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Effects of Shading on Dry Matter Production, Yield

and Nitrate Reductase Activity of Potato

under Two Levels of Spacing

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The effects of shade (C: unshaded control, S1: 48% shading and S2: 76% shading) at different growth stages (stage-I: vegetative to beginning of tuber initiation, stage-II : tuber initiation to initial tuber bulking and stage-III : tuber bulking to maturity) on nitrate reductase (NR) activity, plant growth and yield of field grown potatoes (Solanum tuber-osum L.; cv. May Queen and Dejima) under two levels of spacing were studied. Main stem length was increased by higher intensity of shading and denser plant spacing at all stages of growth. Denser plant spacing also increased the leaf area index (LAI). Shading at early stage delayed tuber initiation. Increasing shading intensity consistently decreased dry matter production and marketable tuber weight and decreased the tuber yield. The yield reduction was greatest (41%) in S2 plants at stage-II and smallest (15%) in S1 plants at stage-III. On an average (cultivar, spacing and growth stages) 19 and 30% yield reduction was observed for the reduction of 48 and 76% solar radiation, respectively. The NR activity in leaves decreased by shading. On an average, 16 and 25% reduction in NR activity was observed for the reduction of 48 and 76% solar energy, respectively. The reduction coefficient of yield or NR activity for light was 0.40 and 0.33 respectively for both levels of shade applied. From this study it could be concluded that shading at stage-II is
very critical for tuber yield and is directly related to the reduction of NR activity and yield.

Keywords: growth stages, nitrate reductase activity, potato (Solanum tuberosum L.),
spacing, tuber yield

INTRODUCTION

The dependency of light as well as nitrate reductase (NR) activity on yield is not studied well in potato plants. In this study we quantificated the yield or NR activity reduction through the reduction of light. Intensity of solar radiation has pronounced effect on the nitrate reduction, production and allocation of photosynthate in many crop plants. The NR activity in photosynthetic tissues depends both on the intensity of light and the concentration of NO3 (Travis et al., 1969; Li and Oaks, 1994). Light apparently supplies reducing power for the enzymatic reduction of nitrate (Klepper and Hageman, 1969) and influences the synthesis or activation (Ingle, 1968) and degradation or inactivation (Travis et al., 1969) of the enzyme as well as the rate of uptake of nitrate (Beevers et al., 1965). It was also found that
the duration of receiving a certain level of radiation of leaves would ultimately affect the result.
The reduction of light intensity at the critical stages of potato plants, its influence on the NR

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activity and its relationship with the growth and yield are not comprehensively studied yet. Therefore, an in-depth study could reveal some of the inherent processes involved in the interrelations.

Shade at different stages of growth significantly decreased the final yield of potato (Gray and Holmes, 1970; Sale, 1976; Oswald et al., 1995), but the amount of yield loss was influenced by many other factors such as duration, timing and intensity of shading, cultivars and growing season. A certain amount of shade is naturally occurred by leaves within the canopy or by prolonged cloudy weather. Shading of different intensity and its timing changed the growth patterns of potatoes. Reduced intensity of light also impede or modify certain physiological processes of plants and as a consequence, the retardation of plant growth and tuber development occur in sweet potato (Oswald et al., 1995). The yield improvements result partly from a better control of weeds, pests and diseases (Willey, 1979) but the major cause of improvement is to better use of growth resources such as soil, water and nutrients and light energy. Shading treatments had a pronounced effect in delaying tuberization, especially if applied shortly after the onset of tuberization (Struik, 1986). Menzel (1985) suggested that both of low light intensity and high temperature brought about increased production of growth substances that inhibit tuber formation. The cloudy period in potato growing areas varies greatly. In conjunction with the plant type and canopy structure, the complete expres-sions of growth and yield potentials are often hindered. Therefore, it is useful to investigate the reduction coefficients of NR activity and yield.
The objectives of this study are to clarify the yield reduction due to light comparing with the physiological processes such as NR activity and also to investigate the growth stage which is the most critical for tuber yield.

