Temperature and Carbon Dioxide Effects on Nutritive Value of Rhizoma Peanut Herbage

Y. C. Newman, L. E. Sollenberger,* K. J. Boote, L. H. Allen, Jr., J. C. V. Vu, and M. B. Hall

ABSTRACT

Studies assessing the impact of climate change have focused on plant production, but forage nutritive value, especially of legumes, has often been overlooked. The objective of this study was to determine the effect of increasing temperature and atmospheric CO_2 concentration on chemical composition and digestibility of rhizoma peanut (RP, *Arachis glabrata* Benth.) leaf and stem. In vitro digestible organic matter (IVDOM), neutral and acid detergent fiber (NDF and ADF), and lignin concentrations were determined for plants grown in all combinations of two CO_2 (360 and 700 μmol mol^{-1}) and four temperature environments (baseline, or ambient temperature in the greenhouse, B; B + 1.5; B + 3.0; and B + 4.5°C). Forage was sampled every 6 to 8 wk during two growing seasons. Neither increasing CO_2 nor temperature affected leaf IVDOM, but stem IVDOM declined from 562 (B) to 552 g kg^{-1} (B + 4.5) with increasing temperature in Year 1 and from 577 to 511 g kg^{-1} in Year 2. Stem NDF increased with increasing temperature from 556 to 561 g kg^{-1} in Year 1 and from 519 to 526 g kg^{-1} in Year 2. Stem ADF (412 to 418 g kg^{-1}) and lignin (80 to 93 g kg^{-1}) increased linearly as temperature increased in 1 of 2 yr. Lignin as a proportion of NDF or ADF (lignin/NDF or lignin/ADF) accounted for a large proportion of the variation in stem IVDOM. The RP nutritive value decreases with increasing air temperature, but it is relatively unaffected by atmospheric CO_2 concentrations in the range studied.

Increasing atmospheric CO_2 to near a doubling of current concentrations and an associated increase in temperature are among changes predicted to occur in the global environment as consequence of the burning of fossil fuels (Keeling et al., 1995). A major research emphasis has been the impact of environmental changes on plant production (Idso and Idso, 2001), but effects on the nutritive value of plants and plant parts consumed by herbivores has often been overlooked. The nutritive value of plants, defined as the chemical composition and their potential digestibility, is a function of chemical, physical, and structural factors inherent to the plant (Moore, 1994), all of which are dependent to some extent on external factors including climate. Thus, increasing CO_2 and temperature may affect plant chemical composition and its feed value for herbivores (Wilson et al., 1991; Idso and Idso, 2001).

Florigraze RP is a warm-season perennial legume used for pasture (Williams et al., 1991) or as conserved forage (Prine et al., 1981). Capable of supporting daily weight gains of 1 kg in beef cattle (*Bos* spp.), RP is persistent under grazing and is regarded as a high quality forage legume by livestock producers (Williams et al., 1991). It has excellent forage quality, usually comparable with that of alfalfa (*Medicago sativa* L.) (Romero et al., 1987).

There have been relatively few experiments that considered the effects of climate change on warm-season legume nutritive value. Such data are needed because of the importance of grassland agriculture in the lower Southern USA and in warm climates throughout the world. The objectives of this experiment were (i) to quantify the effects of increasing CO_2 and temperature on the nutritive value of RP leaf and stem measured through IVDOM, NDF, ADF, and lignin, and (ii) to determine the relationship between the composition of the fiber fraction of the stem and stem IVDOM.

MATERIALS AND METHODS

Site and Greenhouse Description

The study was conducted during 1996 and 1997 in four temperature-gradient greenhouses (TGGs) constructed over undisturbed field soil at the Irrigation Research and Education Park, University of Florida, Gainesville (29°38′ N and 82°22′ W). Stands of RP were planted on 10 Apr. 1995 (Fritschi et al., 1999) and arranged lengthwise in one half of each TGG. A TGG is a semicircular arch structure made of galvanized steel, and covered with SIXLIGHT (Taiyo Kogyo Co., Tokyo, Japan), which is a transparent polyethylene telephtalate film with 90% light transmission. The TGGs were 27.4-m long, 4.3-m wide, and 2.2-m high at the center, and were parallel to each other in a north–south orientation with separation between TGGs of 4.8 m. The first 3.6 m at the air intake end and the last 1.8 m at the outlet ventilation fan end of the greenhouse were not used. Four 5- by 2-m plots were laid out in the remainder of the space in each greenhouse as shown in Fig. 1. A more detailed description is given by Sinclair et al. (1995) and Fritschi et al. (1999).

