Effect of moisture and nitrogen on growth and yield of fababean (Vicia faba L.)

by David Allen Buss

A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science in Agronomy
Montana State University

Abstract:
Fababean (Vicia faba L.) is being investigated for its potential as a rotational crop with cereals in the Northwestern region of the United States. Fababean is capable of a symbiotic relationship with Rhizobium bacteria that can convert atmospheric nitrogen to a usable plant form, therefore decreasing the demand for nitrogen fertilizer. Soil moisture stress is one of the most limiting factors affecting fababean production in semiarid areas. The objectives of this research were to determine the effect of soil moisture and soil nitrogen at various levels on fababean growth and yield.

Field experiments were established in 1982 and 1983. Main treatments of increasing moisture (non-irrigation, low, intermediate and high irrigation) were applied with a modified line-source sprinkler system. Moisture treatments were divided into subplots of applied nitrogen and non-applied nitrogen.

Fababean roots penetrated to 135 cm in all irrigation regimes. Higher root density was found in deeper soil layers in the non and low irrigation regimes compared to intermediate and high regimes. Plant height, shoot dry weight, total plant N, seed yield, seed number pod-1, pod number plant-1, harvest index, grain and total yield WUE were not affected by N application. N application inconsistently affected 1,000 seed weight and leaf-water potential. Fababean utilized applied NO3- in preference to N2 -fixation when NH4NO3 was applied. Plant height, shoot dry weight, total leaf-water potential and total plant N increased with increased ET. Seed yield, harvest index and WUE increased in 1982 and decreased in 1983 with increased ET. The decrease in 1983 was attributed to the short growing season and the effect of moisture on delayed maturation.

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ABSTRACT

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CHAPTER I

INTRODUCTION

Cereal cropping systems in Montana have historically consisted of wheat and barley monocultures. Annual legume crops are being investigated for their potential in rotation with cereals to increase soil fertility; break weed, insect and disease cycles; and increase market stability.

Fababean (*Vicia faba* L.) is a low oil, high protein crop that can be used as either grain or forage for livestock or food for human consumption. Work in Canada has shown fababean to fit well in cereal crop rotations. Fababean is being investigated as an alternative and rotational crop in Montana.

Fababean, like other legume crops, is capable of a symbiotic relationship with *Rhizobium* bacteria. *Rhizobium* converts atmospheric nitrogen to a usable plant form, with the plant providing carbohydrates for the bacteria. Fababean is self-sufficient from symbiotic nitrogen (N_2)-fixation in low NO_3^- soils (Salih, 1980; Sprent and Bradford, 1977). Therefore, fababean may decrease the demand for nitrogen fertilizer.

Fababean is well adapted to a cool climate and short growing season common in Montana. Its production in Montana should be limited either to irrigated areas or where rainfall is above 38 cm (Lockerman et al., 1982). However, limited research information is available in Montana on irrigation management of fababean.

Soil moisture stress is one of the most limiting factors affecting fababean production in Montana. This study was initiated to determine the effect of: (1) soil moisture levels on growth and yield of fababean; and (2) soil nitrogen at various soil moisture levels on growth and yield of fababean.

CHAPTER II

LITERATURE REVIEW

Crop

Fababean (*Vicia faba* L.) is an Old World crop referred to as the bean of antiquity. Probably native to the Near East, fababean is now cultivated in Europe, South America, North Africa, China, Asia and more recently in Canada and the United States. China is the leading producer of fababean, with an estimated production of 4,660,000 metric tons in 1975 (Duke, 1981). In 1975, Switzerland reported the highest yields with 4,000 kg ha^{-1} (Duke, 1981). Fababean was introduced into Canada in 1972 and production has increased steadily (Anonymous, 1975; Rowland and Drew, n.d.).

Fababean is classified into three groups; major, minor and equina. The small to medium seeded cultivars are grown for livestock feed and belong to the minor and equina groups, while the larger seeded cultivars are used for human consumption and belong to the major group (Duke, 1981; Witcombe, 1982). Common names for fababean include broadbean, horsebean, fava bean, Windsor bean, tickbean and Scotchbean (Duke, 1981; Janick et al., 1981).

