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RELATIONSHIP OF SEED WEIGHT TO PHYSIOLOGICAL AND BIOCHEMICAL RESPONSES IN BLUE PANICGRASS, *PANICUM ANTIDOTALE* RETZ.

by

Rollin Howard Abernethy

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I hereby recommend that this dissertation prepared under my direction by Rollin Howard Abernethy

entitled RELATIONSHIP OF SEED WEIGHT TO PHYSIOLOGICAL AND BIOCHEMICAL RESPONSES IN BLUE PANICGRASS, PANICUM ANTIDOTALE RETZ.

be accepted as fulfilling the dissertation requirement of the degree of Doctor of Philosophy

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TABLE OF CONTENTS

	Page
LIST OF TABLES	v
LIST OF ILLUSTRATIONS	viii
ABSTRACT	x
INTRODUCTION	1
LITERATURE REVIEW	3
Origin and Description	3
Seedling Vigor	3
Seed Size and Seedling Vigor	4
Seedling Metabolism and Seedling Vigor	9
Seed Weight Determination	18
MATERIALS AND METHODS	21
Plant Material	21
Growth Evaluation	21
Seed and Seedling Metabolism	23
Seedling Respiration	23
Adenylate and Energy Charge Studies	25
Free Sugars	29
Mitochondrial Protein	29
Inflorescence Gas Exchange Study	30
Statistical Procedures	33
RESULTS AND DISCUSSION	34
Growth Chamber Dry Matter Production	34
Seed and Seedling Metabolism	37
Inflorescence Photosynthesis and Respiration	69
Summary and Conclusions	76
REFERENCES	80

LIST OF TABLES

Table		Page
1.	Selections of blue panicgrass for heavy and light seed weight from six cycles of recurrent selection with seed weight selection pressure and successive restricted recombination	22
2.	Comparison of five procedures for ATP extraction from blue panicgrass seedlings following 24 hr of imbibition	26
3.	Dry-matter production at 7 time periods during the first 54 days growth under growth chamber environment of five heavy and five light seed-weight selections of blue panicgrass	35
4.	Germination percentage of four selections of blue panicgrass measured at 4 time periods during the initial 72 hr of germination	38
5.	Seed and seedling dry weight per 100 seed of two heavy and two light seed-weight selections of blue panicgrass measured at 8 time periods during the initial 72 hr of germination	40
6.	Seed or seedling fresh weight per 100 seed of two heavy and two light seed-weight selections of blue panicgrass measured at 8 time periods during the initial 72 hr of germination	41
7.	Respiratory rates per 100 seed of two heavy and two light seed-weight selections of blue panicgrass measured at 7 time periods during the initial 72 hr of germination	44
8.	Respiratory rates per gram of initial seed weight of two heavy and two light seed-weight selections of blue panicgrass measured at 8 time periods during the initial 72 hr of germination	45
9.	Content of free sugar per 100 seed of two heavy and two light seed-weight selections of blue panicgrass measured at 8 time periods during the initial 72 hr of germination	47

LIST OF TABLES--Continued

Table		Page
10.	Content of free sugar per gram of initial seed weight of two heavy and two light seed-weight selections of blue panicgrass measured at 8 time periods during the initial 72 hr of germination	49
11.	Content of mitochondrial protein per 100 seed of two heavy and two light seed-weight selections of blue panicgrass measured at 7 time periods during the initial 72 hr of germination	51
12.	Content of mitochondrial protein per gram of initial seed weight of two heavy and two light seed-weight selections of blue panicgrass measured at 7 time periods during the initial 72 hr of germination	53
13.	Content of adenosine triphosphate (ATP) per 100 seed of two heavy and two light seed-weight selections of blue panicgrass measured at 8 time periods during the initial 72 hr of germination	54
14.	Content of adenosine diphosphate (ADP) per 100 seed of two heavy and two light seed-weight selections of blue panicgrass measured at 8 time periods during the initial 72 hr of germination	55
15.	Content of adenosine monophosphate (AMP) per 100 seed of two heavy and two light seed-weight selections of blue panicgrass measured at 8 time periods during the initial 72 hr of germination	56
16.	Content of total adenylate phosphates (TAP) per 100 seed of two heavy and two light seed-weight selections of blue panicgrass measured at 8 time periods during the initial 72 hr of germination	57

LIST OF TABLES--Continued

Table		Page
17.	Content of adenosine triphosphate (ATP) per gram of initial seed weight of two heavy and two light seed-weight selections of blue panicgrass measured at 8 time periods during the initial 72 hr of germination	58
18.	Content of adenosine diphosphate (ADP) per gram of initial seed weight of two heavy and two light seed-weight selections of blue panicgrass measured at 8 time periods during the initial 72 hr of germination	59
19.	Content of adenosine monophosphate (AMP) per gram of initial seed weight of two heavy and two light seed-weight selections of blue panicgrass measured at 8 time periods during the initial 72 hr of germination	60
20.	Energy charge values of two heavy and two light seed-weight selections of blue panicgrass measured at 8 time periods during the initial 72 hr of germination	65
21.	Correlation coefficients between several variables per 100 seed of four seed-weight selections of blue panicgrass measured at 7 time periods during the initial 72 hr of germination	68
22.	Photosynthetic rates of inflorescences of five heavy and five light seed-weight selections of blue panicgrass measured at four growth stages	71
23.	Respiration rates of inflorescences of five heavy and five light seed-weight selections of blue panicgrass measured at four growth stages	73
24.	Ratio of photosynthetic to respiration rate (P:R) of five heavy and five light seed-weight selections of blue panicgrass measured at four growth stages	74

LIST OF ILLUSTRATIONS

Figure		Page
1.	Diagram of the closed system used for seed respiration measurements	24
2.	Recorder trace showing changes in CO_2 concentration in the closed system used for measurement of blue panicgrass inflorescence gas exchange	32
3.	Mean relative growth rates ($\overline{RGR}$) of 10 seed-weight selections of blue panicgrass calculated over a 48-day growth period. Bars with the same letter are not significantly different at the .05 level according to Student-Newman-Keul's multiple range test	36
4.	Trends in fresh weight, respiration rate, and free sugar content of four seed-weight selections of blue panicgrass during the initial 72 hr of germination	42
5.	Content of ATP, ADP, AMP, and total adenylate phosphates (TAP) per 100 seed of four seed-weight selections of blue panicgrass measured during the initial 72 hr of germination	61
6.	Energy charge values of unimbibed seed of five heavy and five light seed-weight selections of blue panicgrass. Bars with same letter are not significantly different at the .05 level according to Student-Newman-Keul's multiple range test	67
7.	Photosynthetic rates of inflorescences of five heavy and five light seed-weight selections of blue panicgrass measured at four growth stages. Vertical line at each mean represents one standard error of the mean	70

LIST OF ILLUSTRATIONS--Continued

Figure Page

8. Respiration rates of inflorescences of five heavy and five light seed-weight selections of blue panicgrass measured at four growth stages. Vertical line at each mean represents one standard error of the mean 72

9. Ratio of photosynthetic to respiration rate (P:R) of five heavy and five light seed-weight selections of blue panicgrass averaged over four growth stages. Bars with the same letter are not significantly different at the .05 level according to Student-Newman-Keul's multiple range test 75

ABSTRACT

Seed from selections of blue panicgrass (Panicum antidotale Retz.) for heavy and light seed-weight from six cycles of recurrent selection with seed-weight selection pressure and successive restricted recombination were used to evaluate the relationship between seed weight, seedling vigor, and several aspects of seedling energy metabolism. Maternal clones were used to evaluate factors that influence seed weight during seed development.

Heavy seed-weight selections demonstrated significantly greater dry-matter production up to 54 days after planting when grown under a controlled environment. Mean relative growth rate was significantly higher for some light seed-weight selections.

Comparison of two heavy and two light seed-weight selections demonstrated significantly greater fresh weight, free sugar content, ATP, ADP, and total adenosine phosphate levels per 100 seed throughout the initial 72 hr of germination.

Mitochondrial protein content per 100 seed was significantly higher for heavy seed-weight selections from 36 to 72 hr of germination. When these data were expressed on the basis of seed weight, comparisons among selections were not significantly different. Greater values obtained for heavy seed were attributed to physical seed size.

Energy charge values were not significantly different for the four selections except at 6 hr of imbibition. Comparison of energy

charge values for unimbibed seed of five heavy and five light seed-weight selections revealed a 26% greater energy charge for heavy seed-weight selections. These metabolic functions, in addition to energy charge of unimbibed seed, warrant further consideration as selection criteria for seedling vigor.

Lower apparent photosynthesis and higher dark respiration of inflorescences were found for light seed-weight selections. This finding suggested that part of the difference in seed weight between the selections was due to a decreased amount of assimilate available for storage in developing seed of light seed-weight selections.

INTRODUCTION

Blue panicgrass, Panicum antidotale Retz., has the unique potential for high forage yields under irrigated conditions and tolerance of drouth and associated environmental stresses under aridland conditions in the southwestern United States (Wright, 1966). Plant establishment under aridland conditions is one factor which currently reduces the use of blue panicgrass as a forage grass under aridland environments. Flood plains and other areas of moisture concentration increase the probability of successful establishment of stands.

Selection for heavier seed-weight is one method of improving seedling vigor. Seedlings with greater vigor have a better chance of survival under stress conditions, and may develop plants with higher forage-yielding potential under irrigated conditions.

Physiological selection tools will greatly assist in a grass improvement program to shorten the selection process and strengthen the probability of isolating plants with improved characteristics. Considering the potential influence of heavier seed-weight of other species, recurrent selection was used within blue panicgrass populations for six cycles by Dr. L. Neal Wright, Agricultural Research Service and Department of Agronomy and Plant Genetics, University of Arizona, to isolate germplasm for improvement of seedling vigor and forage yield capabilities.

Objectives of this study were to examine factors that influence seed weight during seed development, and to examine several physiological aspects of seedling metabolism and their relation to subsequent seedling and plant growth in the seed-weight selections. A prime objective was evaluation of seed and seedling energy-levels and energy conservation processes as selection criteria for seedling vigor.

LITERATURE REVIEW

Origin and Description

Blue panicgrass is a forage grass native to southern Asia which was first introduced to the United States in 1912 from collections in India. It is a vigorous bunch grass with an extensive root system. It grows 1 to 2.5 m in height with heavy basal growth, many panicle bearing branches, and vigorous tillering from short, thick, bud-like rhizomes. Seed-head initiation and development are indeterminate and maturity occurs over an extended period. Blue panicgrass is best adapted to semiarid and arid areas of the southwestern United States (Wright, 1966).

Koller and Negbi (1957) considered seedling growth poor under arid conditions the year of establishment, but good forage yields were obtained in subsequent years. Establishment under arid conditions in Arizona has also met with difficulty. Wright (1971) concluded that success in germination and seedling emergence is the major requirement of plants used for revegetation in semiarid and arid regions. Improved seedling vigor would aid in blue panicgrass stand establishment, and consequently extend its area of adaptation and use as a forage grass.

Seedling Vigor

Early definitions of seedling vigor tended to restrict vigor to responses under adverse conditions. From this view two concepts

of vigor have evolved: (a) susceptibility to unfavorable field conditions, and (b) vigor per se as reflected in germination and growth rate of seedlings (Delouche and Caldwell, 1960). Kneebone (1972) defined seedling vigor as a realized capacity for rapid growth in the seedling stage. Both plant genetic potential and environmental attributes are related to seedling establishment.

Two interpretations of seedling vigor are found in the literature. Seed analysts are concerned with reduction in seed vigor due to adverse conditions during harvesting, storage, or treatment; while the agronomic approach is an attempt to understand and improve species or strains with inherently poor seedling vigor (Whalley and McKell, 1973). Several reviews on techniques for assessing seedling vigor in grasses have been presented (Delouche and Caldwell, 1960; Kalton, Delong, and McLeod, 1959; Kneebone, 1972; Whalley and McKell, 1973; and Wright, 1971).

Seed Size and Seedling Vigor

Advantages of large seed for germination and establishment are well documented. Heavy seed may have higher germination percentage (Green and Hansen, 1969; Knipe, 1970). Seedlings from heavy seed emerge faster (Kneebone and Cremer, 1955; Rogler, 1954; Tossel, 1960; Whalley, McKell, and Green, 1966a), emerge from greater planting depth (Arnott, 1969; Lawrence, 1963; Rogler, 1954), and have greater percentage emergence (Knipe, 1970; Kittock and Patterson, 1962; Rogler, 1954; Tossel, 1960; Townsend, 1972) than small seed. These vigor attributes for large seed generally apply only within species (Kneebone and Cremer, 1955; Whalley et al., 1966a).

Bremner, Eckersall, and Scott (1963) varied the relative amounts of embryo and endosperm in wheat (Triticum aestivum L.) by removal of a portion of the endosperm. Seed with small embryos had higher relative growth rates than seed with larger embryos regardless of the amount of seed reserves present during the first six days of germination and initial growth. Growth that followed was dependent on the amount of reserves present. Relationship between seed size and subsequent plant size was governed by the amount of reserves present in the seed. Major and Wright (1970) found that during the first six days of growth, increase of seedling weight was reciprocally related to seed weight decrease in heavy and light seed-weight selections of blue panicgrass.

Increased growth of large seed during the heterotrophic stage, when the seedling is dependent on seed reserves, may or may not persist when the seedling becomes autotrophic. Arnott (1969) reported the relative growth rates of seedlings from perennial ryegrass (Lolium perenne L.) seed of two weight ranges were similar. His findings indicated seed weight conferred no advantage to autotrophic growth other than the initial advantage during the heterotrophic stage.

Black (1956, 1957a, 1957b) conducted an extensive study with subterranean clover (Trifolium subterraneum L.) on seed size classes and vegetative growth. Seedling dry weight in the early vegetative stage was proportional to the initial seed size, but the growth rate of plants grown from different initial seed size was identical. The initial seedling dry weight advantage was related to a greater cotyledonary area from large seed, which resulted in greater initial leaf

area and subsequent dry weight. Thomas (1966) reported the correlation between seed weight and vigor measurements in perennial ryegrass decreased as the plants matured.

Association of greater vigor with heavy seed-weight throughout the vegetative stage of the plant has been reported by several workers. Rogler (1954) reported that leaf development of crested wheatgrass (Agropyron desertorum (Fisch.) Schult.) was more rapid for heavy seedlots from planting depths greater than 35 mm. Twamley (1969) reported improved tillering of plants from large seed in birdsfoot trefoil (Lotus corniculatus L.). Seedlings from larger seed may also be more competitive. Rhodes (1968) found that differences in dry matter production between seedlings grown from large seed versus small seed were increased when plants from varying seed sizes were grown together in comparison to plants from large and small seed grown separately for L. multiflorum Lam. and Phalaris coerulescens Desf. Arnott (1969) suggested that the initial advantage of perennial ryegrass seedlings grown from large seed may be maintained so that with interplant competition the plants were more competitive.

Decline in number of subterranean clover plants over the growth period in mixtures of large and small seed was attributed to death of plants from small seed. Number of plants from large seed remained virtually unchanged according to Black (1958). He attributed death of plants produced from small seed to shading. Plants from small seed accounted for 25% of the leaf area at the first sampling but were located to receive only 10% of the incident light. Plants from small

seed accounted for 10% of the leaf area and received 2% of the incident radiation at the last sampling.

Cooper and McDonald (1970) demonstrated the importance of endosperm reserves in the development of adequate leaf area for photosynthetic capacity in corn (Zea mays L.). Partial endosperm removal decreased the rate of photosynthetic-area expansion. Association of seed weight with leaf-length, -width, -area, rate of leaf appearance, and tiller number was significantly positive during initial growth stages of perennial ryegrass (Thomas, 1966). Burris, Edjie, and Wahab (1973) reported additional cotyledonary and unifoliate leaf-area from large soybean seed resulted in greater total-photosynthesis. However, photosynthetic rate per unit of leaf area was higher in seedlings from small seed.

Maximum radicle elongation may also be dependent on seed reserves. Radicle elongation of six range grasses, wheat, and barley (Hordeum vulgare L.) was limited and growth ceased when seedlings were grown in darkness. Radicle elongation continued with the onset of photosynthesis when seedlings were grown in light. This would suggest that seed reserves limit radicle elongation in the pre-emergence stage according to Tadmor and Cohen (1968). Cohen and Tadmor (1969) suggested, that for small-seeded species of Phalaris, development of cultivars with larger seed should increase the rate of root elongation.

