brunner 1972, Hanks et al. 1973,
Kelsey et al. 1976). Using a chloroform solvent, Kelsey et al. (1982)
separated the external components of sagebrush foliage from the inter-
nal constituents (Figure 2). The terpenoids and possibly the phenolics
are present within glandular trichomes located on leaf surfaces that
are coated with cuticular waxes (Kelsey and Shafizadeh 1980, Kelsey et
al. 1983). These external components are readily available for
solvent extraction. Collectively, the extract of external components
constitute the "crude terpenoids" (Kelsey et al. 1982). The internal
constituents are cell wall polymers, proteins, nonstructural car-
bohydrates and lipids.

The volatile, non-terpenoid organic compounds such as acetone and
methacrolein are probably located in the glandular trichomes (Kelsey
1984, personal communication). Because of their extreme volatility,
they are lost during the extraction process and therefore are not found
in the crude terpenoids (Kelsey 1984, personal communication).

EXTERNAL

Monoterpenes
Crude terpenoids — Sesquiterpene lactones
Phenolics
Cuticular waxes

INTERNAL

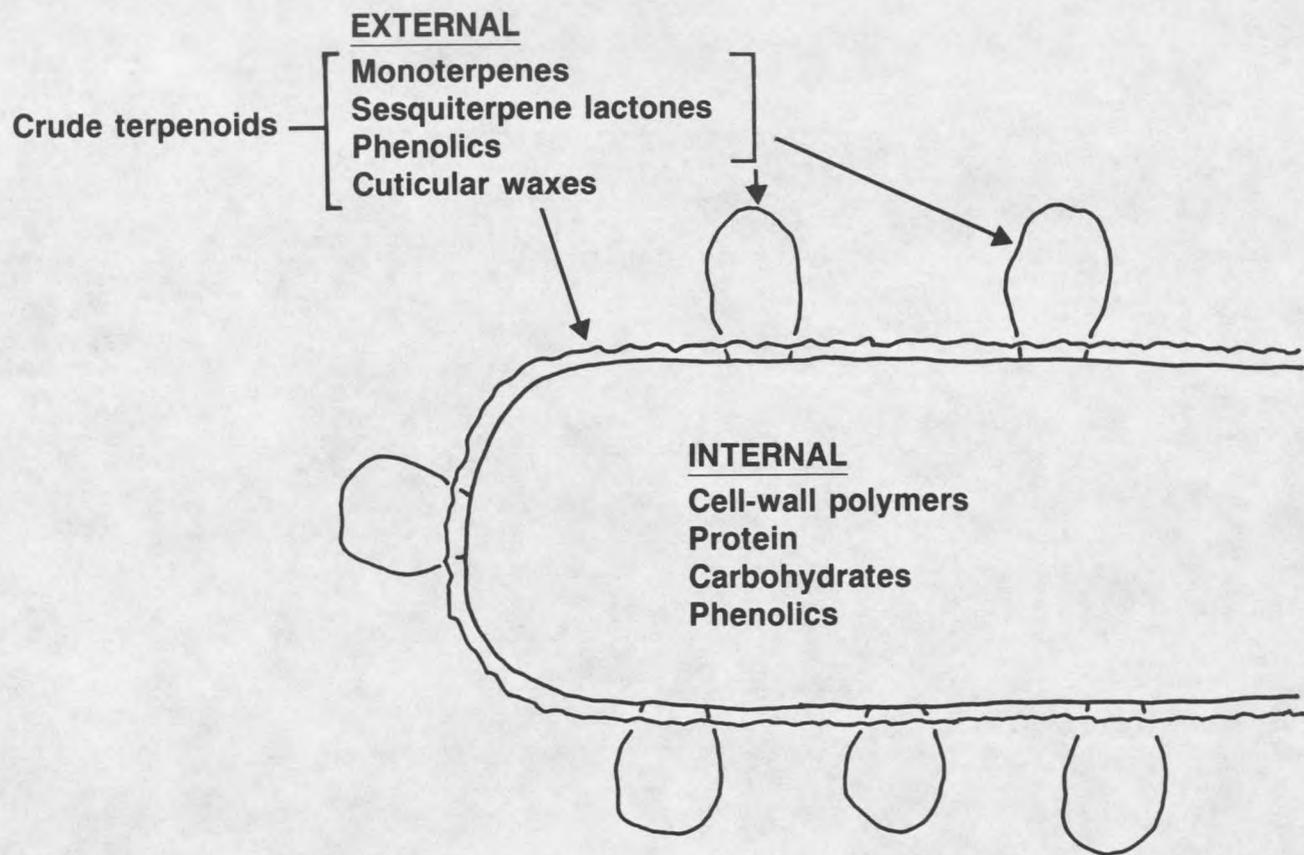Cell-wall polymers
Protein
Carbohydrates
Phenolics

Figure 2. Internal and external components of sagebrush foliage. Leaf shown in cross section with protruding glandular trichomes. Phenolics may be internal and external components. Volatile non-terpenoid hydrocarbons (ie. acetone, methacrolein) probably occur in glandular trichomes.