Fababean is a coarse, upright annual legume with indeterminate growth (Duke, 1981). It has large, unbranched, hollow stems 0.3 to 2 m tall, with 1 or more stems from the base (Duke, 1981). The leaves are compound, usually having 6 large, broad, oval leaflets (Duke, 1981). Indeterminate flowering is prolific with a limited number of set pods (Anonymous, 1975). The white axillary flowers with dark purple markings are born on short pedicels in clusters of 1 to 5 (Duke, 1981). Each flower cluster produces one to four pods 8-20 cm long, 10-30 cm broad, containing 3 to 4 seed initiating approximately 20 cm above ground level (Duke, 1981).

The smooth seed may be either oblong, oval, flattened or rounded. Seed color varies from bright reddish brown, light to dark greenish brown, light to dark purple, and may be obscurely mottled or dotted with colors similar to the base colors (Duke, 1981). Cultivated varieties in the U.S. and Canada are pale buff to buff in color when mature. Seed size varies from 350,000 to 550,000 mg per thousand seed (Anonymous, 1975). Although fababean are mainly self-pollinated, they may be highly cross-pollinated given favorable conditions and appropriate insect populations (Anonymous, 1975; Duke, 1981).

Rooting depth ranges from 80 to 120 cm with 70 to 80% of the root mass in the soil plow-depth layer (Hebblethwaite, 1982; Naimark, 1976). Growth rate of the root system exceeds that of the stem up to the flowering stage (Naimark, 1976). Sprent et al. (1977) reported that root growth ceases when the pods begin to fill.

Fababean is exposed to varied photoperiod, precipitation and thermal regimes since its cultivation ranges from approximately 9 N to more than 40 N longitude and from near 0 to more than 2,000 m above sea level (Saxena, 1982). It is grown as a winter-season crop in subtropical regions with mild winters, at high elevations under tropical conditions, and as a spring-season crop in temperate areas.

Fababean is best adapted to moist growing areas and does best under relatively cool growing conditions (Anonymous, 1975; Rowland and Drew, n.d.). Dantuma et al. (1982) evaluated eight fababean cultivars grown at 22 environments in Western Europe. They concluded that favorable factors for optimum fababean production are moderate temperatures, average amounts of solar radiation and the absence of a long, dry period. They also concluded that water supply was probably the major yield determining factor.

Keatinge and Shaykewich (1977), in a study at 9 locations in Manitoba, reported that seasonal soil-heat accumulation (above 5 C) needs to be greater than 1,000 degree days for satisfactory dry matter production. High ambient temperatures (above 20 C) appeared to be deleterious to crop growth. Hot, dry conditions with low humidity may have a detrimental effect on seedset (Anonymous, 1975; Lockerman et al., 1982; Rowland and Drew, n.d.; Skjelvåg, 1981a). Skjelvåg (1981a) found that dry matter and seed yields decreased with increasing temperature. Growth was mainly affected by day temperature while night temperature had less effect (Skjelvåg, 1981b).

The amount of solar radiation has a differential effect on fababean growth. Increasing insolation reduced plant height, especially at high day temperatures (Skjelvåg, 1981e). Crude fiber and nitrogen content increased with temperature at low insolation levels, but decreased at high levels (Skjelvåg, 1981d). Skjelvåg (1981c) also reported increased seed yields with high insolation during early growth and flowering. However, yields decreased with increased temperature and soil moisture deficit.

Frost tolerance and growing season length are comparable to barley (Lockerman et al., 1982). Time needed for fababean maturation varies because of its indeterminate growth habit. Maturity ranges from 100 to 115 days depending on cultivar, location and year (Lockerman et al., 1982). Late maturity of fababean can be largely offset by early planting since the seedlings are frost tolerant (Anonymous, 1975). Additionally, some fababean cultivars can withstand low Fall temperatures. 'Ackerperle' was not frost killed until the temperature dropped below -4 C in Bozeman, MT during the Fall (1981) season (Lockerman et al., 1982).