Tadmor and Cohen (1968) also observed that shoot growth of seedlings grown in darkness continued after radicle elongation ceased. They suggested this response might indicate that the shoot is able to use seed reserves for a greater length of time than the radicle.

Utilization of seed reserves by the shoot could be a partial explanation for the significant association observed between seed size and emergence from greater planting depths by both monocotyledons (Kalton et al., 1959; Kittock and Patterson, 1962; Lawrence, 1963; Rogler, 1954; Vogel, 1963) and dicotyledons (Black, 1956; Burris et al., 1973; Townsend, 1972). Kneebone (1972) stated that emergence of grasses from deep planting was, however, interrelated with coleoptile length. Kittock and Law (1968) reported that vigor differences between wheat seedlings were largely associated with effects of coleoptile length on emergence, and Hunt and Miller (1965) found a positive association ($r=0.81$) between seed size and coleoptile length in intermediate wheatgrass (Agropyron intermedium (Host) Beauv.).

Increased seed size or weight may also exhibit a positive association with seed yield of the mature plant (Kneebone, 1972). When high seed-weight was transferred to 'Thatcher' spring wheat by backcrossing to 'Selkirk', the backcross lines with high seed-weight outyielded Thatcher on the average (Knott and Talukdar, 1971).

Some range grasses also exhibited an association between size or weight of seed planted and subsequent seed yield (Russian wildrye, Elymus junceus Fisch., Lawrence, 1963; smooth bromegrass, Bromus inermis Leyss., Christie and Kalton, 1960; blue panicgrass, Wright, 1969). However, in some species heavy seed was associated with poor seed-set. In those instances no relation between seed weight and subsequent seed yield would be expected.

Seedling Metabolism and Seedling Vigor

Evidence presented to this point of the review has indicated seedling vigor is closely related to seed size in many species, although the association is not complete. Characteristics in addition to seed size are also responsible for seedling vigor, which was demonstrated by varietal vigor differences when seed size was held constant (Qualls and Cooper, 1968). Differences in metabolism must be included among these factors, and may be involved in the vigor advantage possessed by larger seed.

Excellent reviews on seedling metabolism were presented by Ching (1972) and Mayer and Poljakoff-Mayber (1963). The initial stage of germination of seed is the imbibition phase, which can last from minutes to several hours. Rapid water uptake by seed biocolloids, which results in reactivation of macromolecules and organelles, initiates the energy forming catabolic processes. These catabolic processes are required to drive the numerous anabolic reactions during germination (Ching, 1972). Thus, the rate and efficiency of various catabolic and anabolic reactions may be involved in seedling vigor determination.

Evidence for the immediate activation of respiration upon imbibition was provided by the instantaneous oxygen uptake by seed reported by Abdul-Baki (1969a) and Mayer and Poljakoff-Mayber (1963). Components for protein synthesis are also apparently present in seed before imbibition. Marcus and Feely (1964, 1965) considered ribosomal activation and polysome formation the only requirements for initiation of protein synthesis. Respiration rate and protein synthesis rate

(measured by leucine-^{14}C uptake and incorporation) were similar during the first 12 hr of imbibition of barley seed (Abdul-Baki, 1969a). Synthesis of enzymatic and structural proteins is a prerequisite for growth after initial imbibition. Respiration would provide the required energy for their synthesis.

Macleod (1969) and Murata, Akazawa, and Fukuchi (1968) reported seed-food reserves of most Graminae were present in both the embryo and endosperm. In the embryo the reserves were in the form of sucrose, raffinose, triglycerides, and amino acids and immediately available for use as substrate by the growing seedlings. In the endosperm the reserves were stored for use after hydrolytic breakdown to available forms. Activation of glycolytic and citric acid cycle enzymes after imbibition by seed completed the pathway for immediate sugar catabolism and synthesis of energy in the form of adenosine triphosphate (ATP), (Brown and Wray, 1968; Ching, 1972). Activity of beta-amylase (alpha-1, 4-glucan maltohydrolase EC 3.2.1.2) was present in seed before imbibition of barley (Macleod, 1969); rice, Oryza sativa L. (Palmiano and Juliano, 1972); and crested wheatgrass (Wilson, 1971), and hydrolysis of endosperm starch was initiated upon imbibition to provide additional respiratory substrate. Gibberellic acid induced de novo synthesis of alpha-amylase (alpha-1, 4-glucan 4-glucanohydrolase EC 3.2.1.1) was reported by Paleg (1961), Varner (1964), and Varner and Ram Chandra (1964). Synthesis of alpha-amylase, the principal starch degrading enzyme during later stages of germination, began within 12 to 48 hr after imbibition. Timing was dependent on the species (Macleod, 1969; Murata et al., 1968; Nomura, Kono, and

Akazawa, 1969; Wilson, 1971). Activity of alpha-amylase increased rapidly up to five days in seed of crested wheatgrass (Wilson, 1971) while starch breakdown in rice paralleled alpha-amylase activity after four days. Prior to this time little starch hydrolysis was observed and soluble sugar levels were low (Murata et al., 1968; Nomura et al., 1969). A rapid increase in respiratory oxygen uptake occurred the third day. The respiratory oxygen increase was followed by increased ATP levels which coincided with the rapid increase of hydrolases and degradation of endosperm reserves (Palmiano and Juliano, 1972).

The relationship between immediately available soluble sugars, rate of endosperm breakdown, and seedling vigor were demonstrated in Phalaris sp. by Whalley and McKell (1967). Total soluble sugar levels were significantly higher for the average of all species during the first five days of germination of rapid growing seedlings. Endosperm hydrolysis limited rate of growth. Sugar levels were higher in slow-growing seedlings of one species which indicated the ability of the seedling to utilize sugars as substrate limited rate of growth. Abdul-Baki (1969b) reported a decreased rate of exogenous glucose-^{14}C uptake and utilization during the first 10 hr of germination by low-vigor seedlings of wheat and barley.

Sarkissian, Kessinger, and Harris (1964) reported that the reducing sugar and sucrose content of heterotic hybrid corn seedlings were increased during germination. A nonheterotic hybrid and the parental lines remained constant.

Use of individual enzyme activities during germination to predict seedling vigor have not generally been successful. Roos and

Sarkissian (1968) compared rates of activity of the respiratory enzymes isocitric dehydrogenase (L-isocitrate: NADP oxidoreductase (decarboxylating) EC 1.1.1.42) and isocitric lyase (L-isocitrate glyoxylate-lyase EC 3.1.3.1) in heterotic and nonheterotic corn hybrids. Isocitric dehydrogenase showed no heterotic response. Isocitric lyase gave a heterotic response during the first four days of germination in heterotic hybrids, but none in nonheterotic hybrids.

Glutamic acid decarboxylase (L-glutamate 1-carboxy-lyase EC 4.1.1.15) activity (GADA) during germination was proposed as a measure of seedling vigor (Grabe, 1964). Recently, Abdul-Baki and Anderson (1973) reported that GADA activity was largely dependent on the technique and seed part used for measurement. Data revealed higher activity in low than high vigor seed-lots of soybean (Glycine max (L.) Merrill) when activity was measured manometrically.

Rapid increase in oxygen uptake immediately after the initiation of imbibition is an indication that mitochondria are present in seed before imbibition and only require moisture for activation (Mayer and Poljakoff-Mayber, 1963). Further evidence was reported for cotyledons of germinating peas, Pisum sativum L., (Bain and Mercer, 1966; Nawa and Asahi, 1971; Solomos et al., 1972); beans, Phaseolus vulgaris L., (Malhotra and Spencer, 1970); and in the endosperm of castor bean, Ricinus communis L., (Akazawa and Beevers, 1957a, 1957b). A rapid maturation of mitochondria occurred upon hydration of these dicotyledon storage tissues. The first few hours were marked by increased enzymatic activity, followed by increased protein and lipid content. Mitochondrial cristae membrane development

was complete after two to three days. Within approximately five days the original mitochondria began to break down, and new mitochondria were formed.

Mesocotyl tissue of corn that was cut into sections of increasing physiological age from rapidly dividing to mature cells was characterized by increased mitochondrial protein and membranous development in mature cells (Key et al., 1961).

McDaniel (1969) demonstrated the relationship between mitochondrial number and efficiency, and seedling vigor of barley seed-weight classes. Seedling fresh-weight, mitochondrial protein, and mitochondrial biochemical-activity, measured by phosphorylative efficiency (ADP:O ratio), and respiratory rate were positively associated with seed weight when expressed on a per seed basis. Mitochondrial activity per unit of mitochondrial protein was not significantly different between seed-weight classes. Results suggested heavy seed have more mitochondria, consequently they were capable of greater ATP synthesis.

A significant association between seedling respiration rate two to three hr after the start of imbibition and axis length of corn seedlings three days later has been reported (Woodstock, 1965; Woodstock and Grabe, 1967). Cantrell, Hodges, and Keim (1972) obtained a positive association ($r=0.93$) between kernel respiration at 24 hr and shoot length with the use of heat treatments to obtain seed quality groups of corn. Conflicting results were reported previously by Throneberry and Smith (1955). Variations in respiratory oxygen consumption did not explain the differences in viability and vigor of

31 seed lots of corn. Mahadevappa (1967) found significant differences in respiration between hybrids of pearl millet, Pennisetum typhoides (Stapf.) Hubb., and their parents which did not differ significantly in germination capacity. Kittock and Law (1968) considered respiration primarily a measure of nongenetic factors of seedling vigor which they termed seed quality.

Seed germination requires a tremendous amount of biological energy in the form of ATP. Availability of ATP is a definite controlling factor in germination and seedling growth (Ching, 1972). Atkinson (1969) in a review of metabolic regulation, stated that sequences which are involved in the regeneration of ATP such as glycolysis and the citrate cycle should be controlled by the energy level of the cell, or the balance between adenosine monophosphate (AMP), adenosine diphosphate (ADP), and ATP. The stimulatory effects of AMP on key regulatory enzymes of glycolysis and the citrate cycle led to development of the adenylate-control hypothesis (Atkinson, 1969).

Atkinson and Walton (1967) defined "energy charge" as one half the number of anhydride-bound phosphate groups per adenine moiety, thus ATP would have an energy charge of one, and AMP an energy charge of zero. In a biological system the relative energy charge is calculated as: $[ATP] + \frac{1}{2}[ADP] / [ATP] + [ADP] + [AMP]$. The adenylate control hypothesis predicted and data showed that regulatory enzymes from sequences which generated ATP were active at low energy charge and activity decreased with an increase in energy charge above 0.75. Conversely, the regulatory enzymes from biosynthetic sequences that utilized ATP exhibited little activity at low energy charge levels,

while the activity increased rapidly above an energy charge of 0.75 (Atkinson, 1969; Atkinson and Fall, 1967; Atkinson and Walton, 1967; Chapman, Fall, and Atkinson, 1971). It was suggested that the adenylate nucleotides were maintained in equilibrium at this energy charge level through the action of adenylate kinase (ATP:AMP phosphotransferase EC 2.7.4.3) by Bomsel and Pradet (1968); Pradet (1969); Pradet, Narayanan, and Vermeersch (1968); and Santarius and Heber (1965).

Evidence in support of the adenylate-control hypothesis was obtained with the bacterium Escherischia coli (Migula) Castellani and Chalmers (Chapman et al., 1971), and unicellular alga, Polytoma uvella Ehr. (Mangat, 1971) grown in cultures. Cells went through a lag phase of little growth prior to the logarithmic phase of rapid growth, when the energy charge was 0.80 to 0.90. Cells entered a stationary phase when the substrate was depleted and the energy charge dropped to approximately 0.50. This response indicated that systems that utilized ATP predominated and in the absence of substrate, ATP could not be regenerated.

Brown and Short (1969) found an accumulation of high-energy compounds during the lag phase in Acer pseudoplatanus L. cell cultures. During rapid growth these compounds decreased in concentration. Energy charge values calculated from the data of Brown and Short were 0.80 during the lag phase and 0.70 during rapid growth. This response is difficult to explain with Atkinson's hypothesis (Atkinson, 1969), but could indicate ATP formation was limiting during rapid growth.

Energy charge values of dry seed were 0.50 or lower according to Chapman et al. (1971) and Ching and Kronstad (1972). Adenine

nucleotide content and energy charge rose dramatically to 0.70 after a short imbibition period. Levels of ATP were generally low in dry seed, ADP levels intermediate, and AMP levels high. Levels of ATP increased 250% or more within the first 4 to 16 hr of germination. Levels of ADP remained fairly stable, and AMP decreased parallel to ATP increases (Brown, 1965; Ching and Kronstad, 1972; Pradet, Narayanan, and Vermeersch, 1968; Wilson, Nelson, and Goebel, 1970).

Total adenylate levels of pea seed decreased after two days germination (Brown, 1965; Brown and Wray, 1968). However, total adenylate levels of lettuce (Lactuca sativa L.) seed and wheat seed continued to increase (Ching and Kronstad, 1972; Pradet et al., 1968). Chapman et al. (1971) concluded that energy charge values determined for whole seed mainly reflected the energy level of the storage tissue, and were not stabilized to the degree the energy charge would be in actively growing tissue.

Evidence presented to this point of the review indicated the adenylate nucleotide levels may control major metabolic trends to a large extent. This assumption leads to the suggestion that seedling growth potential may be predicted by the energy charge or energy levels of seed or germinating seedlings. Cherry et al. (1963) measured changes in nucleotide concentration of a corn hybrid and the inbred parents during germination. Concentration of ATP per embryonic axis was 2.5 fold greater in the hybrid than in either parent after two days germination. One of the inbred lines had the highest ATP level by the fourth day. Content of ATP increased at a faster rate in the hybrid.

Ching and Kronstad (1972) compared the adenylate energy level and energy charge during germination in two wheat cultivars, 'Yamhill' and 'Hyslop'. Yamhill emerged and grew more rapidly than Hyslop under field conditions, but in this study seed weight, rate of germination, and respiration rate were not different. Shoot length of Yamhill was 30% greater. Dry seed of both cultivars were similar in total adenylate level and energy charge. Yamhill had a slightly higher level of total adenylates than Hyslop after 4 hr of imbibition, although the energy charges were still similar. Energy charge of Yamhill seedlings was higher than that of Hyslop seedlings at 40, 44, and 48 hr of germination. Although ATP and ADP concentrations maintained an upward trend throughout the 48 hr study, concentration dropped at radicle emergence and again at shoot emergence. Magnitude of the decreases and subsequent recovery was greater in Yamhill than Hyslop. The differing response suggested a more dynamic synthesis and utilization in more vigorous Yamhill seedlings which suggested that energy charge reflected seedling vigor.

Ching (1973a) determined ATP levels of seedlings imbibed for 4 hr. Seedlings of species with starchy, proteinaceous, and fatty seed reserves of three seed-size classes of each species were studied. Content of ATP per seed for all three species was associated with seed weight, seedling fresh-weight, dry weight, and shoot length. Ching concluded that ATP content alone may be used to predict seedling vigor.

Seed Weight Determination

Ultimate weight of the seed is determined by both genetic and environmental factors (Bingham, 1966; Carleton and Cooper, 1972; Ryle, 1966; Stoy, 1965; Whalley, McKell and Green, 1966b). Seed size differences that are genetically determined are more likely to be associated with subsequent seedling performance than environmentally determined differences (Carleton and Cooper, 1972).

Excellent reviews on the relationship of the availability of photosynthetic assimilate to grain yield of cereal, including grain weight as one of the yield components have been presented by Stoy (1965), Thorne (1966), and Yoshida (1972). Ryle (1966) reviewed physiological aspects of seed yield of forage grasses. Seed weight of forage plants has received minimum research effort.