The irrigation system had 32 microjet spray heads; 16 of them were along each side of the TGG and they were spaced 1.8 m from each other. Irrigation was applied three times per week using a double-overlapping microjet sprinkler pattern. This method of application provided 7 to 8 mm d^{-1} on average during the 8- to 9-mo growing season. During winter, the rate was reduced approximately in half. The total annual irrigation averaged for the 2-yr period and expressed as a rainfall equiva-

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Abbreviations: ADF, acid detergent fiber; B, baseline temperature; DM, dry matter; IVDOM, in vitro digestible organic matter; NDF, neutral detergent fiber; OM, organic matter; PAR, photosynthetically active radiation; RP, rhizoma peanut; TGG, temperature-gradient greenhouse.

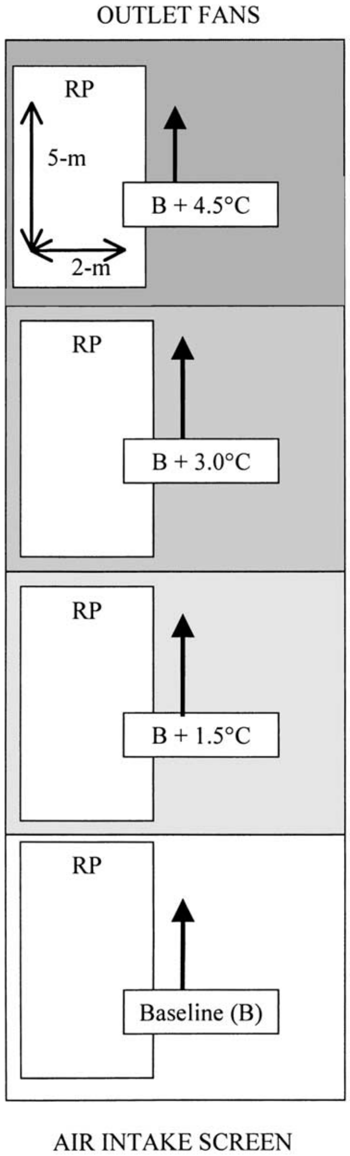

Fig. 1. Example of treatment layout in a temperature-gradient greenhouse (not to scale). Unidirectional arrows indicate the direction of air flow. One greenhouse represents one replicate of one CO_2 treatment. Adapted from Newman et al. (2001). RP = rhizoma peanut.

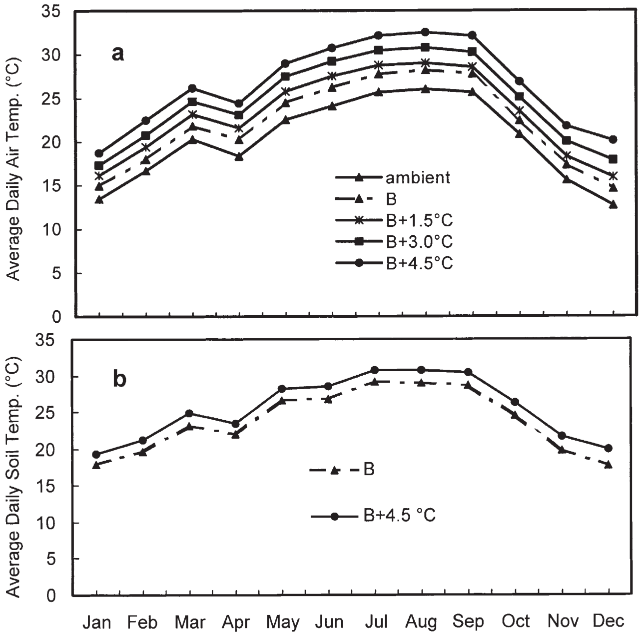

Fig. 2. (a) Monthly averages of average daily air temperature in Greenhouse 1 for baseline (B) through B + 4.5°C temperature treatments during 1997. (b) Monthly averages of average daily soil temperature in Greenhouse 1 for B through B + 4.5°C temperature treatments during 1997.

lent, was 2020 mm yr^{-1}. The average annual rainfall (years 1961–1990) is 1342 mm.