Fababean is grown in North America primarily as a high protein supplement or high protein silage for on-the-farm use or for sale to local markets (Lockerman et al., 1982). When supplemented with methionine, fababean is an excellent protein source for livestock (Anonymous, 1975; Lockerman, et al., 1982; Rowland and Drew, n.d.).

Protein in the present world collection ranges from 6.9 to 34.4% (El Sayed et al., 1982). Protein content of commonly cultivated cultivars often approaches 30% with a low fat content of 1-2% (Marquardt, 1978). Fababean contains 60% less crude protein than soybean (*Glycine Max* (L.) Merrill) meal, but 27 and 147% more than field peas (*Pisum sativum* L. subsp. *arvense* L. Poir.) and barley (*Hordeum vulgare* L.), respectively (Marquardt, 1978). Digestible energy content of fababean is similar to or slightly less than that of corn (*Zea mays* L.) silage (Ingalls et al., 1976; Ingalls et al., 1979). According to Blair (1977), approximately 900 g of fababean are equivalent in feeding value to 450 g of soybean meal plus 450 g of barley.

Whole-plant fababean silage intake by dairy heifers and lactating cows is significantly higher than that of grass/legume silage or grass silage (Bareeba, 1980; Ingalls et al., 1976; Ingalls et al., 1979). Marquardt (1978) reported that daily liveweight gains of calves fed fababean, corn and grass/legume silage were 1544, 1317 and 1226 g, respectively. However, Ingalls et al. (1976 and 1979) reported no difference in average daily liveweight gains in dairy heifers fed fababean or grass/legume silage.

Milk yields and milk composition were not significantly different when dairy cows were fed grass/legume or corn silage untreated or treated with urea or Pro-sil or whole-plant fababean silage untreated, direct cut, wilted or treated with formaldehyde (Bareeba, 1980). Ingalls et al. (1980) also found no significant differences in milk yield when fababean replaced soyameal in the diet. Additionally, with similar amounts of dietary fiber, replacing soya by fababean had no apparent effect on milk fat, but milk protein was significantly reduced.

Thorlacius and Beacom (1981) reported high energy digestibility and voluntary intake of whole crop fababean silage by lambs. Additionally, dry matter intake and average daily gain was significantly greater for lambs given fababean than those fed on corn or oat (*Avena sativa* L.) silage (Thorlacius and Beacom, 1981). Ingalls et al. (1976) reported that dry matter digestibility of silages for sheep was 60.3, 59.7, 65.9 and 69.0% for barley, grass, corn and fababean, respectively.

Mateos and Puchal (1981) studied the nutritional value of fababean for swine and suggested that fababean may be used safely in diets for starting and finishing pigs at 20% supplemental levels.

Fababean is also being utilized as a protein source in human diets. In Egypt, fababean occupies a prominent position in the national diet (Gabrial, 1982). In 1978, fababean provided 250,000,000 of the 376,000,000 kg of pulse, nut and seed crops produced in Egypt (Gabrial, 1982). Eighty-one and six-tenths g of the daily per capita protein intake of 94.9 g is of vegetable origin (Gabrial, 1982). Approximately 14 g of fababean is consumed daily per capita accounting for 3 g of protein (Gabrial, 1982).

Fababean in Egypt are prepared and eaten in several ways. Green immature seeds are eaten fresh, fresh immature pods are boiled and dried seeds may either be stewed, germinated and cooked, or soaked and made into a paste and fried (Gabrial, 1982).

Fababean seed amino acid balance is good, except for the sulphur amino acids, in particular methionine (El Mubarak et al., 1982). El Mubarak et al. (1982) also concluded that 100 g of germinated, cooked or baked fababean would supply, with the exception of methionine and threonine, a major proportion of the human daily requirement for essential amino acids.

Water Stress Effects on Seed Yield

According to Sprent et al. (1977), water supply may be a more important factor controlling fababean yield than either solar radiation or plant competition. Montana fababean production should be limited either to the irrigated areas or areas where rainfall exceeds 38 cm (Lockerman et al., 1982). Seed yield rarely exceeds 1344 kg ha^{-1} in Montana when precipitation is below 38 cm.