Importance of photosynthetic assimilate to grain weight was demonstrated in experiments where grain weight was reduced by ear shading (Kriedemann, 1966; Stoy, 1965; Thorne, 1963a, 1966). Total grain-weight is a function of photosynthetic assimilate translocated to the grain from the shoot before anthesis and during kernel development, plus photosynthetic assimilate from the inflorescence minus the assimilate lost by respiration (Lupton and Ali, 1966; Thorne, 1966). The contribution by preanthesis assimilate to grain weight was small in grain sorghum (Sorghum vulgare Pers.) (Fischer and Wilson, 1971a; Goldsworthy, 1970) and the cereals (Thorne, 1966). The major part of the grain weight was provided by a assimilate from the leaves near the developing inflorescence and by inflorescence photosynthesis (Carr and Wardlaw, 1965; Evans and Rawson, 1970; Fischer and Wilson, 1971b;

Lupton, 1968, 1969; Porter, Pal, and Martin, 1950; Thorne, 1963a, 1963b, 1965). The contribution of ear or inflorescence photosynthesis to grain was low in corn and rice (Yoshida, 1972). Inflorescence photosynthesis was relatively high in wheat and barley (Evans and Rawson, 1970; Lupton, 1968; Porter et al., 1950; Thorne, 1965, 1966). Inflorescence photosynthesis accounts for 10 to 40% of the grain weight in wheat (Evans and Rawson, 1970; Kriedemann, 1966), 30 to 40% in grain sorghum (Goldsworthy, 1970), and 50 to 60% in barley (Thorne, 1963a, 1966). Inflorescence photosynthesis was greater than respiration at anthesis and shortly after anthesis, however, as maturity approached respiration tended to become equal or greater. The response was associated with a decline in photosynthesis and increase in respiration (Carr and Wardlaw, 1965; Evans and Rawson, 1970; Porter et al., 1950). Gaastra (1963) emphasized the high respiratory rates of reproductive inflorescences. Respiratory carbon losses by the inflorescence may account for 20 to 30% of the total carbon fixed (Evans and Rawson, 1970; Thorne, 1963a).

Greater duration of the period of grain maturation was associated with increased grain size in cereals (Yoshida, 1972).

Evans et al. (1970) examined the phloem area and vascular bundle number at the tip of the main stem of diploid, tetraploid, and hexaploid wheats. There was a marked increase in the amount of assimilate that was translocated to the grain with an increase of the ploidy level (Evans and Dunstone, 1970). More phylogenetically advanced hexaploid species had the greatest number of vascular bundles. Maximum phloem assimilate flow rate was linearly related to phloem

area, and the authors postulated that the import of assimilate by the inflorescence would be approximately proportional to grain number and weight. They were unable to conclude that phloem area supplying the inflorescence limited yield.

Evidence that translocation of sucrose into the developing grain, which limited starch accumulation and subsequently seed weight, was presented by Jenner and Rathjen (1972). Detached peduncles of the ear were cultured in sucrose solutions which provided an unlimited sucrose supply. If photosynthetically supplied sucrose limited starch accumulation, an increase in grain starch would be found in the cultured ears. Cultured ears did not increase in starch content, which suggested translocation of sucrose limited starch accumulation in the grain.

MATERIALS AND METHODS

Plant Material

Selections of blue panicgrass for heavy and light seed weight (Table 1) from six cycles of recurrent selection with seed-weight selection pressure and successive restricted recombination were established in separate polycross nurseries in 1970. Nursery and research facilities of the research laboratory of the Agricultural Research Service located at the Tucson Plant Materials Center, Soil Conservation Service, and the Department of Agronomy and Plant Genetics, University of Arizona were used for the investigations. Design of each crossing block was a randomized complete-block with 10 replications. Polycross seed of each selection was used for seed and seedling studies. Plants were established from rhizomes in field plots for photosynthetic and respiratory studies.

Growth Evaluation

Dry-matter production was determined for five heavy and five light seed-weight selections in a growth chamber. One hundred seed were planted in 12 cm plastic pots. Growth chamber conditions were 12 hr light at 38 C with light intensity of 41 klux and 12 hr dark at 21 C. Experimental design was 4 randomized complete-blocks. Plants were thinned to ten per pot. Plant material was dried at 70 C for 48 hr, and dry weight of ten plants was determined. Measurements

Table 1. Selections of blue panicgrass for heavy and light seed weight from six cycles of recurrent selection with seed weight selection pressure and successive restricted recombination

Selection no.	Weight per 100 seed (mg)
	Heavy selections
4	122
70	110
12	100
75	92
95	82
	Light selections
100	60
97	58
66	57
72	54
62	52
61	45

were made at 6, 9, 12, 18, 30, 42, and 54 days after planting. Mean relative growth rate ($\overline{RGR}$) was calculated for each selection over the 6 to 54 day growth period. The equation; $\overline{RGR} = \frac{\log_e W_2 - \log_e W_1}{t_2 - t_1}$ as described by Radford (1967) was used.

Seed and Seedling Metabolism

Selections 4, 95, 72, and 62 were used for seedling metabolism studies. They were considered representative of the heavy and light seed-weight groups. Disposable plastic petri-dishes (9 cm) were used as germination containers with two circles of autoclaved Eaton and Dikeman No. 617 filter paper. Filter paper was wetted with 9 ml of deionized water. Seed were placed in small nylon sacks and surface sterilized for 8 min in 0.5% sodium hypochlorite. Sacks with seed were rinsed 8 times with deionized water and twice with sterile water. Seed were then transferred to the petri dishes. Germination was conducted in an Environator growth chamber at 30 C for 72 hr in darkness. Two petri dishes of each selection were removed at 0, 6, 12, 24, 36, 48, and 72 hr of imbibition.

Seedling Respiration

Respiration was determined as CO_2 evolution by each dish of 100 seed using a Beckman 215A Infrared Gas Analyzer and closed system of 0.72 liter volume (Fig. 1). A Manostat Varistaltic tubing pump was used to circulate air through the system at a rate of 3.5 liters per min. Air was pumped out of the glass plant chamber through two drying columns located on the intake and exhaust side of the pump to alleviate pressure fluctuations. The air then passed through the

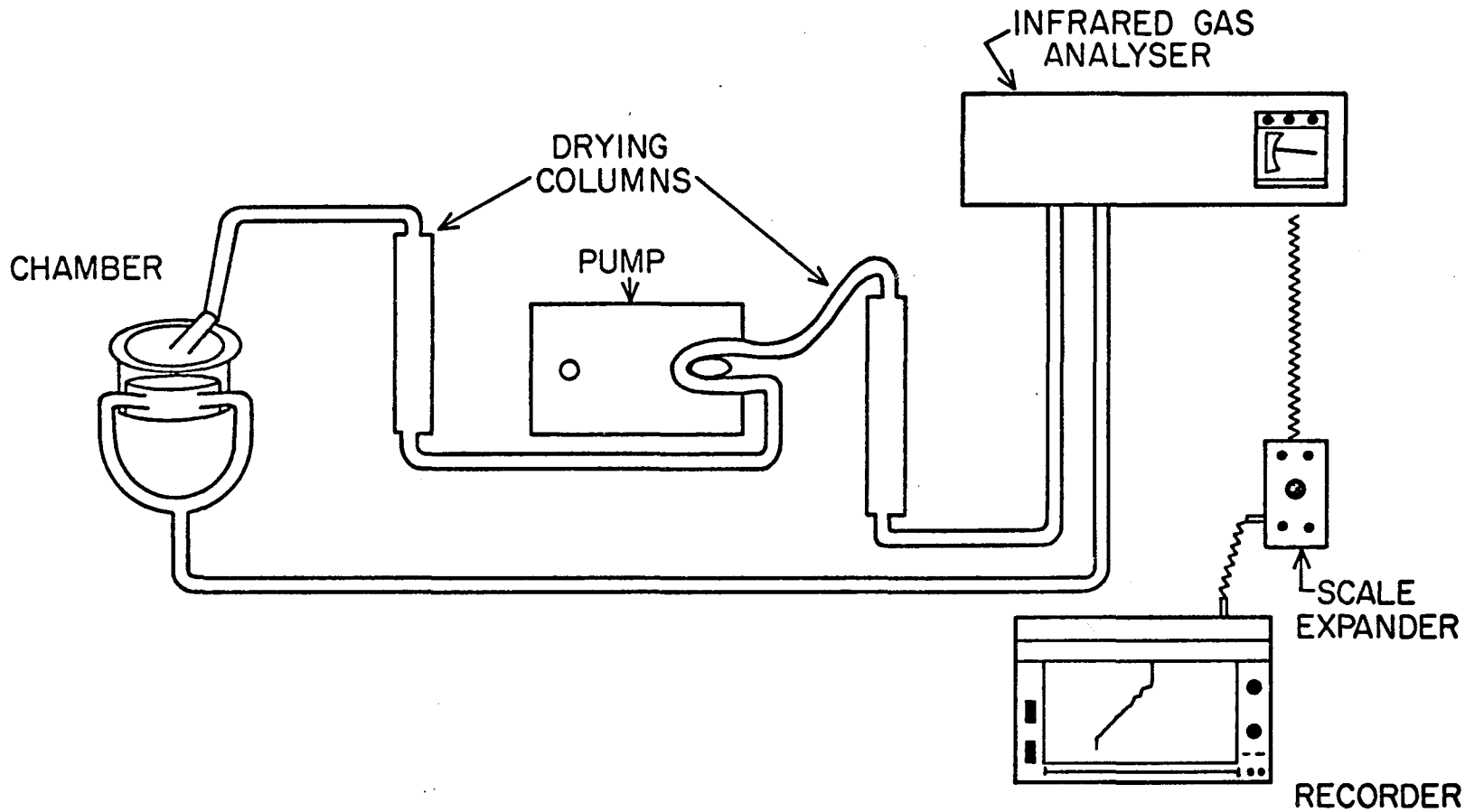

Fig. 1. Diagram of the closed system used for seed respiration measurements

analyzer and was reintroduced into the chamber. Increase in CO_2 concentration per unit of time was monitored on a Leeds and Northrup Speedomax recorder. Determinations were conducted between 400 and 270 ppm CO_2. Change per unit of time of ppm CO_2 was converted to μmole CO_2 hr^{-1}, corrected for temperature and pressure, and expressed on a 100 seed (μmole CO_2 100 $seed^{-1}$ hr^{-1}) or unit initial seed weight basis (μmole CO_2 evolved g initial seed $weight^{-1}$ hr^{-1}).

Germination percentage was determined by testa separation and evidence of radicle protrusion as the criterion for germination. Thirty seed were randomly removed from each dish, surface moisture blotted away, and fresh weight determined. Dry weight of the 30 seed sample was obtained after oven drying at 75 C for 72 hr. Results were converted to a 100 seed basis.

Adenylate and Energy Charge Studies

Twenty seed were selected at random from each dish immediately after the respiration measurements were completed, and crushed in liquid N_2 in a 1.5 x 10 cm test tube with a large glass rod. Samples were maintained at -25 C prior to adenine nucleotide extraction. Adenine nucleotides were extracted by a modification of the method used by Ching and Kronstad (1972) after a comparison of several methods (Table 2). The test tube containing the sample was placed in a boiling water bath and 4 ml boiling 20 mM Tris, 5 mM disodium ethylenediaminetetraacetate (Na_2EDTA) pH 7.0 extraction buffer were immediately injected into the tube. After boiling 5 min, the tubes were held in ice until assayed for adenine nucleotides. Concentration

Table 2. Comparison of five procedures for ATP extraction from blue panicgrass seedlings following 24 hr of imbibition

Extraction procedure	ATP content (nmoles per 100 seed)	Mean
Boiled 25 mM Tris-SO_4, 25 mM magnesium acetate, pH 7.5, 5 min	2.52 2.82 3.32	2.88
Cold 5% TCA 5 min, neutralized with KOH	2.26 2.41 2.89	2.52
Cold 5% TCA 5 min, TCA removed by 5 ethyl ether extractions	1.05 1.14 1.21	1.13
Boiled 20 mM Tris-SO_4, pH 7.0 5 min	2.70 2.53 3.64	2.96
Boiled 20 mM Tris-SO_4, 5 mM Na_2EDTA, pH 7.0, 5 min	3.27 3.73 3.04	3.35

of ATP decreased with storage so adenine nucleotide assays were performed within 1 hr after extraction.

Concentration of ATP was determined by means of the luciferin-luciferase reaction. The luciferin and luciferase were extracted from dessicated firefly tails as described by Strehler and Trotter (1954). One hundred mg firefly lanterns were ground approximately 5 min in a chilled mortar and pestle with 10 ml of 0.1 M sodium arsenate buffer, pH 7.4, and transferred to a Corex test tube. The mortar was washed with 3 ml additional buffer. The extract was then centrifuged at 12,000 x g for 5 min. The supernatant was decanted into a tube containing 100 mg $MgSO_4$ and stored at 8 C for 48 hr prior to use to allow depletion of endogenous ATP.

Adenylate concentrations in seed extracts were determined after a 2X dilution as described by Pradet (1967), with ADP and AMP conversion to ATP. For ATP determinations, 0.1 ml extract was added to 0.9 ml reaction buffer (25 mM Tris-SO_4, 25 mM magnesium acetate, pH 7.5). For ATP plus ADP determination 0.1 ml extract was added to 0.9 ml reaction buffer with addition of 1 µmole phosphoenolpyruvate and 20 µg pyruvate kinase. For total adenylate determination, 0.1 ml extract was added to 0.9 ml reaction buffer with 1 µmole phosphoenolpyruvate, 20 µg pyruvate kinase, and 40 µg adenylate kinase. The three mixtures were incubated at 30 C for 10 min, then held at 4 C until ATP assay. ADP and AMP concentrations were determined by difference.

Adenylate kinase was dialyzed for 4 hr at 4 C against 250 ml of 10 mM Tris-Cl, 1 mM Na_2EDTA, 0.1 mM dithiothreitol prior to use (Ching, 1973b).

Reaction buffer (0.6 ml) and firefly extract (0.1 ml) were added to a scintillation vial and placed in the refrigerated sample chamber of a Model 3320 Packard Tri-Carb liquid scintillation spectrometer for the ATP assay. Spectrometer gain was set at 100% with coincidence correction off (Stanley and Williams, 1969). After temperature equilibration the vial was lowered into the counting chamber for a 1 sec background count to determine the endogenous firefly extract ATP levels and photomultiplier tube noise. Then, 0.1 ml sample was injected into the vial with an Eppendorf automatic pipet and a 1 sec sample count was made. The initial background count was subtracted from the sample count.

Standard ATP solutions from 0.5 to 15.0 pmoles, prepared daily in reaction buffer, were used to quantitate sample ATP concentrations. Known concentrations of each adenylate were added to two selected samples at each sampling interval to determine recovery. Recovery percentages were variable, but averaged 100, 90, and 70% for ATP, ADP, and AMP respectively.

Energy charge values were calculated as $E.C. = [ATP] + \frac{1}{2}[ADP] / [ATP] + [ADP] + [AMP]$, as initially defined by Atkinson and Walton (1967).

Dessicated firefly tails, pyruvate kinase, adenylate kinase, and dithiothreitol were obtained from Sigma. Phosphoenolpyruvate was obtained from Calbiochem.

Free Sugars

Free sugars were extracted from samples of 70 seed of each selection. Seed were frozen in liquid N_2, lyophilized for 24 hr, and stored at -25 C. Free sugars were extracted after grinding the seed in liquid N_2 in a 1.5 x 15 cm test tube with a glass rod. Ten ml of 80% ETOH was introduced into the test tube, and the tube was placed in a sand bath at 60 C for 2 hr. Samples were filtered into test tubes through Whatman #1 filter paper (gravity filtration). The ETOH was subsequently removed by evaporation under a stream of N_2 gas in the 60 C sand bath, and the sample volume reduced to approximately 0.5 ml. Samples were brought to a constant volume and free sugars were determined with the anthrone reagent (Yemm and Willis, 1954). One ml of extract was transferred to a pyrex test tube and 5 ml of 70% anthrone reagent (728 ml H_2SO_4, 272 ml dist. H_2O, 2 g anthrone, and 1 g thiourea) was added, thoroughly mixed, and placed into ice. The tube was then placed into boiling water for 10 min and immediately back into ice. After reaching room temperature, absorbance at 620 nm was determined with a Beckman DB-G grating spectrophotometer. Free sugar concentrations were determined from a standard curve prepared with 10 to 100 µg/ml glucose.