MATERIALS AND METHODS

The experiment was conducted in spring 1998 at the experimental field of the Faculty of Agriculture, Kagawa University. Three levels of shade treatment (C : unshaded control, S1: 48% shading and 52 : 76% shading) were imposed at three different stages of growth (stage-I: vegetative to beginning of tuber initiation, stage-II : tuber initiation to initial tuber bulking and stage-III : tuber bulking to maturity). Treatments were initiated from 10 d after emer-gence and succeeded for 15 d. Two potato cultivars, May Queen (leafy type) and Dejima (stem type) were used (Fonseka and Asanuma, 1996). Two plant spacings (66 cm X 30 cm and 66 cm X 15 cm) were maintained. Fertilizers at the rate of 101 kg N, 212 kg P2o5 and 98 kg K20 per ha were applied just before planting and mixed well with the soil. About 50 g of seed tubers were planted over the ridge by hand on March 17, 1998. A unit plot (total 96 unit plot) size of 1.98 m2 contain 15 plants for higher spacing (30 cm) and 30 plants (15 cm) for denser plant spacing. The experimental design was factorial randomized complete block design with three replications. Plants were sampled at the end of each treatment for growth studies and at the final harvest for yield and yield components. Three plants per replication were harvested and separated into leaves, stems, stolons, tubers and roots. The measurements included the length of the main stem, leaf area and fresh and dry weight of each organ. For yield determination 10 plants per replication were harvested and total yield, marketable yield (>50 g) and yield components were recorded. Nitrate reductase activity was determined after
Kapoor and Li (1982). Fully expanded leaf (3rd and 4th leaf from the apex) samples were collected (five replicates) and analyzed at different growth stages. Reduction coefficient for
light on yield or NR activity were calculated by dividing the reduction of yield or NR activity
by the reduction of light. All statistical analyses were performed by MSTAT-C (Michigan
State University, USA) software. The climatic factors observed during the growing season

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Table 1 Mean of monthly climatic factors observed during the growing season.

Source : Agro-meteorological Center, Kagawa University.

are shown in Table 1. At the later part of the growing season rainfall was relatively high.

RESULTS

1. Morphological changes
Main stem length was increased by higher intensity of shading and denser plant spacing
at all stages of growth (Fig. 1). Denser plant spacing also increased the leaf area index (LA!). Stolon number per plant decreased by the increase of shading intensity for both plant spacing at stage-I and stage-II but at stage-III, no appreciable change was observed. Tuber number per plant decreased by shading at stage-I and stage-II but at stage-III, it remained unchanged. Denser plant spacing increased the stolon and tuber numbers per unit of ground area.

2. Dry matter production
Total dry matter production decreased by shading (Fig. 2). Decreases in stem, leaf, tuber and total dry weight were greater at stage-I for higher intensity of shading in both cultivars. At stage-II, cultivar differences were observed. In May Queen, dry matter production of plant organs decreased by shading in both spacing. In case of Dejima, on the other hand, stem and leaf dry weights increased by S1 treatment but tuber dry weight decreased, and in S2 plants the dry weight of all plant organs decreased. At stage-III, stem, leaf, tuber and total dry matter production decreased for higher intensity of shading in both cultivars at each spacing.

3. Yield and yield components
Shading at all stages of growth decreased the total tuber yield at final harvest (Table 2). Tuber yield differed significantly for different treatments except for Dejima in denser (15 cm) spacing where the effect was not significant. Tuber number decreased more at stage-I, and in some cases number increased for S1 plants (stage-II) and remained nearly unchanged at stage-III. The mean weight of marketable (>50 g) tubers at all stages of growth decreased significantly by shading in both cultivars.
The percentage of yield reduction varies between cultivars and spacing (Table 3). Yield reduction was relatively greater in May Queen than Dejima. The yield reduction was the greatest in SZ plants (41 %) at stage-II and the smallest in S1 plants (15%) at stage-III. On total average (cultivar, spacing and growth stages), the reduction in yield was 19 and 30% for S1 and SZ plants over control. Reduction coefficient of yield for light was 0.40 for both S1 and SZ (Table 3). It means yield reduction is directly related to per unit reduction of light.