Seed yield increases with increased irrigation (El Nadi, 1970; Farah, 1981a; Keatinge and Shaykewich, 1977; Krogman et al., 1980; McEwen et al., 1981; Olivares and Recalde-Martinez, 1982; Stock and El Naggar, 1980). Yield may decrease as a result of water stress at any growth stage, however, some growth stages are more sensitive than others (El Nadi, 1970). Most researchers agree that the greatest detrimental effect of moisture stress is during the early reproductive development phase (El Nadi, 1970; Keatinge and Shaykewich, 1977; Stock and El Naggar, 1980).

El Nadi (1970) applied four irrigation treatments [(wet, wet), (dry, wet), (wet, dry) and (dry, dry)] to fababean at two different growth phases from emergence to early fruit set and from early fruit set to harvest. Plants not stressed had the highest number of pods plant^{-1} and seed weight. Plants stressed early had higher yields than plants stressed late due to high seed weight and more seeds pod^{-1}. The number of pods plant^{-1} were higher in the later stressed plants.

Annual legume crops other than fababean have not shown consistent results from water applications. Zablotowicz et al. (1979) working with cowpea (*Vigna unguiculata* (L.) Walp.) and Robertson et al. (1980) with soybean found no difference in yield between well-watered and droughted treatments. Summerfield et al. (1976) reported that repeated wilting prior to flowering of cowpea markedly reduced seed yields compared with the unstressed controls, whereas wilting after flowering did not reduce yield. Turk et al. (1980a) reported no effect of water stress during the vegetative stage when environmental conditions were conducive to rapid recovery in field grown cowpea. However, water stress during flowering and pod fill reduced yields. Other studies have found that irrigation of pea (*Pisum sativum* L.) and soybean at pod fill increased yield more than irrigation at any other growth stage (Ashley and Ethridge, 1977; Doss et al., 1973; Miller et al., 1977; Pumphrey and Schwanke, 1974; Rathore et al., 1981). Mederski and Jeffers (1972) reported that soil moisture effects on soybean seed yield varied among cultivars.

Water Stress Effects on Seed Quality

Literature addressing the effect of water stress on pea, cowpea and soybean seed quality is limited and inconsistent. At Vauxhall, Alberta from 1974 to 1977, seed crude protein yield was strongly dependent upon increased water supply (Krogman et al., 1980). Seed crude protein content increased from 30.8 to 33.2% as irrigation level increased. However, at Brooks, Alberta in 1974 and 1976 there was no response of seed crude protein content with increased irrigation (Krogman et al., 1980). Additionally, 1,000 seed weight was not dependent upon total water received. Farah (1981b) reported that water shortage reduced amounts of seed nitrogen (N), phosphorus (P) and potassium (K).

Results on the effect of water stress on pea, cowpea and soybean seed quality are also inconsistent. Moisture stress did not affect oil or protein content of pea, cowpea or soybean at any growth stage (Hunt et al., 1980; McLean et al., 1974; Rathore et al., 1981; Sionit and Kramer, 1977). Miller et al. (1977) reported a relationship between water used and seed size at constant water applications. However, Pumphrey and Schwanke (1974) found irrigated peas to have lower processing quality than non-irrigated peas.

Water Stress Effects on Dry Matter Production

Irrigation increases fababean total dry matter and moisture stress reduces dry matter production (Farah, 1981a; Krogman et al., 1980; McEwen et al., 1981; Shaaban et al., 1979). McEwen et al. (1981) predicted fababean forage yields of at least 5,000 kg ha^{-1} at Rothamsted without irrigation and 6,000 kg ha^{-1} with above average rainfall or irrigation. According to Lockerman et al. (1982), Canadian reports indicate that irrigated fababean has a forage potential of 8,960 to 17,920 kg ha^{-1}.

In the Sudan, El Nadi (1970) reported reductions in fababean relative growth rate when water stress was applied from emergence until early fruit set. Additionally, more crown branches were produced when drought up to early fruit set was followed by watering. In contrast, soybean plants suffered less injury when the plants were stressed before flowering (Sionit and Kramer, 1976).