Mitochondrial Protein

A mitochondrial fraction was obtained by modifications of the method reported by McDaniel (1969). Fifty seed were ground for 1 min in a prechilled mortar and pestle with 4 ml cold 0.5 M sucrose, .05 M phosphate buffer, .003 M Na_2EDTA grinding buffer, pH 7.2. The

suspension was then washed into a glass tissue homogenizer with 2 ml grinding buffer. The homogenate was filtered through Mira-Cloth (Calbiochem) into a centrifuge tube after 30 sec homogenization and washed with an additional 4 ml grinding buffer. After centrifugation at 500 x g for 5 min the supernatant was decanted and centrifuged at 12,000 x g for 10 min. The mitochondrial pellet obtained was resuspended in 1 ml of 0.5 M sucrose and used for mitochondrial protein assay.

Mitochondrial protein was determined using Chaykin's (1966) modification of the Lowry, et al. (1951) method. Five ml of reagent C (50 ml of 2% Na_2CO_3 plus 1 ml of 0.5% $CuSO_4.5\ H_2O$ in 1% sodium tartrate) prepared each day, was added to a 0.5 ml sample and mixed thoroughly. After 10 min at room temperature 0.5 ml Folin phenol reagent (Fisher) was added and mixed immediately. Absorbance at 600 nm was determined after 10 min at room temperature with a Beckman DB-G spectrophotometer.

Bovine serum albumin (Sigma Fraction V) in 0.02 M phosphate buffer was used to prepare a standard curve from 10 to 200 µg protein. Sample concentration was determined from a curve prepared each day.

Inflorescence Gas Exchange Study

Rhizomes were removed from dormant plants in the early spring of 1972, transplanted to pots, and maintained under greenhouse conditions. Plants were transplanted to the field in June in separate crossing blocks of heavy and light seed-weight selections with 10 and 8 replications, respectively. Plants were cut to 25 cm height

following establishment and regrowth collected for the gas exchange measurements.

Inflorescences were selected at 5 day intervals at four stages of maturity. Maturity stages were as inflorescence emerged, at early anthesis, at late anthesis, and dough stage. Each culm was placed in a 120 ml bottle of distilled water and allowed to equilibrate at 25 C over night. The next morning apparent photosynthesis and dark respiration rates of the inflorescences were determined using a Beckman 215A Infrared Gas Analyzer and closed system with a volume of 2.54 liters, similar to that used for seedling respiration measurements. Air was pumped out of the glass plant-chamber, through a single drying column, and then through a 250-ml flask to alleviate pressure fluctuations before the gas entered the analyzer. Air was then reintroduced into the plant chamber. The change in CO_2 concentration per unit of time was monitored on a Leeds and Northrup Speedomax recorder.

Following photosynthesis and dark respiration measurements, inflorescences were oven-dried at 70 C for 48 hr for dry weight determination.

Change in concentration of CO_2 (ppm per unit of time) was obtained from the recorder trace. A representative recorder trace is shown in Figure 2. Concentrations were converted to mg CO_2 hr^{-1}, corrected for temperature and pressure, and expressed on a unit inflorescence weight (mg CO_2 g dry wt $^{-1}$ hr^{-1}) basis.

Light for the photosynthetic measurements was provided by seven 500 watt, 130 volt Sylvania reflector-flood lamps, which

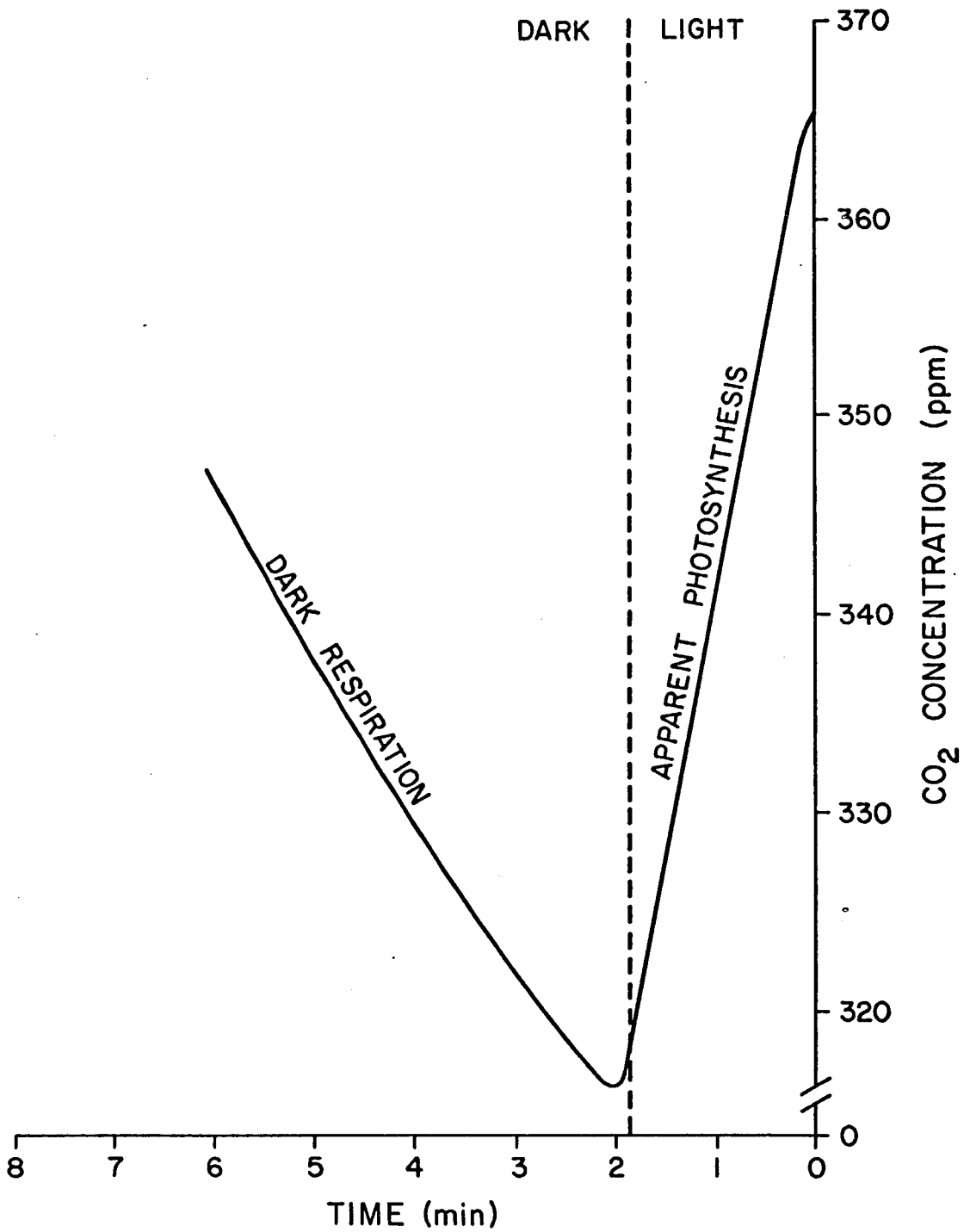

Fig. 2. Recorder trace showing changes in CO_2 concentration in the closed system used for measurement of blue panicgrass inflorescence gas exchange

developed 75.3 klux intensity. Lamps were submerged in 15 cm of circulating water to exchange heat. The plant chamber was covered with aluminum foil for dark respiration measurements. Photosynthesis and dark respiration measurements were made between 380 and 270 ppm CO_2.

Statistical Procedures

Steel and Torrie (1960) served as a guideline for statistical procedures. Analysis of variance was made on all measured variables. Means were separated with the method described by Newman (1939). Means were the result of 6 replications for seedling fresh weight, dry weight, and respiration rate. Four replications were used for all other variables measured. Correlations were made between selected variables. Covariance analysis was used to obtain treatment means adjusted for germination percentage for seedling metabolism studies and the adjusted means separated by the method of Finney (1946).

Analyses were performed by the Agricultural Experiment Station Statistician in cooperation with the University of Arizona Computer Center.

RESULTS AND DISCUSSION

Growth Chamber Dry Matter Production

Dry matter production of the heavy seed-weight selections was significantly greater than that of the light seed-weight selections at all sampling dates (Table 3). Thus, dry matter production was closely associated with seed-weight selections. Within each seed-weight group selections were similar for dry-matter production. Since the seed-weight groups were extremes of seed-weight selection pressure, little variation would be expected in dry-matter production.

Heavy seed provided a definite dry-matter production advantage during the first 54 days growth of blue panicgrass. These results are in agreement with other reports of seed weight enhanced dry-matter production (Black, 1956, 1957a; Kneebone, 1972).

The calculated mean relative growth rate ($\overline{RGR}$) suggests that the advantage of dry-matter production of heavy seed-weight selections may not persist beyond the initial growth period (Fig. 3). Overall $\overline{RGR}$ values of the light seed weight selections were 10% greater than the $\overline{RGR}$ values of the heavy seed-weight selections. Calculation of $\overline{RGR}$'s over intervals from 6 to 18, 18 to 30, 30 to 42, and 42 to 54 days after planting demonstrated greater values for light seed-weight selections at all intervals. This indicated that the light seed-weight selections produced more dry-matter per gram dry-matter already

Table 3. Dry-matter production at 7 time periods during the first 54 days growth under growth chamber environment of five heavy and five light seed-weight selections of blue panicgrass

Selection no.	Dry weight (g per 10 plants)						
	Days from planting						
	6	9	12	18	30	42	54
				Heavy selections			
4	0.005 b*	0.010 c	0.028 b	0.157 c	1.258 abc	4.816 bc	8.902 ab
70	0.005 b	0.017 a	0.033 ab	0.185 bc	1.449 a	4.462 c	10.244 a
12	0.007 a	0.009 c	0.033 ab	0.167 bc	1.186 bc	4.848 bc	8.018 b
75	0.005 b	0.012 bc	0.035 a	0.195 b	1.081 c	5.202 ab	8.156 b
95	0.005 b	0.015 ab	0.030 ab	0.235 a	1.322 ab	5.790 a	8.560 b
				Light selections			
100	0.002 c	0.004 d	0.009 d	0.066 d	0.371 e	2.878 de	5.798 c
66	0.002 c	0.004 d	0.014 c	0.078 d	0.633 d	3.252 d	5.610 c
72	0.001 c	0.003 d	0.008 d	0.060 d	0.492 de	2.696 de	5.636 c
62	0.001 c	0.004 d	0.010 cd	0.062 d	0.614 d	2.590 e	5.886 c
61	0.002 c	0.004 d	0.012 cd	0.057 d	0.502 de	1.878 f	6.602 c

*Means in the same column followed by the same letter are not significantly different at the .05 level according to Student-Newman-Keul's multiple range test

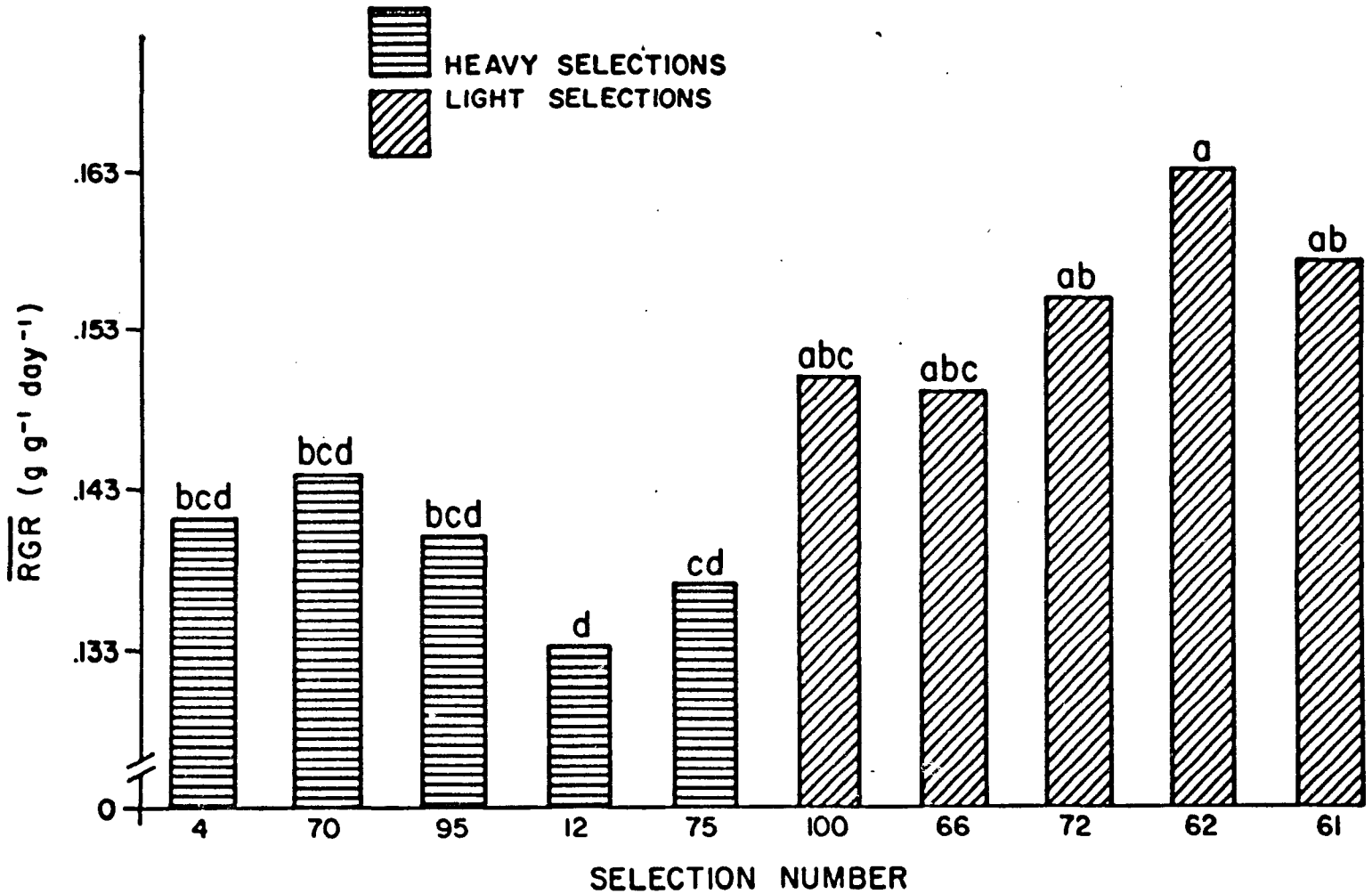

Fig. 3. Mean relative growth rates ($\overline{RGR}$) of 10 seed-weight selections of blue panicgrass calculated over a 48-day growth period. Bars with the same letter are not significantly different at the .05 level according to Student-Newman-Keul's multiple range test.

present. Arnott (1969) reported similar results for $\overline{RGR}$'s of perennial ryegrass seed weight classes.

Heavy seed-weight selections possess greater seed reserves for initial growth. Yet, these reserves are apparently not associated genetically with the $\overline{RGR}$ of a developing perennial plant. This hypothesis suggests that the systems are genetically different.

Assuming $\overline{RGR}$ of the light seed-weight selections is manifested in regrowth, then the genetic system controlling increased seed reserves (heavy seed weight) and the genetic system controlling plant growth and development are independent systems.

Seed and Seedling Metabolism

Radicle emergence was initiated at 36 hr and coleoptile emergence was noted at 48 to 60 hr of germination for the four blue panicgrass selections (heavy seed-weight selections 4 and 95 and light seed-weight selections 62 and 72), Table 4. Germination percentage of selection 4 was significantly greater than the other three selections at 72 hr of imbibition. Germination percentage of selection 95 was similar or significantly lower than the two light seed-weight selections. Germination percentage was not consistently greater for the heavy seed-weight selections of blue panicgrass.

Germination percentage could affect respiration rate, adenylate levels, and other determinations. Covariance analysis was used to obtain treatment means adjusted for germination percentage. Relative efficiency of the covariance analysis was very low, and only in isolated cases was germination percentage responsible for differences

Table 4. Germination percentage of four selections of blue panicgrass measured at 4 time periods during the initial 72 hr of germination

Selection no.	Percentage of germination			
	Hours of imbibition			
	36	48	60	72
4	21 a*	32 a	36 a	54 a
95	11 b	16 b	19 a	25 c
72	17 ab	24 ab	29 a	40 b
62	15 ab	16 b	24 a	27 c

*Means in the same column followed by the same letter are not significantly different at the .05 level according to Student-Newman-Keul's multiple range test

between biochemical parameters of the seed-weight selections. Thus, unadjusted arithmetic means are presented.

