Dry matter and nitrogen partitioning in sweet corn (*Zea mays* L.) for processing: plant density and nitrogen nutrition effects.

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Abstract

Increasing land values without comparable increases in yield or reduced input costs have reduced the attractiveness to growers of processing sweet corn (*Zea mays* L.) as a cropping enterprise at Gisborne, New Zealand. As a consequence, the problem of consistently sourcing adequate volumes of raw material has been one factor leading the region's major sweet corn processor to consider withdrawing from the region. Hence, the development of agronomic practices which reduce crop production costs, improve marketable yields, or both, will be important for maintaining the viability of the sweet corn processing industry in Gisborne for both growers and processors alike.

Two of the most important factors influencing yield of sweet corn are plant density and nitrogen (N) nutrition. The density range which maximised marketable yield of cobs and kernels for Jubilee and SS42, the two prominent cultivars grown at Gisborne, was 69-77,000 plants per hectare. Although yield response to fertiliser N was also investigated in the same study, the yield response was either negligible (SS42) or did not follow a trend consistent with incremental increases in N rate (Jubilee). The limited response was attributed to high background levels of soil available N (269 kg/ha). A second experiment was designed to investigate the yield response to fertiliser N on a soil with a low available N level. Although only 92 kg N/ha was available from the soil, yield response in this experiment was also negligible with N rates greater than 73 kg/ha. Combining the two years' results indicated that yield response to N fertiliser will be limited when soil available N levels are > 213 kg/ha.

The rate of yield improvement could be enhanced by greater understanding of the physiological processes limiting yield in maize and sweet corn. The study of source-sink relationships can provide useful insights into yield determinants. A field experiment was established with Jubilee and SS42 to study how variables influencing weight of primary and secondary ears (e.g., silk delay, tiller number per plant) adjust to plant density and N nutrition. Path analysis and canonical discriminant analysis indicated that tillers were important for supplying the secondary ears of both cultivars with photoassimilate at low densities (e.g., 40,000 plants per hectare) and were important for Jubilee, but not SS42, at high densities (e.g., 100,000 plants per hectare). A short silk delay for both the primary and secondary ear was important for both cultivars at low

densities to establish a large ear sink. Thus, at low densities, the presence of a secondary ear at low densities appeared to enhance kernel development on the primary ear.

To further understand the partitioning of DM and N to kernels, further experiments quantified sink strength (or source strength) of an organ (i.e., leaves, stems, roots, kernels, rachis, husk, or shank) between defined ontogenetic stages. Sweet corn grown at 70,000 plants per hectare with rates of applied N ranging from 0 to 230 kg/ha were harvested throughout ontogeny until R4. Although N rate generally did not influence partitioning of N or dry matter (DM) to any organ, significant cultivar differences were detected. Kernel sink strength of Jubilee was two-fold greater for DM than SS42 and three-fold greater for N between R1 and R3. As a consequence, kernels of Jubilee contained 34% more DM than those of SS42 at R4 and were significantly more efficient than SS42 kernels at translating endogenous N into kernel DM. The observation that DM was partitioned to vegetative organs during reproductive growth while N was being remobilised from these organs indicated that both Jubilee and SS42 were source limited for N, yet sink limited for current photoassimilate.

No published studies have been sighted which have identified a link between the source limitation for N and the sink limitation for DM in *Z. mays*. Investigating source-sink relationships indicated that the two events are linked and initiated by low kernel sink strength during early grain filling. SS42 partitioned large proportions of DM to both husks and stems between R1 and R3, in contrast to Jubilee which partitioned most DM directly to kernels. As partitioning DM to vegetative tissue and husks reflects photoassimilate not consumed in reproductive growth, excess photoassimilate resulting from limited sink strength may have decreased photosynthetic rates through 'feedback' inhibition. Consequently, the ability of Jubilee to partition DM to roots for N assimilation between R3 and R4 may reflect less inhibited photosynthesis than for SS42.

A subsequent experiment provided further evidence that kernel sink strength influences N and DM partitioning. This experiment also indicated that low kernel sink strength during early grain filling may actually initiate an inhibitory cycle. When maximum leaf area in maize and sweet corn is reached around R1, the ear is a relatively weak sink and unable to accumulate all the photoassimilate being produced. Although the excess is partitioned to stems and husks, these

organs can only accumulate a limited quantity before they become saturated. When the stem and husks become saturated, photoassimilate may accumulate in leaves causing feedback inhibition of photosynthetic enzymes to reduce the supply of photoassimilate. However, as N assimilation rate is dependent on the rate of photoassimilate supply to roots, the inhibited photosynthesis reduces N uptake and as a consequence, remobilisation of N is stimulated. Excessive remobilisation of N from leaves may further impair photosynthetic activity to further restrict the photoassimilate supply for root and shoot functions including grain filling. Hence, an inhibitory cycle may evolve from the limited capacity of kernels and rachis to accumulate photoassimilate. Since SS42 (*sh2* mutant) had a significantly lower kernel sink strength than Jubilee (*su1* mutant) during early grain filling, SS42 was apparently more influenced by the inhibitory cycle than Jubilee.

To add support to the theory that limited kernel sink strength during early grain filling may lead to an inhibitory cycle, a final experiment investigated the association of the endosperm storage protein, zein, with kernel sink strength. A high correlation (r=0.91) was observed between kernel DM and the level of zein. Further, the wild type (Furio) contained 25 and 49% more zein at R4, and accumulated 18 and 49% more DM, respectively than the *su1* (Jubilee) and *sh2* (SS42) mutants. Similarly, kernels of Jubilee, which contained 31% more zein than those of SS42., accumulated 38% more DM. Together these results indicate that the level of zein is associated with kernel sink strength and thus lends support to the inhibitory cycle theory.