Pea and cowpea dry matter production respond to water stress similar to fababean (Lee et al., 1973; McLean et al., 1974; Miller et al., 1977; Pumphrey and Schwanke, 1974; Shouse et al., 1981; Turk and Hall, 1980c). A greenhouse study where four constant moisture levels were applied to pea showed a relation between water used and total dry matter (Miller et al., 1977). Shouse et al. (1981) reported that dry matter production was linearly related to transpiration.

Water Stress Effects on Plant Height

Limited information is available on the effect of water stress on fababean plant height. Most of the literature relates plant growth mainly to shoot dry matter. El Nadi (1970) reported that water stress from emergence to early fruit set resulted in a relative growth reduction. Fababean is reported to have a strong stem (Anonymous, 1975). However, McEwen et al. (1981) reported that fababean grain in 1977, in a field study at the Rothamsted experiment station, could not be harvested because of lodging. Therefore, it is suggested that plant height, internode number and length may have serious implications if they are affected by high precipitation or irrigation.

Pea and cowpea plant height increased with increased water application and water use efficiency (Manning et al., 1977; Miller et al., 1977). Irrigation timing may also affect plant height. Miller et al. (1977) in a greenhouse study applied combinations of two water levels of high (80 to 100% of field capacity) and low (40 to 60%) to pea over each of three different growth stages. Greatest plant height occurred when high water was applied during flowering to early pod fill.

Water Stress Effects on Leaf and Internal Water

High moisture stress reduced fababean leaf area (El Nadi, 1970; Farah, 1981a). Farah (1981a) applied constant field irrigation treatments designated as wet, medium and dry to fababean. Leaf area was reduced as well as rate of leaf appearance and leaf longevity as moisture stress increased. In another field experiment, water stress from emergence to early fruit set reduced leaf area (El Nadi, 1970). Additionally, water stress applied from emergence to early fruit set decreased moisture content of shoot tissue compared with the well-watered plants. In a growth room experiment, moisture content of shoot tissue at the permanent wilting point was only 2% less than that of plants growing at field capacity (El Nadi et al., 1969). This suggests a tendency toward drought resistance in fababean.

Water stress decreased leaf area, leaflet number and average leaflet area of cowpea, although water stress increased specific leaf weight (Turk and Hall, 1980c). Manning et al. (1977), in a greenhouse experiment, found water use efficiency (WUE) positively correlated with leaf area. WUE represents yield per unit of water used by the plant. Water stress also affects other structural components of pea leaves. Increased soil moisture stress increased the stomatal density, while upper leaves had more stomata per area than lower leaves (Manning et al., 1977). Additionally, the cross-sectional diameter of the xylem correlated with WUE (Manning et al., 1977).

Plant responses (leaf-water potential, leaf-air temperature differential and leaf-diffusion resistance) are sensitive to water deficits during the late vegetative stage in southern pea (*Vigna sinensis* L.) (Clark and Hiler, 1973). All three plant measurements indicated water deficit to some degree, however, leaf-water potential was most responsive and leaf-diffusion resistance was least responsive (Clark and Hiler, 1973). Additionally, plant response was less sensitive during the pod development stage (Clark and Hiler, 1973). Predawn leaf-water potential was a better indicator of crop water stress than midday in cowpea (Shouse et al., 1981; Turk and Hall, 1980b).

The literature does not explain the effect of water stress levels on leaf-water potential of fababean. More work should be done to examine the utility of leaf-water potential as an index of fababean water stress.

Water Stress Effects on Water Use

Water use by a crop may be expressed as WUE, evapotranspiration (ET) or crop transpiration (T). Additionally, water use efficiency may be based either on evapotranspiration or crop transpiration. The difference may be important since suppression of soil evaporation and prevention of weed transpiration may improve WUE based on ET, but may not improve WUE based on T (Tanner and Sinclair, 1983). However, ET is easier to measure than T and is the most commonly used.