The dry weight of seed and seedlings during germination and initial growth of the four selections (Table 5) showed a slight trend toward decrease in dry weight. This lack of dry-weight decrease might be partially attributed to the low germination percentage observed up to 72 hr, however, Ching (1972) presented evidence that dry weight loss for seed of several species was not detectable until after 48 hr of germination. Major and Wright (1970) reported seed weight diminished by 50% after 144 hr of germination for the same heavy and light seed weight selections used in this study. The response obtained in this study suggested endosperm utilization and respiratory carbon loss for blue panicgrass was not of great magnitude until after 72 hr of germination.

Dramatic differences in fresh weight increase during germination and initial growth were obtained (Table 6). Selection 4 was significantly greater than selection 95, and selections 4 and 95 significantly greater in fresh weight than selections 72 and 62 throughout the initial 72 hr of germination. These differences were partially a reflection of the initial differences in seed weight. When absolute growth rates (weight increase per hr) are calculated over the 72 hr germination period, selections 4, 95, 72, and 62 had growth rates of 1.12, 0.61, 0.51, and 0.30 mg per hr, respectively. Most of the greater absolute growth rate for heavy seed can be related to their ability to imbibe more water due to physically greater size. During the 0 to 6 hr period of rapid imbibition (Fig. 4),

Table 5. Seed and seedling dry weight per 100 seed of two heavy and two light seed-weight selections of blue panicgrass measured at 8 time periods during the initial 72 hr of germination

Selection no.	Dry weight per 100 seed (mg)							
	Hours of imbibition							
	0	6	12	24	36	48	60	72
					Heavy selections			
4	113 a*	117 a	113 a	104 a	115 a	112 a	111 a	111 a
95	75 b	78 b	75 a	78 b	77 b	74 b	78 b	74 b
Mean	94 x	97 x	94 x	91 x	96 x	93 x	94 x	92 x
					Light selections			
72	47 c	47 c	45 c	46 c	48 c	45 c	45 c	46 c
62	48 c	50 c	47 c	48 c	48 c	47 c	47 c	46 c
Mean	47 y	48 y	46 y	47 y	48 y	46 y	46 y	46 y

*Selection means and means of selections within the same column followed by the same letter are not significantly different at the .05 level according to Student-Newman-Keul's multiple range test

Table 6. Seed or seedling fresh weight per 100 seed of two heavy and two light seed-weight selections of blue panicgrass measured at 8 time periods during the initial 72 hr of germination

Selection no.	Fresh weight per 100 seed (mg)							
	Hours of imbibition							
	0	6	12	24	36	48	60	72
				Heavy selections				
4	122 a*	147 a	153 a	149 a	168 a	179 a	186 a	203 a
95	81 b	101 b	101 b	110 b	113 b	115 b	121 b	125 b
Mean	101 x	124 x	127 x	129 x	140 x	147 x	153 x	164 x
				Light selections				
72	50 c	58 c	60 c	66 c	69 c	72 c	77 c	87 c
62	52 c	63 c	63 c	68 c	71 c	71 c	75 c	74 c
Mean	51 y	60 y	61 y	67 y	70 y	71 y	76 y	80 y

*Selection means and means of selections within the same column followed by the same letter are not significantly different at the .05 level according to Student-Newman-Keul's multiple range test

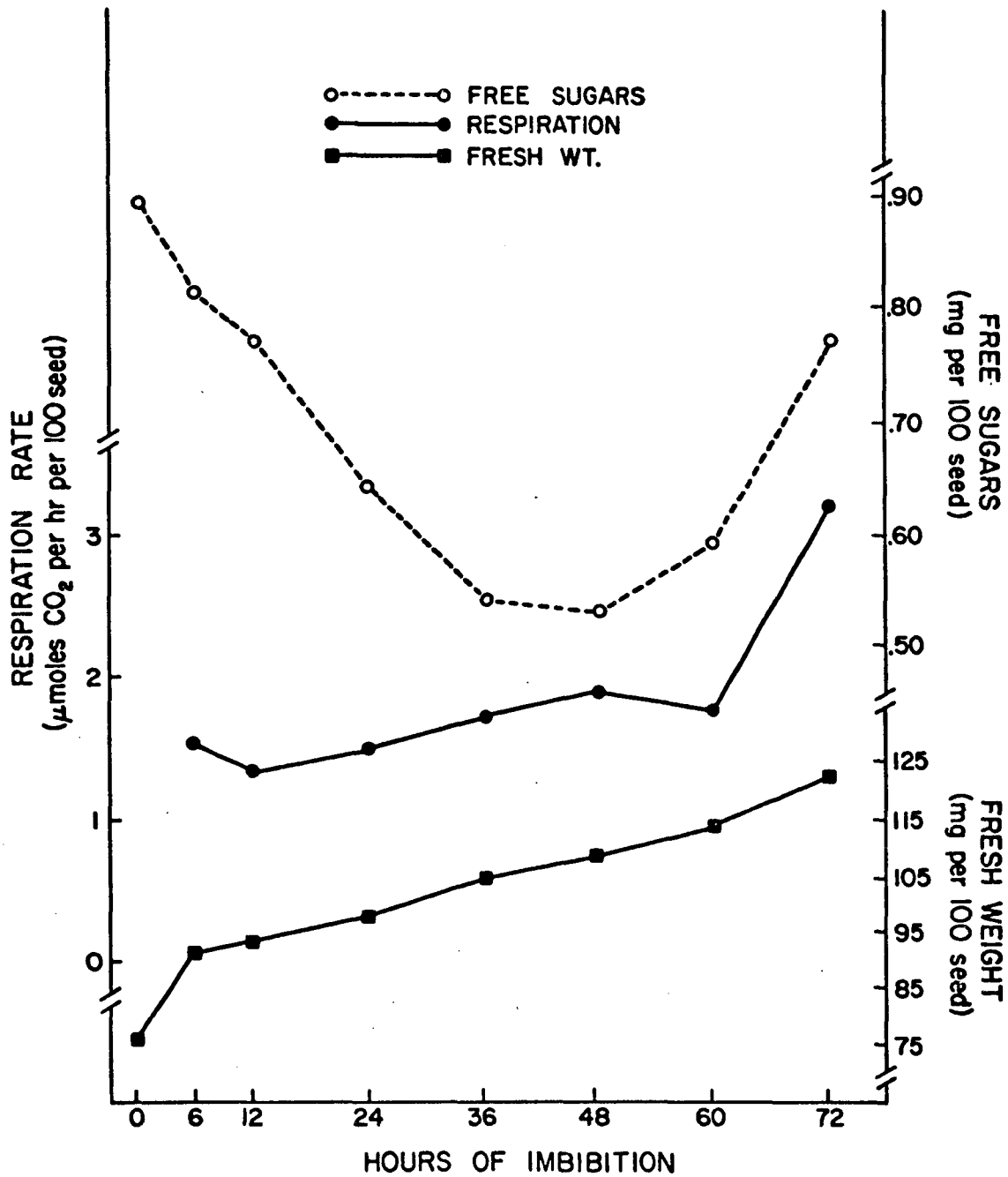

Fig. 4. Trends in fresh weight, respiration rate, and free sugar content of four seed-weight selections of blue panicgrass during the initial 72 hr of germination

fresh weight increase for heavy seed was more than twice that of the light seed selections (3.83 mg per hr versus 1.50 mg per hr). Water uptake alone would be primarily responsible for this initial difference in rate. However, absolute growth rates of 0.85 mg per hr, 0.36 mg per hr, 0.44 mg per hr, and 0.17 mg per hr for selections 4, 95, 72, and 62 respectively, were obtained for the 6 to 72 hr of germination period (calculated from Table 6). Selection 4 was considered the most vigorous from these data, selection 62 the least vigorous, with little difference between selections 95 and 72.

Respiration rates per 100 seed (Table 7) were higher for the heavy seed-weight selections throughout the 72 hr germination period. However, rates were significantly higher only at the 48 hr measurement. A low, but significantly positive association ($r = +.57$) was obtained between respiration rate and fresh weight at 6 hr. The association was not significant at subsequent measurements. Respiration rate during the initial hours of germination was the basis for a proposed seedling vigor test for corn (Woodstock, 1965; Woodstock and Grabe, 1967; Cantrell et al., 1972). Lack of significant differences in respiration rates obtained in this study for blue panicgrass selections agree with reports by Mahadevappa (1967) and Throneberry and Smith (1955). They found little relationship between seedling vigor and respiration rate.

Expression of respiratory rates on the basis of initial seed weight (Table 8) showed greater rates for light seed-weight selections. Differences were significant at 48 and 72 hr of imbibition. Burris, Wahab, and Edjie (1971) reported similar findings for soybean seed-size

Table 7. Respiratory rates per 100 seed of two heavy and two light seed-weight selections of blue panicgrass measured at 7 time periods during the initial 72 hr of germination

Selection no.	Respiration rate (μmoles CO_2 hr^{-1} 100 $seed^{-1}$)						
	Hours of imbibition						
	6	12	24	36	48	60	72
	Heavy selections						
4	1.98 a*	1.66 a	1.82 a	1.96 a	2.11 a	2.20 a	3.68 a
95	1.43 a	1.39 a	1.61 a	1.75 a	2.01 a	1.66 a	2.74 a
Mean	1.71 x	1.52 x	1.71 x	1.85 x	2.06 x	1.93 x	3.21 x
	Light selections						
72	1.50 a	1.26 a	1.44 a	1.67 a	1.75 ab	1.45 a	3.28 a
62	1.20 a	1.13 a	1.07 a	1.41 a	1.50 b	1.33 a	2.95 a
Mean	1.35 x	1.19 x	1.28 x	1.54 x	1.62 y	1.39 x	3.11 x

*Selection means and means of selections within the same column followed by the same letter are not significantly different at the .05 level according to Student-Newman-Keul's multiple range test

Table 8. Respiratory rates per gram of initial seed weight of two heavy and two light seed-weight selections of blue panicgrass measured at 8 time periods during the initial 72 hr of germination

Selection no.	Respiration rate (μmoles CO_2 hr^{-1} g initial seed weight^{-1})						
	Hours of imbibition						
	6	12	24	36	48	60	72
				Heavy selections			
4	16.20 a*	13.62 a	14.93 a	16.06 b	17.35 c	18.09 a	30.16 a
95	17.57 a	17.12 a	19.79 a	21.55 ab	24.81 b	20.46 a	33.70 a
Mean	16.88 x	15.37 x	17.36 x	18.80 x	21.08 x	19.27 x	31.93 x
				Light selections			
72	30.01 a	25.12 a	28.74 a	33.27 a	35.03 a	28.98 a	65.47 a
62	23.04 a	21.67 a	20.51 a	27.18 ab	28.91 ab	25.61 a	56.83 a
Mean	26.52 x	23.39 x	24.62 x	30.22 x	31.97 y	27.29 x	61.15 y

*Selection means and means of selections within the same column followed by the same letter are not significantly different at the .05 level according to Student-Newman-Keul's multiple range test

classes. Large seed-size classes exhibited higher respiratory rates than small seed-size when expressed on a per seed basis. However, when expressed on a dry weight basis small seed showed a higher respiratory rate. Increased respiration rates for light seed were hypothesized a function of relative amounts of meristematic tissue that respired rapidly and structural tissue that respired slowly. The results obtained in this study can be explained in a similar manner. Heavy seed of blue panicgrass could contain a greater proportion of endosperm and structural tissue. This relationship would result in reduced respiration rate when based on seed weight. If light seed utilized a greater percentage of the endosperm during early germination, more of the total seedling weight would be composed of meristematic tissue as germination progressed. Absolute decreases in dry weight (Table 5) were similar for all four selections. This suggests that on a percentage basis utilization of endosperm by light seed was greater.

Additional evidence in support of the hypothesis was provided by data presented in Tables 9 through 18. Free sugar content, mitochondrial protein, and adenylate phosphate levels were higher for heavy seed weight selections when expressed on a 100 seed basis. When expressed per gram of unimbibed seed weight, light seed exhibited equivalent or higher values.

Content of free sugar per 100 seed for the heavy seed-weight selections was significantly greater than that for the light seed-weight selections throughout the initial 72 hr of germination (Table 9).

Table 9. Content of free sugar per 100 seed of two heavy and two light seed-weight selections of blue panicgrass measured at 8 time periods during the initial 72 hr of germination

Selection no.	Free sugars per 100 seed (mg)							
	Hours of imbibition							
	0	6	12	24	36	48	60	72
				Heavy selections				
4	1.41 a*	1.32 a	1.18 a	.87 a	.86 a	.80 a	.88 a	1.25 a
95	.88 b	.75 b	.76 b	.73 ab	.54 ab	.52 ab	.53 b	.60 b
Mean	1.15 x	1.03 x	.97 x	.97 x	.70 x	.66 x	.70 x	.93 x
				Light selections				
72	.63 c	.63 c	.62 b	.53 ab	.42 ab	.44 b	.59 ab	.78 b
62	.63 c	.55 c	.53 b	.43 b	.35 b	.35 b	.37 b	.44 c
Mean	.63 y	.59 y	.58 y	.48 y	.39 y	.39 y	.48 y	.61 y

*Selection means and means of selections within the same column followed by the same letter are not significantly different at the .05 level according to Student-Newman-Keul's multiple range test

Selection 95, however, exhibited significantly greater free sugars content than the light seed-weight selections only during very early stages of imbibition.

Wilson (1971) reported synthesis of alpha-amylase began 24 hr after imbibition for crested wheatgrass, and activity increased rapidly from 2 to 5 days. The data suggested that alpha-amylase activity of blue panicgrass increased after 36 hr with greater activity after 60 hr, demonstrated by the increase in free sugar content (Fig. 4). Activity of beta-amylase, present in unimbibed seed (Macleod, 1969; Palmiano and Juliano, 1972; Wilson, 1971), apparently did not hydrolyze endosperm starch reserves at a sufficient rate to meet the requirement for sugar utilization during the initial 36 hr of germination in blue panicgrass.

Examination of data of individual selections revealed quite different patterns of free sugar content (Tables 9 and 10). Trends expressed on a basis of 100 seed and on a basis of seed weight were the same. Selection 4 showed a marked decrease during the first 24 hr. In contrast, selection 72 did not exhibit a decline in free sugar content until 24 hr of imbibition. Free sugar content decreased during the first 6 hr, leveled off at 12 hr, and then decreased to 36 hr for selections 95 and 62. Average rate of decline during the first 36 hr was 15, 9, 6, and 8 μg per hr for selections 4, 95, 72, and 62 respectively, when expressed on a basis of 100 seed. Either differential beta-amylase hydrolytic activity or rate of utilization could account for the variable free sugar trends among selections.

Table 10. Content of free sugar per gram of initial seed weight of two heavy and two light seed-weight selections of blue panicgrass measured at 8 time periods during the initial 72 hr of germination

Selection no.	Free sugars per g initial seed weight (mg)							
	Hours of imbibition							
	0	6	12	24	36	48	60	72
				Heavy selections				
4	11.6 ab*	10.8 a	9.7 a	7.1 a	7.1 a	6.5 a	7.2 a	10.3 b
95	10.9 b	9.2 a	9.4 a	9.0 a	6.6 a	6.4 a	6.5 a	7.4 b
Mean	11.2 x	10.0 x	9.5 x	8.1 x	6.9 x	6.5 x	6.9 x	8.8 x
				Light selections				
72	12.6 a	12.5 a	12.4 a	10.6 a	8.4 a	8.8 a	11.7 a	15.6 a
62	12.2 ab	10.6 a	10.3 a	8.2 a	6.8 a	6.7 a	7.1 a	8.5 b
Mean	12.4 y	11.6 x	11.4 x	9.4 x	7.6 x	7.7 x	9.4 x	12.0 y

*Selection means and means of selections within the same column followed by the same letter are not significantly different at the .05 level according to Student-Newman-Keul's multiple range test

Extractable mitochondrial-protein on a per 100 seed basis (Table 11) was significantly higher for the mean of heavy seed-weight selections after 36 hr of imbibition. Selection 4 was consistently significantly higher than the light seed-weight selections, while selection 95 was significantly different only at 60 and 72 hr of imbibition. McDaniel (1969) reported a three-fold increase in mitochondrial protein of the scutellum of barley seedlings after 3 days germination. Blue panicgrass seedlings exhibited a 10 to 25% increase of mitochondrial protein after 3 days germination. This difference was attributed to utilization of the entire seedling for blue panicgrass. The endosperm of seed was reported to contain few mitochondria (Ching, 1972). The protein content of blue panicgrass increased up to 24 hr, then dropped between 24 and 36 hr with the exception of selection 95. Mitochondrial populations have been reported to undergo changes, that may be related to aging and degradation of the initial mitochondria and formation of new mitochondria, in castor bean tissue at approximately 5 days of germination (Akazawa and Beevers, 1957a, 1957b). The fluctuations in content of mitochondrial protein of blue panicgrass could relate to aging, degradation, and synthesis.