4. Nitrate reductase activity
The NR activity of leaves decreased by shading at stage-I and II. At stage-III, NR
activity increased for some cases in both cultivars (Table 4). The decrease in NR activity was more evident for higher intensity of shading. On the other hand, plant spacing effect was not

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Growth stages

Fig. 1 Effects of shading on some growth characteristics of two potato cultivars at two spacing just after the removal of shade clothes.
Bars represent standard error. At the 3rd stage of treatments leaves senesced and data could't be
taken. LII, control ; /, 48% shade ; ®, 76% shade. S-I, S-II, S-III : stage-I, stage-II and stage-III, respectively.

consistent for NR activity in both cultivars. NR activity was at peak at stage-II and then gradually decreased. Reduction of NR activity was relatively pronounced for 8 d after shading (DAS) as compared to 15 DAS for both cultivars. On an average (cultivars, spacing and growth stages), 16 and 25% reduction in NR activity was observed for the reduction of 48
(S1) and 76% (S2) of solar energy, respectively. Reduction coefficient of NR activity for light
was 0.33 for both S1 and S2 (Table 4), indicating the reduction in NR activity is directly proportional to the per unit reduction of solar energy.

DISCUSSION

Shading increased the plant height in both cultivars. This is a response of plant to grow

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Plant organs

Fig. 2 Effects of shading during different growth stages on dry matter production of two potato cultivars
at two spacing just after the removal of shade clothes.
Bars represent standard error. • , control; •¡, 48% shade; •¬, 76% shade.

longer in search of more light. Bodlaender (1963) showed that stem elongation was very sensitive to daily radiation levels between 1.2 and 6.0 MJ m_2 and lower light intensity increased stem elongation. Closer spacing always increased the LAI. Increasing LAI with decreasing solar energy is a response typical for potato (Sale, 1976). Shading decreased the total dry matter production and the effect was more evident for higher intensity of shading. The decrease in dry matter production may be related to the decrease in photosynthate production under shaded condition. Nosberger and Humphries (1965) found that 60% shade reduced tuber growth more than top growth, with a slight decrease in total dry weight. But Gray and Holmes (1970) applied 85% shade to potato crop for 10 d during the bulking period and found a net decrease in the dry weight of stem, which they attributed to the export of carbohydrate to meet the demand of tuber. Higher levels of shade (S2) in stage-I delayed the tuber initiation. This is supported fairly well by the several reports (Gray and Holmes,1970 ; Sale, 1973a, b, 1976).
Earlier investigations have implicated that reduced light intensity obtained by artificial
shade structures or by increased plant population (Sale, 1976) as a causal factor in the decreased yield of potato and in other crops (Lang et al., 1956; Gregory et al., 1987). The
results of this experiment are also well agreed with the above report. Decreasing plant spacing from 30 to 15 cm increased the total tuber number per unit area of land but decreased

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the individual tuber weight. Closer spacing increased the tuber yield by increasing the number of tuber per unit of land area but decreased the average marketable tuber weight. The yield declined in the current experiments was due to the decrease in photosynthate production and also the reduction of assimilate partitioning to the tubers, hence a decrease in mean tuber weight. Within the potato the photomorphogenic effect of shading, manifest through favored haulm growth at the expense of tuber growth (in part due to delay in tuber initiation ; Midmore, 1990) is most likely manifest through the interplay of plant growth substances (Menzel, 1985). Tuber number is not drastically decreased under shade but size distribution varies markedly (Ewing and Struik, 1992).
Shading at stage-I, delayed the onset of tuber initiation. Shading at stage-II drastically reduced the yield. Shading at stage-III, slightly delayed tuber bulking rate and decreased yield. The yield reduction was greatest (41%) in S2 plants and lowest (15%) in S1 plants. On total average (cultivars, spacings and growth stages), 19 and 30% yield reduction was observed for S1 and S2 plants (Table 3), respectively. Considering the growth stages, it could be concluded that the effect of shading at stage-II when the tuber dry matter is accumulating very rapidly, is very critical for tuber yield than other stages of treatment