Evapotranspiration for the growing season is higher in fababean than cereals. At Lethbridge, Canada from 1974 to 1977, evapotranspiration of fababean receiving high irrigation averaged 544 mm, which was 16% greater than irrigated cereals (Krogman et al., 1980). El Nadi (1970), in field studies at the University of Khartoun in the Sudan, reported the highest WUE in well-watered fababean.

Water stress affects WUE of pea and cowpea similar to fababean. When constant water applications were applied, WUE was positively correlated with moisture regime in pea (Manning et al., 1977) and cowpea (Turk and Hall, 1980d). However, the growth stage in which stress is applied may result in either an increase or decrease in WUE. Shouse et al. (1981) and Turk and Hall (1980d) found that WUE in cowpea increased with vegetative stage drought and decreased with flowering and late season drought. WUE was also positively correlated with total dry matter, seed yield, seed size, seed number $plant^{-1}$, plant height and leaf area of pea (Manning et al., 1977; Miller et al., 1977). Therefore, WUE should be a good parameter to measure plant response to various moisture levels.

Water Stress Effects on Root Growth and Depth of Soil Water Extraction

Root system size and water extraction depth are extremely important since yield and growth parameters are closely related to total water use. There are conflicting reports on the maximum rooting depth of fababean. Naimark (1976), on a dernopodzolic soil in Belorussia, reported rooting depths to 120 cm. However, Hebblethwaite (1982) reported that no roots could be found below 80 cm.

Although there is disagreement on the maximum depth of rooting, most researchers agree on the depth where most of the water is absorbed. Tawadros (1982), Naimark (1976) and Hebblethwaite (1982) reported that the upper 30 cm of the soil profile is the most important absorption area for fababean, since it contains approximately 70% of the active roots.

Literature involving the effect of soil moisture levels on root growth and soil extraction patterns of fababean is limited. El Nadi et al. (1969), in growth chamber experiments, observed that the drier the soil, the deeper the roots penetrate in the growing medium. Additionally, soil moisture influenced root distribution in the profile, but did not affect root weight. Roots reduce the harmful effect of water stress by growing and branching deeper where the soil is less dry.

A physiological explanation has been suggested for compensatory growth of fababean roots in deep layers in dry soils. Growth rate depends on carbohydrate supply and on external conditions. Carbohydrates flowing from the shoot are distributed to all growing parts of the root. Plant parts growing most rapidly constitute the most active sink. High soil moisture is more favorable for rapid growth than low soil moisture, with subsequently more root growth in deeper soil layers of high moisture content (El Nadi et al., 1969).

Soil moisture effects are variable among many crops. Peanut (*Arachis hypogaea* L.) and soybean root growth was not affected by water management, however, corn root growth increased in length with irrigation (Robertson et al., 1980). Water management treatments of (1) rain-fed, no irrigation; (2) light, frequent irrigation-soil wetting depth of 30 cm; (3) medium, infrequent irrigation-soil wetting depth of 60 cm; and (4) light, infrequent irrigation-soil wetting depth of 30 cm were applied to field grown corn. Corn root growth increased in length with irrigation with the largest root length values corresponding to light, infrequent irrigations (Robertson et al., 1980).

Water Stress Effects on Nodulation and N_2-Fixation

Molecular nitrogen (N_2) composes almost 80% of the earth's atmosphere (Havelka et al., 1982). However, the two triple-bond atoms of the N_2 molecule have to be cleaved into single atoms before they combine with hydrogen or oxygen to form either ammonia (NH_3) or nitrate (NO_3^-) compounds for plant use (Havelka et al., 1982). One method of bond cleavage is by the commercial Haber-Bosch process which requires high temperature and pressure (Havelka et al., 1982). Another method is through symbiotic biological N_2-fixation, a unique system possessed by a few prokaryotic organisms in association with legume plants. Nitrogenase catalyzes the conversion of N_2 to NH_3 under mild temperature and normal atmospheric pressure.