All four selections exhibited a decrease in mitochondrial protein at 60 hr of imbibition. The response was associated with coleoptile emergence and a concomitant decline in respiration rates (Table 7). Synthesis of a new mitochondrial population by the rapidly growing coleoptile would be expected, and the decline in mitochondrial protein content at this stage of imbibition could have represented a transition period in mitochondrial populations.

Table 11. Content of mitochondrial protein per 100 seed of two heavy and two light seed-weight selections of blue panicgrass measured at 7 time periods during the initial 72 hr of germination

Selection no.	Mitochondrial protein per 100 seed (μg)						
	Hours of imbibition						
	6	12	24	36	48	60	72
	Heavy selections						
4	1230 a*	1236 a	1432 a	1417 a	1755 a	1706 a	1657 a
95	974 a	1020 a	1198 a	1218 ab	1273 ab	1094 b	1349 a
Mean	1102 x	1128 x	1315 x	1317 x	1514 x	1400 x	1503 x
	Light selections						
72	749 a	781 a	1091 a	778 bc	977 b	702 c	803 b
62	821 a	788 a	987 a	772 c	951 b	625 c	786 b
Mean	785 x	784 x	1039 x	775 y	964 y	663 y	794 y

*Selection means and means of selections within the same column followed by the same letter are not significantly different at the .05 level according to Student-Newman-Keul's multiple range test

Content of mitochondrial protein expressed on a basis of a gram of unimbibed seed-weight (Table 12) showed a trend for higher protein content in light seed, although the difference was significant only at 24 hr of imbibition. McDaniel (1969) obtained similar results with barley seed-weight classes. The response suggests that heavy seed contained a greater content of mitochondria per seed, yet the heavy and light seed contained equivalent amounts of mitochondria per unit of actively growing tissue. A similar conclusion was reached for respiration rate in relation to seed weight.

Heavy seed-weight selections had significantly higher ATP(Table 13) and total adenylate phosphate content per 100 seed (Table 16, see p. 57) than light seed-weight selections throughout the initial 72 hr of germination. Content of ADP was significantly greater in unimbibed heavy seed and toward the end of the time periods of imbibition (Table 14). The response for the mean of heavy seed-weight selections was due primarily to the high ATP and ADP levels of selection 4. Levels of AMP were not significantly different among selections at any period during initial germination (Table 15).

The higher contents of adenylate for heavy seed were apparently associated with relative amounts of metabolically active and inactive tissue similar to the response discussed for respiration rate. Adenylate contents expressed on a gram seed-weight basis (Tables 17, 18, and 19) are approximately equivalent for heavy and light seed-weight selections.

The trends for the mean of the four selections showed ATP and ADP decreased during the first 6 hr of imbibition (Fig. 5). A greater

Table 12. Content of mitochondrial protein per gram of initial seed weight of two heavy and two light seed-weight selections of blue panicgrass measured at 7 time periods during the initial 72 hr of germination

Selection no.	Mitochondrial protein per g initial seed weight (mg)						
	Hours of imbibition						
	6	12	24	36	48	60	72
	Heavy selections						
4	10.1 a*	10.1 a	11.7 c	11.6 a	14.4 a	14.0 a	13.6 a
95	12.0 a	12.6 a	14.7 bc	15.0 a	15.7 a	13.5 a	16.6 a
Mean	11.0 x	11.4 x	13.2 x	13.3 x	15.0 x	13.7 x	15.1 x
	Light selections						
72	14.9 a	15.6 a	21.8 a	15.5 a	19.5 a	14.0 a	16.0 a
62	15.8 a	15.2 a	19.0 ab	14.8 a	18.3 a	12.0 a	15.1 a
Mean	15.4 x	15.4 x	20.4 y	15.2 x	18.9 x	13.0 x	15.6 x

*Selection means and means of selections within the same column followed by the same letter are not significantly different at the .05 level according to Student-Newman-Keul's multiple range test

Table 13. Content of adenosine triphosphate (ATP) per 100 seed of two heavy and two light seed-weight selections of blue panicgrass measured at 8 time periods during the initial 72 hr of germination

Selection no.	ATP per 100 seed (nmoles)							
	Hours of imbibition							
	0	6	12	24	36	48	60	72
				Heavy selections				
4	.26 a*	1.09 a	2.08 a	2.89 a	5.19 a	5.69 a	6.68 a	7.87 a
95	.29 a	.84 b	1.22 ab	2.01 a	2.54 b	2.55 b	2.22 b	3.31 b
Mean	.27 x	.96 x	1.65 x	2.45 x	3.86 x	4.12 x	4.45 x	5.59 x
				Light selections				
72	.11 a	.57 d	.67 b	1.54 a	2.10 b	2.62 b	2.61 b	4.20 b
62	.29 a	.69 c	.81 b	1.49 a	2.00 b	2.16 b	1.80 b	2.18 b
Mean	.20 x	.63 y	.74 y	1.51 x	2.05 y	2.39 y	2.20 y	3.19 y

*Selection means and means of selections within the same column followed by the same letter are not significantly different at the .05 level according to Student-Newman-Keul's multiple range test

Table 14. Content of adenosine diphosphate (ADP) per 100 seed of two heavy and two light seed-weight selections of blue panicgrass measured at 8 time periods during the initial 72 hr of germination

Selection no.	ADP per 100 seed (nmoles)							
	Hours of imbibition							
	0	6	12	24	36	48	60	72
	Heavy selections							
4	1.04 a*	1.93 a	2.63 a	2.33 a	4.95 a	4.38 a	4.93 a	5.90 a
95	.86 ab	1.57 a	1.81 b	2.44 a	2.26 b	1.96 a	2.34 b	3.87 ab
Mean	.95 x	1.75 x	2.22 x	2.38 x	3.60 x	3.17 x	3.63 x	4.88 x
	Light selections							
72	.65 b	1.12 a	1.07 c	1.39 a	2.07 bc	1.59 a	2.12 b	2.72 b
62	.37 c	.94 a	.96 c	1.63 a	1.27 c	1.54 a	1.58 b	2.31 b
Mean	.51 y	1.03 x	1.01 y	1.51 x	1.67 y	1.56 x	1.85 y	2.51 y

*Selection means and means of selections within the same column followed by the same letter are not significantly different at the .05 level according to Student-Newman-Keul's multiple range test

Table 15. Content of adenosine monophosphate (AMP) per 100 seed of two heavy and two light seed-weight selections of blue panicgrass measured at 8 time periods during the initial 72 hr of germination

Selection no.	AMP per 100 seed (nmoles)							
	Hours of imbibition							
	0	6	12	24	36	48	60	72
					Heavy selections			
4	2.54 a*	.37 a	1.09 a	1.29 a	.47 a	1.46 a	.30 a	.53 a
95	2.46 a	.48 a	.47 a	1.23 a	.50 a	.34 a	.17 a	.52 a
Mean	2.50 x	.42 x	.78 x	1.26 x	.48 x	.90 x	.23 x	.52 x
					Light selections			
72	2.13 a	.68 a	.77 a	1.34 a	.26 a	.81 a	.09 a	.75 a
62	1.97 a	.56 a	.66 a	1.12 a	.96 a	.38 a	.38 a	.63 a
Mean	2.05 x	.62 x	.71 x	1.23 x	.61 x	.59 x	.23 x	.69 x

*Selection means and means of selections within the same column followed by the same letter are not significantly different at the .05 level according to Student-Newman-Keul's multiple range test

Table 16. Content of total adenylate phosphates (TAP) per 100 seed of two heavy and two light seed-weight selections of blue panicgrass measured at 8 time periods during the initial 72 hr of germination

Selection no.	TAP per 100 seed (nmoles)							
	Hours of imbibition							
	0	6	12	24	36	48	60	72
	Heavy selections							
4	3.84 a*	3.39 a	5.80 a	6.51 a	10.61 a	11.53 a	11.91 a	14.30 a
95	3.61 a	2.89 b	3.50 b	5.68 a	5.30 b	4.85 b	4.73 b	7.70 b
Mean	3.72 x	3.14 x	4.65 x	6.09 x	7.95 x	8.19 x	8.32 x	11.00 x
	Light selections							
72	2.89 ab	2.37 c	2.51 b	4.27 a	4.43 b	5.02 b	4.82 b	7.67 b
62	2.60 b	2.19 c	2.42 b	4.25 a	4.23 b	4.08 b	3.76 b	5.13 b
Mean	2.74 y	2.28 y	2.47 y	4.26 x	4.33 y	4.55 y	4.29 y	6.40 y

*Selection means and means of selections within the same column followed by the same letter are not significantly different at the .05 level according to Student-Newman-Keul's multiple range test

Table 17. Content of adenosine triphosphate (ATP) per gram of initial seed weight of two heavy and two light seed-weight selections of blue panicgrass measured at 8 time periods during the initial 72 hr of germination

Selection no.	ATP per g initial seed weight (nmoles)							
	Hours of imbibition							
	0	6	12	24	36	48	60	72
					Heavy selections			
4	2.13 a*	8.94 b	17.06 a	23.71 a	42.57 a	46.68 a	54.80 a	64.60 a
95	3.57 a	10.34 ab	15.03 a	24.75 a	31.28 a	31.40 a	27.34 b	40.76 a
Mean	2.85 x	9.64 x	16.04 x	24.23 x	36.92 x	39.04 x	41.04 x	52.68 x
					Light selections			
72	2.20 a	10.96 ab	13.19 a	29.97 a	40.96 a	51.26 a	51.24 a	82.68 a
62	5.58 a	13.77 a	15.90 a	29.31 a	39.37 a	42.60 a	35.09 ab	42.43 a
Mean	3.89 x	12.36 y	14.54 x	29.64 x	40.16 x	46.92 x	43.16 x	62.65 x

*Selection means and means of selections within the same column followed by the same letter are not significantly different at the .05 level according to Student-Newman-Keul's multiple range test

Table 18. Content of adenosine diphosphate (ADP) per gram of initial seed weight of two heavy and two light seed-weight selections of blue panicgrass measured at 8 time periods during the initial 72 hr of germination

Selection no.	ADP per g initial seed weight (nmoles)							
	Hours of imbibition							
	0	6	12	24	36	48	60	72
	Heavy selections							
4	8.53 ab*	15.83 a	21.57 a	19.11 a	40.61 a	35.91 a	40.44 a	48.40 a
95	10.59 ab	19.33 a	22.29 a	30.05 a	27.83 b	24.13 a	28.82 a	47.66 a
Mean	9.56 x	17.58 x	21.93 x	24.57 x	34.22 x	30.02 x	34.62 x	48.03 x
	Light selections							
72	12.97 a	21.53 a	20.97 a	27.10 a	40.45 a	31.21 a	41.78 a	53.30 a
62	7.11 b	18.76 a	18.77 a	32.29 a	24.98 b	30.25 a	30.94 a	45.08 a
Mean	10.04 x	20.14 x	19.87 x	29.69 x	32.71 x	30.73 x	36.36 x	49.29 x

*Selection means and means of selections within the same column followed by the same letter are not significantly different at the .05 level according to Student-Newman-Keul's multiple range test

Table 19. Content of adenosine monophosphate (AMP) per gram of initial seed weight of two heavy and two light seed-weight selections of blue panicgrass measured at 8 time periods during the initial 72 hr of germination

Selection no.	AMP per g initial seed weight (nmoles)							
	Hours of imbibition							
	0	6	12	24	36	48	60	72
				Heavy selections				
4	20.84 b*	3.03 a	8.94 a	10.85 a	3.85 b	11.98 a	2.46 ab	4.35 a
95	30.29 ab	5.91 a	5.78 b	15.15 a	6.16 ab	4.19 a	2.09 b	6.40 a
Mean	25.56 x	4.47 x	7.36 x	12.86 x	5.00 x	8.08 x	2.27 x	5.37 x
				Light selections				
72	42.51 a	13.08 a	15.16 a	26.02 a	5.06 ab	16.10 a	1.73 b	14.85 a
62	37.88 a	11.18 a	13.06 a	22.22 a	18.79 a	7.37 a	7.46 a	12.66 a
Mean	40.19 y	12.07 x	14.11 y	24.12 x	11.92 x	11.73 x	4.59 x	13.75 x

*Selection means and means of selections within the same column followed by the same letter are not significantly different at the .05 level according to Student-Newman-Keul's multiple range test

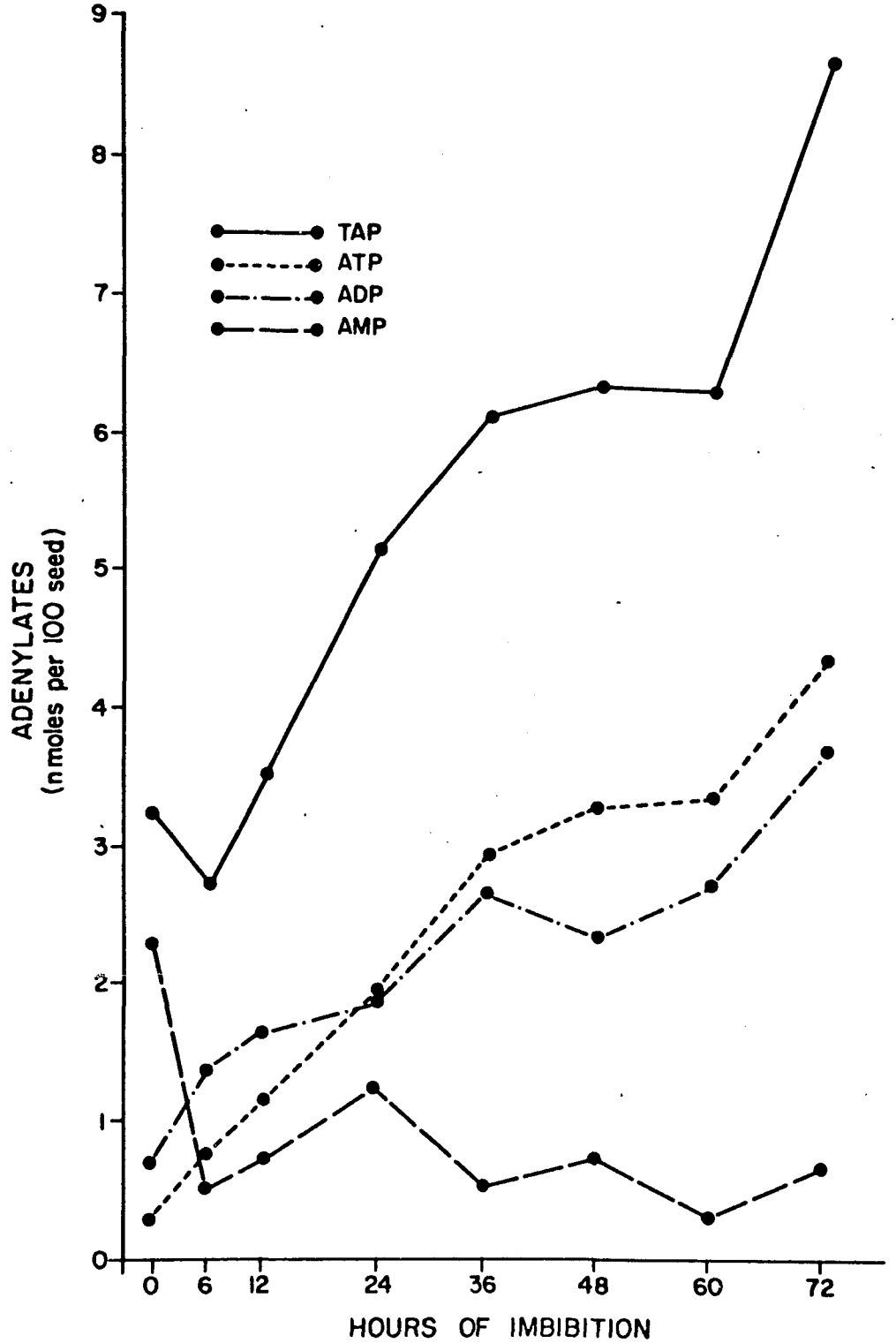

Fig. 5. Content of ATP, ADP, AMP, and total adenylate phosphates (TAP) per 100 seed of four seed-weight selections of blue panicgrass measured during the initial 72 hr of germination

decrease in AMP level than the sum of the increases for ATP and ADP was responsible for the decline in total adenosine phosphates at 6 hr. Pradet et al. (1968) obtained somewhat similar trends for seed of germinating lettuce. Content of AMP decreased by 50% after 30 min of imbibition. They found that ATP represented 80% of the total adenylate nucleotides after one hour, and ADP levels remained low and constant up to 20 hr of germination. Content of ADP of blue panicgrass was greater than ATP content until 24 hr of imbibition. Adenylate kinase mediated conversion of AMP to ADP was observed within 1 hr of imbibition in lettuce seed. Similar reactions might be expected to occur in blue panicgrass, but the decline in AMP due to adenylate kinase conversion would be approximately equal to the sum of ATP and ADP increases (Brown, 1965). The additional decrease in AMP content could be attributed to its conversion to other nucleotide monophosphates.