When touched by feeding herbivores, the glandular trichomes readily burst and release their contents. Thus, a highly concentrated zone of volatile and non-volatile compounds is exposed to the olfactory and gustatory senses of the herbivore. In effect, certain of these compounds might independently or synergistically influence animal selection and digestion (Kelsey et al. 1983).

The literature indicates that the interaction of the secondary metabolites of sagebrush with its forage quality has primarily been evaluated in regard to the influence of the monoterpenes. The total impact of the secondary products of sagebrush on digestibility and forage selection has not been fully researched since the possible influence of the aforementioned classes of compounds not included in the essential oils have been largely overlooked (Kelsey et al. 1983).

Sagebrush Digestibility

Numerous reports on the DDM and TDN contents of big sagebrush indicate that it is moderately to highly digestible relative to alfalfa and winter range forages (Tables 2 and 3). Comparative TDN values determined for alfalfa by Smith (1952), Bissell et al. (1955), Dietz et al. (1962) and Smith (1963) were 64.7%, 65.5%, 54.3% and 59.5% respectively. Smith (1957) discovered that the TDN level in big sagebrush (Table 4) exceeded the amounts found in 7 other deer browse species by at least 12.6%. Ward (1971) determined that big sagebrush had the highest in vitro dry matter digestibility (IVDMD) of 11 winter range forages including 5 grasses, 5 shrubs and 1 forb (Table 5). Urness et al. (1977) ranked the IVDMD of big sagebrush (Table 5) second highest

Table 2. In vivo digestibility of big sagebrush.

Reference	Subspecies Designation	Test Animal	Ave DDM	Ave TDN	DE Kcal/kg	ME Kcal/kg
Smith (1950, 1957)	typica[1]	deer	67.1[2]	78.1	----	----
Cook et al. (1952)	none	sheep	-----	43.4	1946	1130
Cook et al. (1954)	none	sheep	37.6	50.7	2304	1268
Bissell et al. (1955)	none	deer	48.9[2]	55.9	2848[2]	----
Dietz et al. (1962)	none	deer	49.6[2]	58.9	----	----
Smith (1963)	tridentata[3]	sheep	54.5	55.9[2]	2485	1636[2]

[1] Subspecies typica from classification system of Hall and Clements (1923); synonymous with subsp. tridentata of Beetle (1960).
[2] Values calculated from author's reported data.
[3] From classification system of Beetle (1960) which did not recognize subsp. wyomingensis.

Table 3. In vitro digestibility of big sagebrush.

Reference	Subspecies Designation	Test Animal	Ave DDM
Smith (1963)	tridentata[1]	sheep	47.5
Ward (1971)	none	elk	52.3
	none	cow	52.3
Sheehy (1975)	tridentata	unspecified	56.8
	vaseyana	unspecified	53.6
	wyomingensis	unspecified	53.1
Urness et al. (1977)	typica[2]	deer	62.0
Wallmo et al. (1977)	none	deer	59.0
Narjisse (1981)	tridentata	sheep	50.0[3]
	tridentata	goat	51.0[3]
Welch and Pederson (1981)	tridentata	deer	62.1
	vaseyana	deer	53.2
	wyomingensis	deer	51.4
Kufeld et al. (1981)	combination[4]	cow	49.9
Pederson and Welch (1982)	none	deer	67.0

1 From classification system of Beetle (1960) which did not recognize subsp. wyomingensis.
2 Sagebrush remained from Smith (1950) study (Table 2).
3 Digestible organic matter.
4 Average of 3 major subspecies.

among 11 mule deer forages including 8 shrubs and 3 forbs. Alfalfa was the only forage having more IVDMD than big sagebrush out of a set of 4 native and 2 domestic forages tested by Pederson and Welch (1982). For black sagebrush, Cook et al. (1954) detected 38.6% DDM and 47.2% TDN while Sheehy (1975) reported 53.1% IVDMD.

A variety of digestibility techniques and animal species were used in compiling the data in Tables 2 and 3. Smith (1950, 1957) and Bissell et al. (1955) (Table 2) used single species diets while Dietz et al. (1962) and Smith, (1963) (Table 2) used the by-difference method whereby the diet consisted of sagebrush and another forage. Cook et al. (1952, 1954) (Table 2) used the lignin-ratio technique and allowed animals to graze single-species stands. All in vitro digestion trials (Table 3) utilized variations of the Tilley and Terry two-stage technique, except Smith (1963), who used a one-stage method. It is not the purpose of this review to evaluate the relative digestive efficiency of experimental techniques or animal species. However, it should be noted that many factors affect the digestibility of a particular plant species, including environmental conditions, stage of plant maturity, animal species, animal selectivity and nutritive balance of the ration (Cook et al. 1954). The digestibility of an individual plant species when eaten separately may be different than when other species are included in the diet (Cook et al. 1954, Dietz et al. 1962). Therefore, the establishment of exact digestion coefficients under controlled conditions may be only an approximation of the actual digestibility on mixed species ranges (Cook et al. 1954,