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Reduction in light intensity by artificial shade reduced the level of NR activity in leaves
of both cultivars. Reduction of 48 and 76% light from the non-shaded plants resulted in 16

and 25% reduction of NR activity. Similarly in corn plants, Hageman et al. (1961) reported that 30% reduction of solar radiation brought a decrease in NR activity by 23 and 25% in two hybrid cultivars. The results of this experiment also proved that low intensity of solar radiation reduced the activity of NR in potato leaves. Since, nitrate is freely available for absorption by the plant, the accumulation of nitrate in shaded plants may be the direct result of lower NR activity in this experiment (Palmer, 1981). The NR activity was relatively high in plants grown in wider spaces and the activity decreased rapidly with increasing shade compared to those in plants of closer spacing. The lower enzymatic activity is directly related to the level of incident light on the leaf surfaces and the growth of the leaf. In this experiment, NR activity at stage-III was relatively higher in shaded plants. Delayed leaf senescence in the shade plants would result in the prolonged active canopy at later stages of growth (Struik, 1986; Demagante and Vander Zagg, 1988).
The existence of constant reduction coefficient is an important result indicating the dependency of NR activity and yield on the incident solar radiation. This reduction coefficient may be considered as a physiological constant for potato. However, only two cultivars were employed in this experiment. For standardization of this coefficient similar experiment with other type of cultivars should be done in further work.
Reduction coefficient for yield was the same (0.40) for both 48 and 76% reduction of light

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meaning that the reduction of light is directly proportional to the reduction of yield. Furthermore, reduction coefficient value for NR activity was 0.33 for both 48 and 76% reduction of light, meaning that NR activity reduction is also directly proportional to the reduction of light under sufficient nitrogen supply. Reduction coefficient value for yield is higher than that of NR activity. The yield reduction as well as by the reduction of dry matter production may be occurred by the reduction in activity of many enzymes including nitrate reductase. From this study it can be concluded that shading at stage-II is most critical for
tuber yield or NR activity and yield of potato depends on light

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<和文抄録>
異なる栽植密度条件下における遮光処理がジャガイモの乾物生産,
収量および硝酸還元酵素活性に及ぼす影響
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2段階の栽植密度条件でジャガイモ2品種(メークイン,デジマ)を栽培し,生育時期別に遮光
処理が生育,収量および硝酸還元酵素(NR)活性に及ぼす影響について検討した.遮光処理は無
処理(100%,C区),弱遮光(48%遮光,Sl区),および強遮光(76%遮光,S2区)として寒冷紗を
用いて行った.生育時期を三つの時段階(1期:萌芽から塊茎形成期,II期:塊茎形成期から塊茎
発達期,III期:塊茎発達期から成熟期)に区分し,それぞれのステージに遮光処理を行った.す
べての遮光処理区,および密植区で草丈は高くなり,葉面積指数は密植区で増加した.初期の遮光
区では塊茎形成期が遅延した.遮光程度が強くなるほど乾物生産,上イモ収量および全塊茎重が低
下した.収量の低下程度はII期のS2区で最大(41%),III期のSl区で最小(15%)であった.品
種,栽植密度,全生育段階を含めた平均値でみると,C区に比べ,弱遮光区で19%,強遮光区で30%
の減収となった.葉のNR活性は遮光処理区で抑制され,C区に比べ,平均値で弱遮光区は16%,
強遮光区は25%低下した.両処理条件での光強度に対する収量およびNR活性の減少係数はそれ
ぞれ0.40,0.33であった.以上の結果は光強度の低下が収量およびNR活性の低下と直接関連して
いることを示唆している.本研究より,II期が塊茎収量に対する光の影響の最も大きな時期であ
り,NR活性および収量低下に直接関連しているものと結論した.
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