The stabilization of ATP, ADP, and TAP content during the 36 to 60 hr period (Fig. 5) coincided with radicle and coleoptile emergence. Ching and Kronstad (1972) reported a similar pattern at radicle and coleoptile emergence for wheat seed during germination. They suggested that requirement for cellular energy by these events resulted in greater utilization than synthesis of adenylate phosphates.

Rate of ATP increase during the first 6 hr of imbibition was 140, 90, 80, and 60 pmoles per hr per 100 seed for selections 4, 95, 72, and 62 respectively (Table 13). Rates of ATP formation demonstrated the relationship between energy available during early imbibition and subsequent growth rates. Absolute growth rates from 6 to 72 hr, which were previously discussed, separated the selections into

three vigor groups similar to the rate of ATP increase. The absolute growth rate for selection 72 was greater than that for selection 95 during this period, while selection 95 exhibited a more rapid rate of ATP increase.

Rate of ATP formation during the 0 to 6 hr period was associated with greater initial seed weight and might be a function of the greater content of mitochondrial protein (Table 11) and respiration rate (Table 7). Ching (1973a) obtained a highly significant association between seed weight and ATP content per seed ($r = +.90$) for annual ryegrass (Lolium multiflorum L.).

Initial seed-weight per 100 seed was 31 mg greater for selection 95 than selection 72. Rate of ATP increase during the first 6 hr of imbibition was slightly greater for selection 95. In contrast, the absolute growth-rates from 48 to 72 hr were 0.41 and 0.62 mg per hr for selections 95 and 72, respectively, and was primarily responsible for the growth rate difference calculated over the 6 to 72 hr imbibition period. The difference in growth can be attributed to differences in metabolism between the two selections. Content of ATP of selection 72 surpassed that of selection 95 at the 48 hr measurement (Table 13), although the difference was not significant. The rate of increase of free sugars from 48 to 72 hr, calculated from Table 9, was more rapid for selection 72 (14 and 3 µg per hr for selections 72 and 95, respectively). In addition, the respiration rate of selection 72 surpassed that of selection 95 at 72 hr of imbibition (Table 7). The responses suggested that selection 72 exhibited earlier and a more rapid rate of endosperm hydrolysis which provided additional

respiratory substrate. Utilization of this substrate was expressed by enhanced ATP formation and absolute growth rate.

Whalley and McKell (1967) suggested that rate of endosperm hydrolysis was limiting to growth rate for some Phalaris sp. Sarkissian et al. (1964) reported alpha-amylase activity for a heterotic corn hybrid increased at a greater rate and reached a higher level of activity than the parent lines. Examination of Fig. 4 indicated alpha-amylase synthesis may be initiated in blue panicgrass at the 36 to 60 hr stage of germination. Differential rates of alpha-amylase synthesis or level of activity for selections 95 and 72 could partially explain their similarity in growth rate from 6 to 72 hr.

Selection 95 also exhibited a decline in TAP content (Table 16) from 24 to 60 hr of imbibition, caused by decreased ADP and AMP content (Tables 14 and 15). ATP content increased from 24 to 36 hr (Table 13). The decrease in free sugar content (Table 9) and increased respiration rate (Table 7) for selection 95 over this time period suggests phosphorylation of ADP was not limiting. The continued decline in ADP content and subsequent decrease in ATP content after 36 hr of imbibition might suggest a lowered capacity for adenylate nucleotide formation. Comparison of dry-matter production for selections 95 and 72 (Table 3) indicated that selection 95 apparently overcame this effect after 72 hr.

Energy charge values were not significantly different for the four selections except at 6 hr of imbibition (Table 20). Selection 72 was significantly lower than the other selections at this time. Selections for heavy seed weight showed a trend toward higher energy charge

Table 20. Energy charge values of two heavy and two light seed-weight selections of blue panicgrass measured at 8 time periods during the initial 72 hr of germination

Selection no.	Energy charge value: Hours of imbibition 0	6	12	24	36	48	60	72
				Heavy selections				
4	.21 a*	.61 a	.59 a	.64 a	.72 a	.68 a	.77 a	.76 a
95	.21 a	.57 a	.60 a	.58 a	.69 a	.71 a	.72 a	.69 a
Mean	.21 x	.59 x	.59 x	.61 x	.70 x	.69 x	.74 x	.72 x
				Light selections				
72	.15 a	.49 b	.49 a	.53 a	.72 a	.72 a	.76 a	.73 a
62	.18 a	.56 a	.54 a	.57 a	.62 a	.70 a	.68 a	.64 a
Mean	.16 x	.52 y	.51 x	.55 x	.67 x	.71 x	.72 x	.68 x

*Selection means and means of selections within the same column followed by the same letter are not significantly different at the .05 level according to Student-Newman-Keul's multiple range test

the first 24 hr of imbibition. An increase in number of replications might show significance for energy charge values. Ching and Kronstad (1972) demonstrated higher energy charge values for a more vigorous wheat cultivar at 40, 44, and 48 hr of germination. The significantly lower energy charge for selection 72 contradicted its seedling vigor categorization. This response suggests the relationship between seedling vigor and energy charge during germination may not be of the magnitude required for its use as a selection tool in blue panicgrass.

Comparison of energy charge values of unimbibed seed of five heavy and five light seed-weight selections revealed significant differences between seed-weight selections (Fig. 6). Energy charge values of heavy seed selections were 26% greater than light seed. The findings suggested that heavy seed in the dormant state contained a greater proportion of the adenylate phosphate compounds stored in an "energy rich" form. When energy charge of unimbibed seed was compared with dry matter production (Table 3), a positive relationship was determined. Additional studies of the energy charge of unimbibed seed of equal seed weight but with different forage production potential might elucidate the potential use of the energy charge as a selection tool for seedling vigor.

Selected correlation coefficients of the associations between ATP, ADP, and TAP with fresh weight demonstrated the effect of seed weight on their contents per 100 seed (Table 21). Energy charge was not significantly associated with fresh weight for the four selections examined during the initial 72 hr of germination.

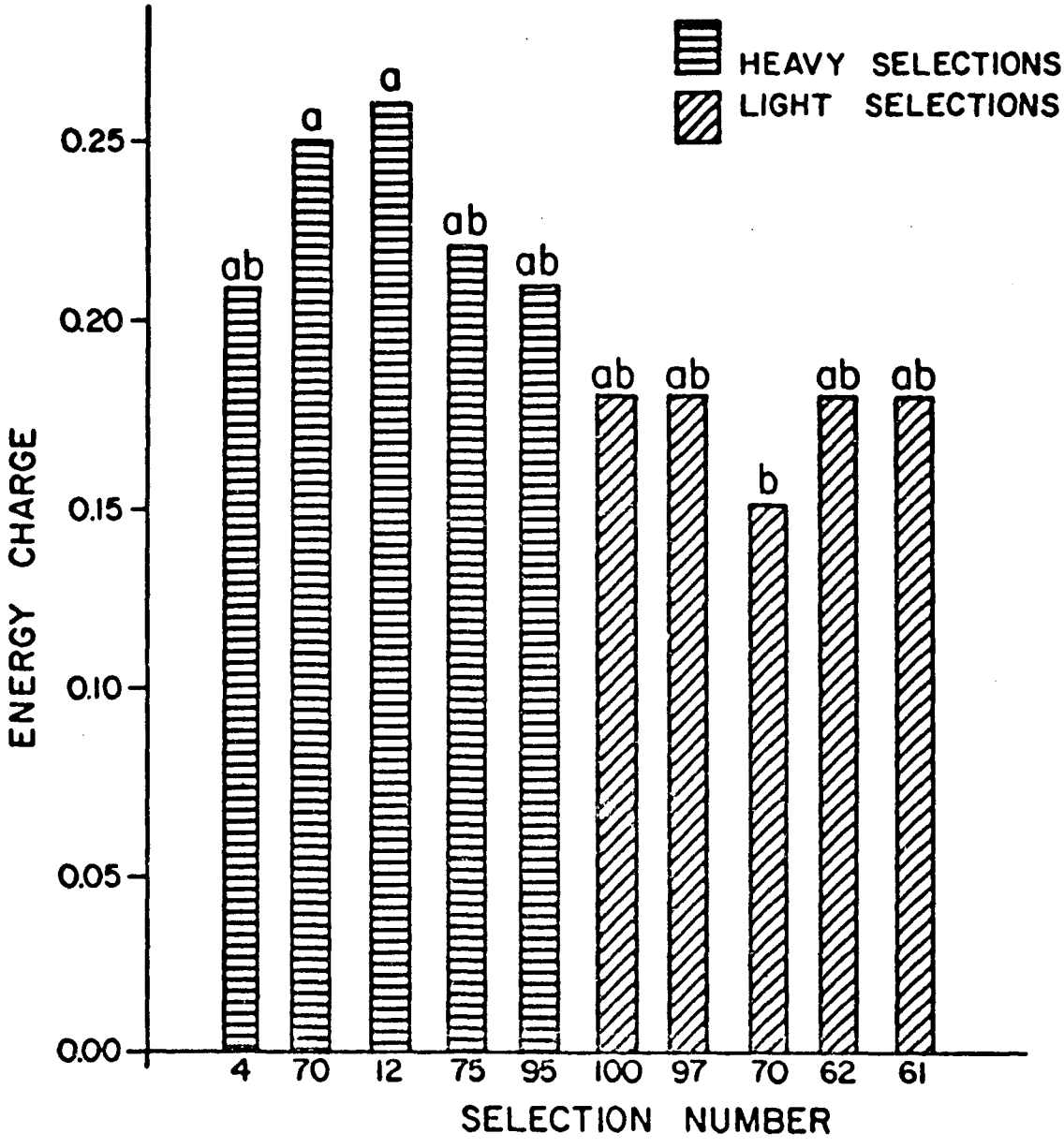

Fig. 6. Energy charge values of unimbibed seed of five heavy and five light seed-weight selections of blue panicgrass. Bars with same letter are not significantly different at the .05 level according to Student-Newman-Keul's multiple range test.

Table 21. Correlation coefficients between several variables per 100 seed of four seed-weight selections of blue panicgrass measured at 7 time periods during the initial 72 hr of germination

Components	Respiration	ATP	ADP	AMP	TAP	Energy charge
Fresh weight	.34	.68*	.77*	.04	.73*	.38
Respiration		.38	.37	-.06	.36	.30
ATP			.87*	-.01	.95*	.61*
ADP				-.06	.91*	.53*
AMP					.24	-.67*
TAP						.40

*Significant at the 5% level

Inflorescence Photosynthesis and Respiration

Photosynthetic CO_2 fixation by inflorescences of heavy seed-weight selections was greater than that of light seed-weight selections during seed development (Fig. 7). Significant differences were obtained at anthesis and dough stages for some selections (Table 22). Respiratory CO_2 evolution by inflorescences was greater for light seed-weight selections until late anthesis. At this stage of development the rates were similar for all selections (Fig. 8). The respiratory rates were significantly different for some selections during anthesis (Table 23).

The decline in photosynthetic rates of blue panicgrass selections after early anthesis were similar to those reported for wheat (Carr and Wardlaw, 1965; Evans and Rawson, 1970). Similarly, the decline of respiration rate after early anthesis obtained for blue panicgrass was also reported for wheat (Carr and Wardlaw, 1965). Maximum respiratory rate for wheat occurred at anthesis.

Photosynthetic rates were equivalent to or greater than respiration rates after the inflorescence emerged. However, the difference between photosynthetic and respiratory rates was greater for heavy seed-weight selections than for light seed-weight selections. This was demonstrated by the ratio of photosynthetic rate to respiration rate, P:R, (Table 24). Average P:R ratios for the four growth stages demonstrated a trend for some significantly greater values for heavy seed-weight selections (Fig. 9).

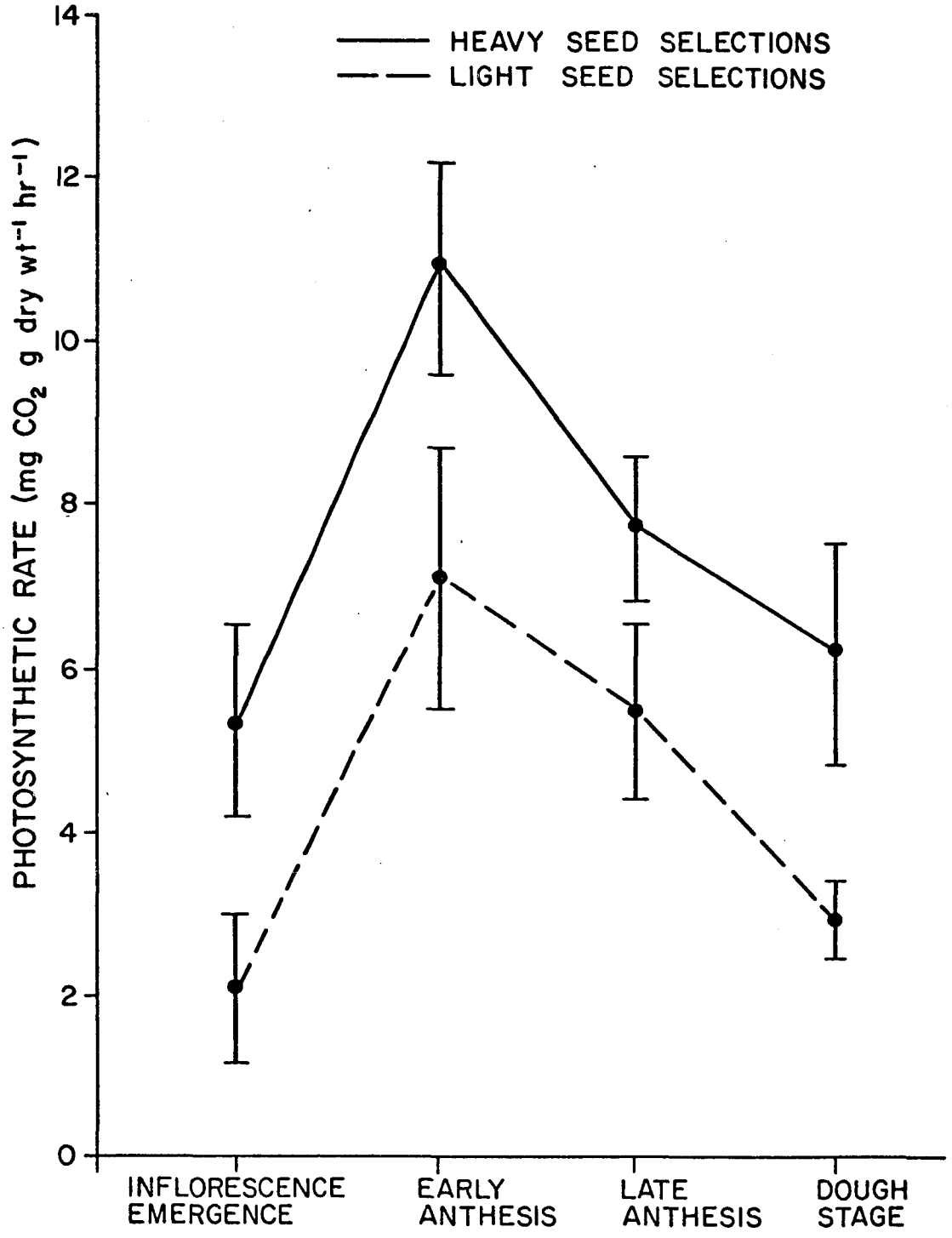

Fig. 7. Photosynthetic rates of inflorescences of five heavy and five light seed-weight selections of blue panicgrass measured at four growth stages. Vertical line at each mean represents one standard error of the mean.