The soil was a Millhopper fine sand with a pH of 6.2 to 6.7. Soil organic matter (OM) ranged from 12 to 15 g kg^{-1}, and Mehlich-I extractable Ca concentration ranged from 240 to 340 mg kg^{-1}, Mg from 98 to 115 mg kg^{-1}, P from 79 to 97 mg kg^{-1}, and K from 6 to 11 mg kg^{-1}. On the basis of soil analyses and assuming a hay production management scheme, all plots were fertilized in 1996 with 70 kg ha^{-1} N, 30 of P, and 58 of K; and during 1997, with 80 kg ha^{-1} N, 36 of P, 173 of K, 65 of Mg, and 128 of S. Nitrogen was applied to the legume to avoid variation in fertilizer inputs in concurrent companion studies that were comparing RP and bahiagrass (*Paspalum notatum* Flügge). In 1996 there were three harvests. Before Harvest 1, 10 kg ha^{-1} N, 4 kg ha^{-1} P, and 8 kg ha^{-1} K were applied. Subsequently, fertilizer was split applied in six equal doses (5 kg N ha^{-1}) during each of the growth periods preceding Harvests 2 and 3 (total of 12 applications, approximately every 1.5 wk.). In 1997 there were four harvests, and fertilizer was applied in four equal split doses (5 kg N ha^{-1}) in each of the four growth periods preceding Harvests 1 through 4 (total of 16 applications). The N source was ammonium nitrate, the P source was triple super phosphate, the K source was KCl, and the S source was magnesium sulfate.

Weeds were controlled manually. During winter, the major weed was narrow-leaf cudweed (*Gnaphalium falcatum* Lam) of the Compositae family, and during summer it was longstalk phyllanthus (*Phyllanthus tenellus* Roxb.) of the Euphorbiaceae family, a C_4 broadleaf plant. The major pests of RP were spider mites (*Tetranychus urticae* Koch), black aphids (*Aphis* spp.), and thrips, very likely the species *Frankliniella fusca* (Hinds). Control was exerted as required with labeled sprays.

Treatments and Data Analyses

The complete factorial arrangement of two levels of CO_2 concentration (360 and 700 μmol mol^{-1}) and four temperatures [B (1.5°C above outside ambient), and 1.5, 3.0, and 4.5°C above B] constituted the treatments. The experimental design was a split-strip plot where CO_2 was the whole-plot factor and was allocated to greenhouses at random, with two greenhouses per level of CO_2 (two replicates). Temperature was the subplot treatment, and plot size was 5 × 2 m (Fig. 1).

Temperature and Carbon Dioxide Control

Temperature treatments were imposed in the four TGGs such that each strip corresponded to a temperature zone. Temperature treatments were maintained throughout the year (Fig. 2A). Year 1996 was cooler than 1997; there were only 3 d with maximum temperatures above 40°C in 1996, while in 1997 there were 22 d. In addition to the air temperature, soil temperature was also monitored with thermocouples placed at 0.09 m beneath soil surface. Soil temperature response is illustrated for one TGG during the 1997 season (Fig. 2B).

In each TGG, the 4.5°C temperature gradient was created through the control of the unidirectional ventilation rate from inlet to outlet end of the TGG (Horton, 1999). Each temperature zone (5-m strip of land) was obtained through incident solar radiation plus the additional heated air (120°C) infused into each strip when natural solar radiation was insufficient to obtain the desired temperature. The injection of heated air at increments of 5.5 m along the length of the TGGs and the use of overhead paddle fans at each strip made it possible to achieve a step gradient of 1.5°C increments. A greater than 4.5°C gradient between the inlet and outlet points triggered an increase in speed of the exhaust fan located at the outlet end of each TGG. Likewise, when the temperature difference was below 4.5°C, the exhaust fan speed was diminished and/or heaters were triggered. The operation of the exhaust fan was governed by a controller/data acquisition system based on thermocouples that monitored air temperature at 0.9 m above soil level over the strips corresponding to B and B + 4.5°C in each TGG. The hardware of the supervisory controller and data acquisition (SCADA) system was obtained from Keithley Metrabyte (Keithley Instruments, Inc., Cleveland, OH), and the FIX DMACS proprietary software was obtained from Intellution, Inc. (Foxborough, MA).