The best known and most agriculturally important microorganism capable of biological N_2-fixation is *Rhizobium* bacteria. *Rhizobium* infect the root of legumes, form nodules and conduct a symbiotic relationship with the host plant. The host plant (macrosymbiont) supplies the bacterium (microsymbiont) with an energy supply, and the bacterium supplies the plant with reduced N_2. However, symbiotic N_2-fixation is not without cost to the host plant. Estimates suggest that from 15 to over 30% of the total assimilatory capacity of a plant may be utilized to sustain the process of N_2-fixation and NH_4^+ assimilation (Schubert, 1982).

Fababean has a symbiotic relationship with *Rhizobium leguminosarum*. However, water stress is a major factor affecting nodulation and nitrogen fixation in fababean (Day et al., 1980a; Sprent, 1972; Sprent, 1976a and b; Sprent and Bradford, 1977). Water potential gradients exist in nodules. Water is lost from the surface and resupplied by the vascular system of the root (Sprent, 1972; Sprent, 1976b). Sprent (1972) showed a high degree of correlation between soil-water content and nitrogen-fixing activity in field grown fababean. Slow natural drying over 6 weeks progressively reduced N_2-fixation and was restored by irrigation (Sprent, 1972).

Maximum nitrogen fixation occurs at field capacity, however, nodule formation and nitrogen fixation are reduced by waterlogging (Sprent, 1972; Sprent, 1976a). Day et al. (1980b) working with fababean and Zablotowicz et al. (1979) with cowpea reported that irrigation increased nodule dry weight, total and specific nitrogenase activity and total N content. Nodulation and nitrogenase activity are differentially affected by water stress, depending on the plant growth stage. Summerfield et al. (1976) observed that nitrogenase activity of cowpea decreased with repeated wilting prior to flowering and was less affected when wilting occurred after flowering.

Several hypotheses explaining how nitrogen fixation is affected by water stress have been suggested. Sprent (1976b) suggested two alternatives: (1) depressed O_2 uptake inhibits oxidative phosphorylation which produces ATP and $NADPH_2$ required for the metabolic reduction of NO_3^- to NH_3 and (2) water stress affects membrane characteristics which in turn affect the function of the membrane bound enzyme essential for N_2-fixation. Effects of moderate stress may be overcome by increasing the O_2 concentrations (Sprent, 1976b).

Pate et al. (1969) suggested that limitations in water supply to the nodule may affect nodule activity by restricting fixation products which may accumulate in inhibitory concentrations. Sprent (1971) observed a close link between nitrogen-fixing and respiratory activities. However, other researchers have reported that inhibition of shoot photosynthesis accounts for the inhibition of nodule acetylene-reduction at low water potentials (Finn and Brun, 1979; Huang et al., 1975a; Huang et al., 1975b). Huang et al. (1975a), in a controlled environment experiment, observed that as soil was desiccated below –0.2 MPa acetylene-reduction decreased and the decrease was correlated with decreased photosynthesis and transpiration. It was concluded that either photosynthesis, transpiration or some direct effect on the nodule other than that caused by respiration was more likely the reason for acetylene-reduction inhibition at soil-water potentials below –0.2 MPa. In further experiments, Huang et al. (1975b) found that acetylene-reduction inhibition caused by low soil-water potentials could be reproduced by depriving shoots of atmospheric CO_2 even though the soil-water potentials were favorable for rapid acetylene-reduction. Additionally, the inhibition of acetylene-reduction at low soil-water potentials could be reversed by exposing shoots to high concentrations of CO_2. It was concluded that inhibition of shoot photosynthesis accounted for acetylene-reduction inhibition at low soil-water potentials.

Other effects of water supply may be on multiplication and movement of *Rhizobium* in the soil. Shimshi et al. (1967) found that shallow placement of inoculum in soils gave best nodulation in peanut at depths of 3-4 cm, despite higher soil moisture at greater depth. They also concluded that *Rhizobium* multiply rapidly following irrigation, and migrate in the soil while sufficient moisture is available. Soil-water tensions of –0.8 MPa reduced the movement of *Rhizobium trifolii*, and migration cessation occurred when water-filled soil pores became discontinuous (Hamdi, 1970).