Table 22. Photosynthetic rates of inflorescences of five heavy and five light seed-weight selections of blue panicgrass measured at four growth stages

Selection no.	Photosynthetic rate (mg CO_2 g dry wt.$^{-1}$ hr^{-1})			
	Growth stage			
	Inflorescence emergence	Early anthesis	Late anthesis	Dough stage
			Heavy selections	
4	3.43 a*	9.39 bc	4.78 ab	3.48 ab
70	2.70 a	9.88 bc	8.52 b	5.57 ab
12	7.06 a	12.61 bc	9.85 b	9.01 b
75	9.26 a	14.85 c	7.43 ab	3.23 ab
95	4.05 a	8.01 bc	7.90 ab	9.53 b
			Light selections	
100	.78 a	1.04 a	1.53 a	1.53 a
66	.94 a	10.60 bc	7.44 ab	4.16 ab
72	1.40 a	5.80 ab	4.77 ab	1.69 a
62	4.91 a	11.77 bc	7.72 ab	3.62 ab
61	2.62 a	6.28 ab	6.44 ab	3.62 ab

*Means in the same column followed by the same letter are not significantly different at the .05 level according to Student-Newman-Keul's multiple range test

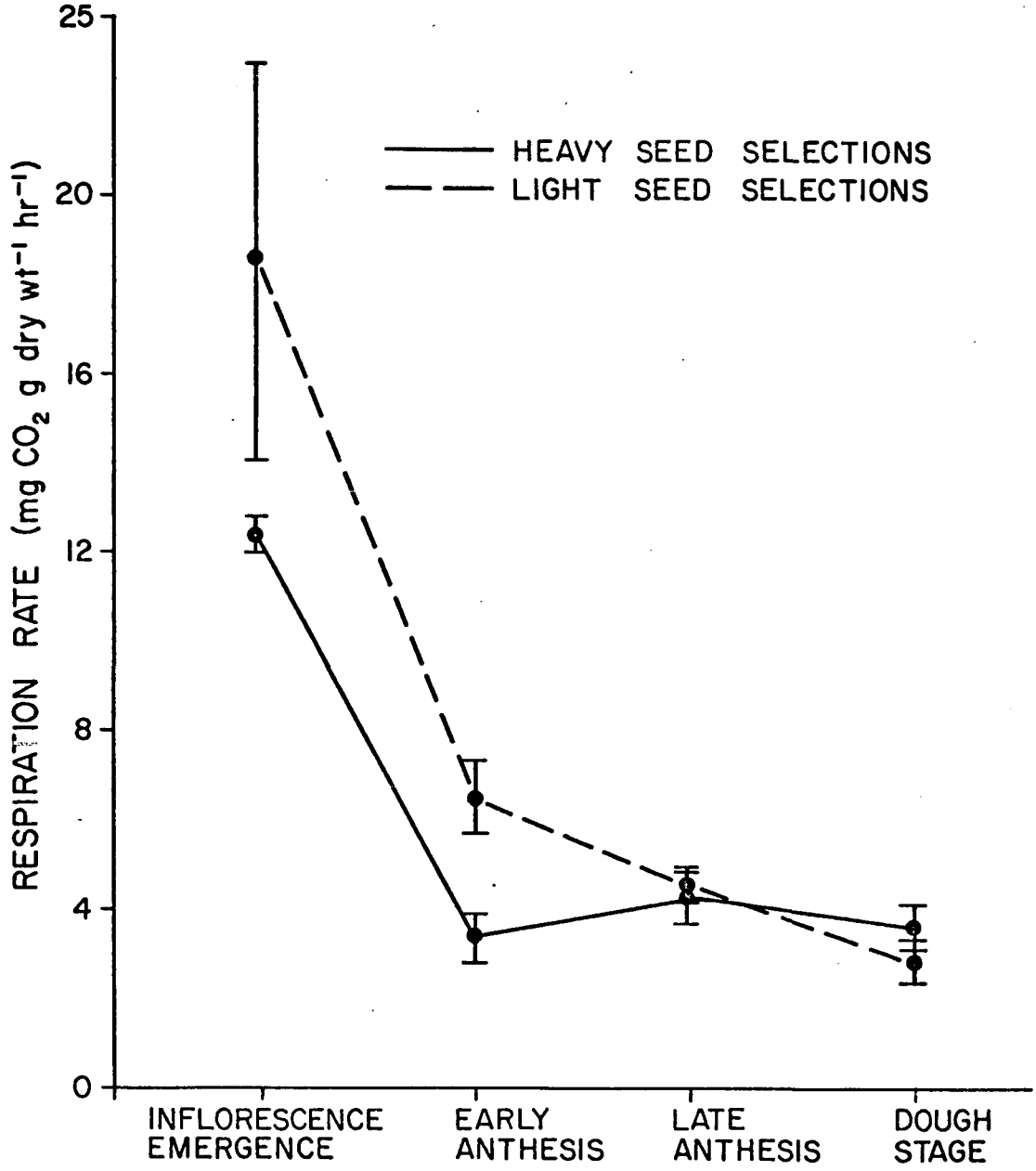

Fig. 8. Respiration rates of inflorescences of five heavy and five light seed-weight selections of blue panicgrass measured at four growth stages. Vertical line at each mean represents one standard error of the mean.

Table 23. Respiration rates of inflorescences of five heavy and five light seed-weight selections of blue panicgrass measured at four growth stages

Selection no.	Respiration rate (mg CO_2 g dry wt.$^{-1}$ hr^{-1})			
	Growth stage			
	Inflorescence emergence	Early anthesis	Late anthesis	Dough stage
			Heavy selections	
4	11.48 a*	3.62 abc	3.94 abc	4.07 a
70	10.93 a	2.45 a	5.16 bc	4.48 a
12	12.77 a	4.89 abc	3.68 abc	2.35 a
75	13.29 a	3.68 abc	4.40 abc	2.15 a
95	13.03 a	1.98 a	3.90 abc	4.37 a
			Light selections	
100	8.30 a	2.78 ab	2.06 a	2.72 a
66	29.66 a	6.99 bc	5.31 bc	3.22 a
72	9.68 a	8.18 c	4.05 abc	1.78 a
62	30.98 a	8.15 c	4.67 abc	3.18 a
61	15.72 a	6.11 abc	5.59 c	3.78 a

*Means in the same column followed by the same letter are not significantly different at the .05 level according to Student-Newman-Keul's multiple range test

Table 24. Ratio of photosynthetic to respiration rate (P:R) of five heavy and five light seed-weight selections of blue panicgrass measured at four growth stages

	P:R ratio			
	Growth stage			
Seed weight selections	Inflorescence emergence	Early anthesis	Late anthesis	Dough stage
Heavy	0.59	3.72	2.13	2.10
Light	0.15	1.04	1.08	1.09

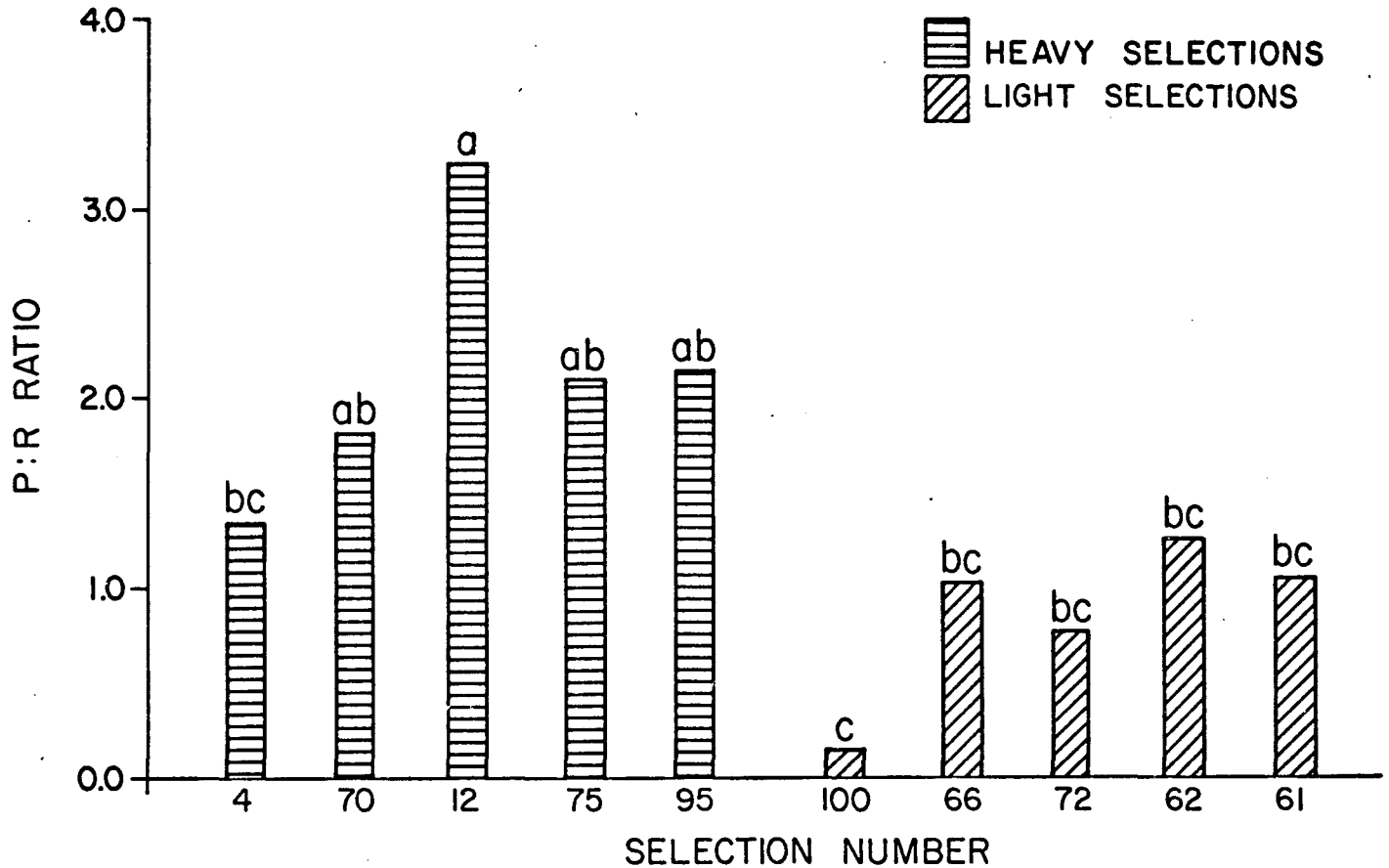

Fig. 9. Ratio of photosynthetic to respiration rate (P:R) of five heavy and five light seed-weight selections of blue panicgrass averaged over four growth stages. Bars with the same letter are not significantly different at the .05 level according to Student-Newman-Keul's multiple range test.

The findings suggested that one of the factors which contributed to lighter seed-weight of the blue panicgrass selections studied, was a lower contribution of photosynthetic assimilate by the inflorescence. This response was coupled with a higher respiration rate of the inflorescence during the early period of seed development and maturation. The net result was a decreased amount of assimilate available for storage in the developing seed, which was reflected by seed weight.

Translocation of assimilate from the vegetative portion of the plant was not studied but may be associated with development and determination of seed-weight differences of these selections. Growth hormones, such as cytokinins, may be related to movement of assimilate to developing seed (Burrows and Carr, 1970; Hall, 1973; Oritani and Yoshida, 1971). Seth and Wareing (1967) reported that hormones applied exogenously stimulate movement and accumulation of assimilate to the application site. Michael and Seiler-Kelbitsch (1972) reported that small barley caryopsis have lower cytokinin activity than large caryopsis. Difference in cytokinin activity was detectable before difference in size.

Regardless of the contribution of these factors to difference in seed weight for blue panicgrass, the higher overall P:R ratios found for heavy seed-weight selections must be considered an important factor.

Summary and Conclusions

Heavy seed-weight selections of blue panicgrass demonstrated significantly greater dry-matter production than light seed-weight

selections up to 54 days after planting when grown under a controlled environment. Mean relative growth rate tended to be higher for the light seed-weight selections. The trend suggested dry-matter production of light seed-weight selections could approach production of heavy seed-weight selections over an extended period. The hypothesis was made that genetic systems for seed weight and $\overline{RGR}$ during vegetative growth were separate.

Two heavy and two light seed-weight selections were studied during the initial 72 hr of germination. Heavy seed-weight selections exhibited significantly greater fresh weight, free sugar levels, ATP, ADP and total adenosine phosphate levels throughout the initial 72 hr of germination when expressed on a 100 seed basis. Mitochondrial protein when expressed on a per 100 seed basis was significantly higher for heavy seed-weight selections from 36 to 72 hr of germination.

Expression of the same data on the basis of unimbibed seed weight demonstrated that, for a given weight of seed, the difference between heavy and light seed was not generally significant. This response was attributed to proportionally more metabolically active tissue per unit weight of light seed-weight selections. Greater values obtained for heavy seed-weight selections on a 100 seed basis were apparently related to physically larger size.

Substrate levels of free sugar and adenylate phosphate contents per seed for the heavy seed were greater and reflected in a greater absolute rate of growth for heavy seed-weight selection 4. Heavy seed-weight selection 95 was similar in growth rate to the most vigorous

light seed-weight selection 72 during the later stages of germination. This was attributed partially to a decreased ability for this selection to mobilize endosperm reserves during the period studied. Thus, the relationship between seed weight and greater seedling vigor, determined by rate of increase of fresh weight, was not complete.

Rate of ATP increase during the first 6 hr of germination appeared to be related to the rate of fresh weight increase for the following 66 hr, and was apparently a function of mitochondrial protein content and respiration rate, which were associated with seed weight.

Trends in free sugar content were reflected in respiration rate and ATP levels. This demonstrated the importance of free sugars for respiratory substrate, and their potential involvement in seedling vigor determination.

Energy-charge values were not significantly different for the four selections except at 6 hr of imbibition. The significantly lower energy-charge value obtained for selection 72 contradicted its seedling vigor categorization, and raised questions about the relationship between seedling vigor and energy charge during germination. Heavy seed-weight selections showed a trend toward higher energy charge the first 24 hr of imbibition. Comparison of the energy charge values for unimbibed seed of five heavy and five light seed-weight selections revealed significant differences between selections. Energy-charge means for heavy seed were 26% greater than means for light seed. Heavy seed appeared to store a greater proportion of the adenylate nucleotides in a "high-energy" form. If this relationship occurs in heavy seed generally, it can be hypothesized that heavy seed have a higher level of biological

energy available for the catabolic and anabolic reactions which occur immediately after initiation of imbibition. This would allow a more rapid initiation of synthesis of the enzymatic and structural proteins required for subsequent seedling growth and development, and could be one explanation of the enhanced seedling vigor which has been observed for heavy seed. This suggests that energy charge measurements of unimbibed seed have potential as a selection tool for seedling vigor.

Although the use of seed-weight selections complicated evaluation of the seedling energy parameters examined in this study, the rate of ATP increase during the first 6 hr of germination and ATP content per seed warrant further examination as physiological selection criteria for seedling vigor.

Lower apparent photosynthesis and higher dark respiration of inflorescences were found for light seed-weight selections. This suggested that part of the difference in seed weight between the selections was due to a decreased amount of assimilate available for storage in developing seed of light seed-weight selections.

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