Carbon dioxide was provided from a supply tank outside the TGG and injected into a predilution distribution system placed approximately 1.2 m inside the inlet end of the TGG. The CO_2 concentration was measured every 20 s from air samples drawn through a manifold at 0.6 m above soil surface and about 6 m downflow from the injection distribution system. The amount of CO_2 released to maintain 700 μmol mol^{-1} was controlled with a variable gas valve, depending on the speed of the exhaust fan using a proportional and integral adjustment algorithm based on deviation from the CO_2 control setpoint. The standard deviation of CO_2 concentration from setpoint ranged from 31 to 53 μmol mol^{-1} (Liu, 1999). Photosynthetically active radiation (PAR) was measured with a calibrated quantum sensor (LI-COR, Lincoln, NE) located at the north end outside of the TGGs. Data collection and processing for temperature, CO_2, and PAR are described in Newman et al. (2001).

Sample Collection and Laboratory Analyses

Plots were harvested three times in 1996 and four times in 1997 (at ≈8 and 6 wk of regrowth, respectively). The three-cut system in 1996 followed a schedule similar to that recommended for RP hay production in North Florida (Prine et al., 1981). Rapid growth in the TGGs led to lodging of forage before harvests in 1996; therefore, in 1997 there were four harvests. Harvest dates were 14 June, 13 Aug., and 18 Nov. 1996; and 9 May, 3 July, 21 Aug., and 21 Nov. 1997.

Fresh forage samples of RP were clipped to a 3-cm stubble and immediately separated into leaf and stem fractions. Leaf and stem samples were oven dried for 48 h at 55°C and analyzed for dry matter (DM), OM, IVDOM, NDF, ADF, and lignin concentrations. A 1-g aliquot was used for determining absolute DM (drying at 105°C for 15 h; AOAC, 1990). Total OM was determined by ashing for 15 h at 550°C (AOAC, 1990). The two-stage technique of Moore and Mott (1974) was used to determine IVDOM. Neutral detergent fiber was analyzed using the method described by Golding et al. (1985), and is reported on an ash-free basis. Acid detergent fiber was determined as described by Van Soest (1963), and lignin was analyzed using the permanganate method of Van Soest and Wine (1967).

Statistical Analyses

Data were analyzed using mixed model methodology (Littell et al., 1996). In all models, effects of CO_2 concentration, temperature, and their interactions were considered fixed effects. Greenhouses nested within CO_2 levels were modeled as random effects. Data were analyzed using PROC MIXED (SAS Institute, 1996). The nature of temperature effects was assessed using orthogonal polynomial contrasts. All means reported in the text are least square means. Values of $P \leq 0.10$ were considered significant. Ratios of stem fiber components (NDF, ADF, and lignin) were calculated for each temperature treatment in 1997, and regression analysis with PROC REG (SAS Institute, 1996) was used to determine the relationship between the ratios and stem IVDOM. Each point in the regression equations is a temperature treatment mean across 16 observations (average of four harvests, two CO_2 levels, and two replicates).

RESULTS AND DISCUSSION

Leaf Nutritive Value

There were no CO_2 or temperature effects on leaf IVDOM, NDF, or lignin in 1996 (Table 1), and there were no effects on leaf IVDOM, NDF, ADF, or lignin in 1997 (Table 2). Only in 1996 there was a linear temperature effect on ADF ($P = 0.021$), and leaf ADF increased from 248 g kg^{-1} at B to 256 g kg^{-1} at B + 4.5°C (Table 1). This slight change in leaf ADF had no impact on leaf IVDOM. This, plus the lack of any effect of temperature on ADF in 1997, suggests that the response observed in 1996 was of limited biological significance. Likewise, Marks and Lincoln (1996) reported no effect of elevated CO_2 on the nutritive value of tall fescue (*Festuca arundinacea* Schreb.) leaves. Averaged across years in the current study, leaf IVDOM, NDF, ADF, and lignin were 721, 370, 240, and 38 g kg^{-1}, respectively. Leaf IVDOM means were similar to those reported previously for RP (Ocumpaugh, 1990; Saldivar et al., 1990; Terrill et al., 1996). Neutral detergent fiber and ADF means were slightly lower than those reported by Romero et al. (1987) and Johnson et al. (2002), and are indicative of the high nutritive value of RP leaf herbage.

Table 1. Temperature and CO_2 effects on rhizoma peanut leaf in vitro digestible organic matter (IVDOM), neutral detergent fiber (NDF), acid detergent fiber (ADF), and lignin concentrations during 1996. Data are averages across three harvests.

	IVDOM	NDF	ADF	Lignin
	g kg^{-1}			
Temperature, °C				
B†	**716**	**401**	**248**	**38**
B + 1.5	**714**	**380**	**253**	**38**
B + 3.0	**714**	**388**	**256**	**38**
B + 4.5	**710**	**400**	**256**	**39**
SE	**2**	**10**	**3**	**0.7**
Contrast‡	**ns**	**ns**	**L, 0.021**	**ns**
CO_2, μmol mol^{-1}				
360	**710**	**387**	**253**	**38**
700	**717**	**392**	**253**	**39**
SE	**2**	**7**	**4**	**0.6**
***P* value**	**0.144**	**0.689**	**0.960**	**0.166**

† Baseline temperature defined as ambient temperature in the greenhouse.

‡ Orthogonal polynomial contrast for temperature effect. L = linear, ns = not significant; number following letter is *P* value for linear effect.

Table 2. Temperature and CO_2 effects on rhizoma peanut leaf in vitro digestible organic matter (IVDOM), neutral detergent fiber (NDF), acid detergent fiber (ADF), and lignin concentrations during 1997. Data are averages across four harvests.

	IVDOM	NDF	ADF	Lignin
	g kg^{-1}			
Temperature, °C				
B†	**722**	**372**	**232**	**37**
B + 1.5	**733**	**376**	**230**	**38**
B + 3.0	**728**	**380**	**238**	**38**
B + 4.5	**728**	**393**	**235**	**38**
SE	**9**	**10**	**5**	**0.7**
Contrast‡	**ns**	**ns**	**ns**	**ns**
CO_2, µmol mol^{-1}				
360	**727**	**380**	**234**	**38**
700	**728**	**381**	**233**	**38**
SE	**2**	**7**	**5**	**0.6**
***P* value**	**0.932**	**0.957**	**0.961**	**0.927**

† Baseline temperature defined as ambient temperature in the greenhouse.
‡ Orthogonal polynomial contrast for temperature effect. ns = not significant.

Table 4. Temperature and CO_2 effects on rhizoma peanut stem in vitro digestible organic matter (IVDOM), neutral detergent fiber (NDF), acid detergent fiber (ADF), and lignin concentrations during 1997. Data are averages across four harvests.

	IVDOM	NDF	ADF	Lignin
	g kg^{-1}			
Temperature, °C				
B†	**577**	**519**	**388**	**80**
B + 1.5	**540**	**515**	**386**	**80**
B + 3.0	**522**	**526**	**393**	**93**
B + 4.5	**511**	**528**	**397**	**93**
SE	**10**	**6**	**5**	**1.8**
Contrast‡	**L, 0.01**	**L, 0.03**	**L, 0.158**	**L, 0.05**
CO_2, µmol mol^{-1}				
360	**518**	**521**	**391**	**82**
700	**558**	**524**	**391**	**81**
SE	**11**	**8**	**8**	**1**
***P* value**	**0.123**	**0.809**	**0.982**	**0.625**

† Baseline temperature defined as ambient temperature in the greenhouse.
‡ Orthogonal polynomial contrast for temperature effect. L = linear, and number following letter is *P* value for linear effect.

Stem Nutritive Value

There was no CO_2 effect on stem nutritive value ($P >$ 0.13), but there was a temperature × year interaction ($P = 0.062$). The effect of temperature on stem nutritive value was more pronounced in 1997, when plots were harvested every 6 wk, than in 1996, when they were cut every 8 wk. Stem NDF and ADF were lower in 1997 than in 1996, and this can be attributed in part to the shorter interval between harvests in 1997. Stem IVDOM tended to be greater in 1997 than 1996 at B, as expected, but at B + 3.0 and B + 4.5°C, stem IVDOM was greater in 1996. The reason for the latter response is not totally clear, but temperatures were greater in 1997 than in 1996 (22 vs. 3 d with B maximum temperature ≥ 40°C). This may have accentuated the negative IVDOM response to the elevated temperature treatments in 1997. This argument is supported by the greater stem lignin concentration in 1997 than in 1996 for B + 3.0 and B + 4.5°C treatments.

During 1996, temperature affected all measures of stem nutritive value (Table 3) except for lignin (average of 90 g kg^{-1} across treatments). Averaged across three harvests, stem IVDOM decreased from 562 to 552 g kg^{-1} as temperature increased from B to B + 4.5°C. Stem NDF increased with increasing temperature (linear and quadratic; $P = 0.07$ and $P = 0.03$, respectively), but the greatest proportion of this increase occurred between B (556 g kg^{-1}) and B + 1.5°C (562 g kg^{-1}). Stem ADF increased linearly from 412 g kg^{-1} at B to 418 g kg^{-1} at B + 4.5°C.

Table 3. Temperature and CO_2 effects on rhizoma peanut stem in vitro digestible organic matter (IVDOM), neutral detergent fiber (NDF), acid detergent fiber (ADF), and lignin concentrations during 1996. Data are averages across three harvests.

	IVDOM	NDF	ADF	Lignin
	g kg^{-1}			
Temperature, °C				
B†	**562**	**556**	**412**	**90**
B + 1.5	**555**	**562**	**417**	**89**
B + 3.0	**554**	**565**	**422**	**90**
B + 4.5	**552**	**561**	**418**	**90**
SE	**10**	**5**	**5**	**0.7**
Contrast‡	**L, 0.05**	**L, 0.07** **Q, 0.03**	**L, 0.01**	**ns**
CO_2, µmol mol^{-1}				
360	**552**	**561**	**418**	**90**
700	**559**	**561**	**416**	**88**
SE	**9**	**4**	**3**	**1**
***P* value**	**0.203**	**0.934**	**0.656**	**0.293**

† Baseline temperature defined as ambient temperature in the greenhouse.
‡ Orthogonal polynomial contrast for temperature effect. L = linear, Q = quadratic, ns = not significant; number following letter is *P* value for linear or quadratic effect.

During 1997, stem IVDOM decreased linearly with increasing temperature (Table 4), but the rate of decrease was much greater than in 1996. Difference in IVDOM between B and B + 4.5°C was 66 g kg^{-1} in 1997 compared with 10 g kg^{-1} in 1996. The linear decrease in IVDOM was associated with a linear increase in NDF and lignin and a trend toward increasing ADF (P = 0.158). Stem NDF, ADF, and lignin ranged, respectively, from 519, 388, and 80 g kg^{-1} at B to 528, 397, and 93 g kg^{-1} at B + 4.5°C.

Most measures of RP stem nutritive value showed a negative effect of increasing temperature in both years, consistent with accelerated maturation at higher temperature. Deinum and Dirven (1972, 1975) associated increases in temperature from 24 to between 28 and 33°C with greater stem weight and increased crude fiber of both C_3 and C_4 forage grasses. Although the negative effect of increasing temperature is not consistent across all species and conditions, Wilson et al. (1991) demonstrated this response for C_3 grasses, and Henderson and Robinson (1982) for C_4 grasses. Data for forage legumes are limited. Wilson and Minson (1984) reported lower digestibility of the tropical legume Siratro [*Macroptilium atropurpureum* (DC.) Urb.] with increasing growth temperature. This decrease was associated with an increase in cell wall and lignin concentration, mainly in the stem fraction. It has been suggested that temperature effects on nutritive value of tropical legumes are often not as great as those on grasses where lignin accumulation in the cell wall was observed throughout the plant (Wilson et al., 1991).

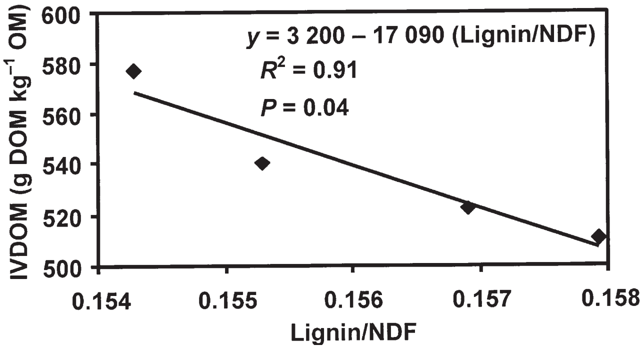

Fig. 3. Relationship between in vitro digestible organic matter (IVDOM) and ratio of lignin to neutral detergent fiber (NDF) concentration (Lignin/NDF) for rhizoma peanut stem in 1997. Each point is a temperature treatment mean and is the average of 16 observations (four harvests, two CO_2 levels, and two replicates).

Relationship of Fiber Components and Stem IVDOM

Data from 1997 showed a much greater range in stem IVDOM than in 1996, so 1997 data were used to assess the relationship between IVDOM and fiber components and IVDOM and ratios of fiber components. Although tending to be positively correlated with IVDOM, individual fiber components did not explain a significant amount of the variation in IVDOM ($P > 0.158$). The proportion of ADF in stem NDF varied only from 0.748 to 0.751 across temperatures, and stem ADF/NDF ratio did not explain a significant amount ($P > 0.630$) of the variation in stem IVDOM. In contrast, stem lignin/NDF ratio ($R^2 = 0.914$) and lignin/ADF ratio ($R^2 = 0.853$) explained a high proportion of the variation in IVDOM (Fig. 3 and 4).

These results show that lignin, when expressed as a proportion of NDF or ADF, is an important indicator of RP stem IVDOM, and these ratios are better predictors than individual fiber components. Moore and Coleman (2001) suggested that expressing lignin as a proportion of individual fiber components may be a useful tool in predicting forage digestibility. When lignin is expressed as a ratio with either NDF or ADF, we are not only associating a measure of fiber concentration, but also accounting for the negative effect of lignin concentration on fiber digestibility.

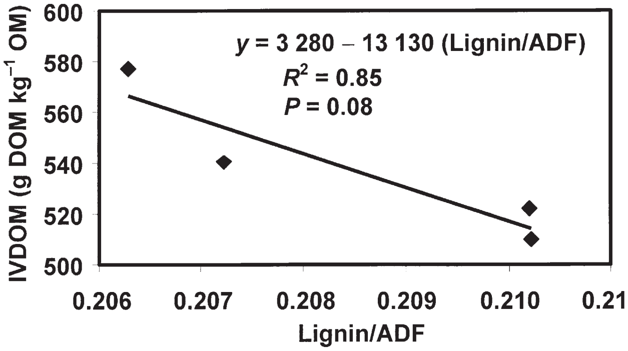

Fig. 4. Relationship between in vitro digestible organic matter (IVDOM) and ratio of lignin to acid detergent fiber (ADF) concentration (Lignin/ADF) for rhizoma peanut stem in 1997. Each point is a temperature treatment mean and is the average of 16 observations (four harvests, two CO_2 levels, and two replicates).

CONCLUSIONS

Data from this study showed no effect of increasing atmospheric CO_2 concentration (in the absence of water stress) on nutritive value of RP leaf or stem. Leaf nutritive value was also unaffected by air temperature, but increasing temperature caused stem IVDOM to decrease in both years, and concentration of fiber components to increase or tend to increase. Individual stem fiber components were relatively weak predictors of stem IVDOM, but ratios of lignin/NDF and lignin/ADF explained a significant and large proportion of the variation in stem IVDOM. We conclude that, in the absence of water stress, the primary climate change factor that will affect nutritive value of RP is increasing air temperature. On the basis of these results, and especially those from the second year of study, the decrease in RP nutritive value when grown at elevated temperatures may be sufficient to lower animal production.

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