Key words: **canonical discriminant analysis, endosperm mutants, nitrogen nutrition, non-linear regression, path analysis, photoassimilate partitioning, plant density, process sweet corn, *sh2*, *su1*, zein.**

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List of abbreviations

1^o	primary
2^o	secondary
^{14}C	carbon isotope
^{15}N	nitrogen isotope
^{32}P	phosphorous isotope
λ_i	*i*th eigenvalue of canonical discriminant function
$\bar{x}$	sample mean
$\sigma_{\bar{x}}$	standard deviation of the sample means
δ	rate of change between two ontogenetic stages
χ^2	chi-square statistic
a.i.	active ingredient
ADP	adenosine diphosphate
ANOVA	analysis of variance
bt2	*brittle*-2 endosperm mutant
C	degrees Celsius
CDA	canonical discriminant analysis
CDF_1	first canonical discriminant function
CEC	cation exchange capacity
DAP	days after pollination
DEFITS	Cook's D statistic (scaled and squared)
DM	dry matter
DMPC	dry matter partitioning coefficient
F	F-statistic
fl2	*floury*-2 endosperm mutant
GDD	growing degree day
Gw	grain dry weight
HI	harvest index
KCl	potassium chloride
kDa	kilo-Dalton
LSD	least significant difference
M	molar concentration
n	number of observations
N	nitrogen
Ns	quantity of nitrogen applied
Nt	total N content of the plant
NIWA	National Institute of Water and Atmospheric Research Ltd
NPC	nitrogen partitioning coefficient
NUPE	nitrogen uptake efficiency
NUSE	nitrogen use efficiency
NUTE	nitrogen utilization efficiency

o2	*opaque*-2 endosperm mutant
P	probability
PEPCase	*phosphoenolpyruvate carboxylase*
P_{ij}	path coefficient between the variables *i* and *j*
PPDK	*pyruvate pyrophosphate dikinase*
PPFD	photosynthetic photon flux density
pph	plants per hectare
PS	current photoassimilate
R1	silking stage (i.e., silks from the tip of the prophyll are visible)
R2	blister stage (i.e., kernels resemble a blister in shape)
R3	milk stage (i.e., kernel displays yellow colour on the outside and the inner fluid is milky white)
R4	dough stage (i.e., endosperm fluid is pasty in appearance)
R6	physiological maturity
r^2	coefficient of determination
R^2_{adj}	adjusted coefficient of determination
RER	rough endoplasmic reticulum
r_{ij}	correlation coefficient between the variables *i* and *j*
rpm	revolutions per minute
RSS	residual sum of squares
RUBISCO	*ribulose 1,5-bisphosphate oxygenase-carboxylase*
SD	standard deviation
SE	standard error of the mean
SEOD	standard error of difference between means
SMC	seed moisture content
SDS	sodium dodecyl sulphate
SDS-PAGE	sodium dodecyl sulphate polyacrylamide gel electrophoresis
su1	*sugary*-1 endosperm mutant
sh2	*shrunken*-2 endosperm mutant
T_{50}	time at which 50% of plants have 'silked'
t/ha	tonnes per hectare
TSS	total sum of squares
USDA	United States Department of Agriculture
V3	ligule of the third leaf is visible
V5	ligule of the fifth leaf is visible
X_1	$\log_e$ nitrogen uptake efficiency
X_2	$\log_e$ nitrogen utilization efficiency
z^*	z-score

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Chapter 1

Introduction

1.1 Introduction

Over the last ten years, increasing land values, fuelled by the development of markets for higher value crops in the Gisborne region (New Zealand's major sweet corn growing area) have reduced the attractiveness to growers of processing sweet corn as a cropping enterprise (Brooking and McPherson, 1986). With gross margins declining and growers choosing more profitable alternative crops, sweet corn processors face problems consistently sourcing adequate volumes of raw material. This has led the region's major sweet corn processor (Heinz Wattie's Australasia) to consider withdrawing from the region. Hence, the development of agronomic practices which reduce crop production costs, improve marketable yields, or both, will be important for maintaining the viability of the sweet corn industry in Gisborne for both growers and processors alike.

Two dominant factors influencing yield of sweet corn in Gisborne are planting density and nitrogen (N) nutrition. Under current agronomic practices, seed of the two major[1] cultivars, *Zea mays* 'Jubilee' and *Z. mays* 'SS42' (hereafter, Jubilee and SS42), is sown in rows 760 mm wide at 55,000 plants per hectare. Between 100 and 150 kg N/ha is incorporated into the soil in two applications (Davis, pers. comm.). The first occurs at sowing with about 75 kg N/ha drilled with the seed. A further 75 kg N/ha is side-dressed at the V3-V5 stage of growth (Ritchie and Hanway, 1984). There is, however, no experimental evidence which demonstrates that this regime maximises yield and the efficiency with which fertiliser N is used under Gisborne conditions. Surveys of American maize growers have shown that many commonly apply more fertilizer N than is economically optimal (Blackmer et al., 1989; El-Hout and Blackmer, 1990; Morris and Blackmer, 1989). Similarly, with the development of improved sweet corn cultivars (Guzman, 1973; Wolf, 1978) more tolerant of high densities (Brown et al., 1970; Guzman, 1972; Tollenaar, 1991; Vyn and Tollenaar, 1998) due to increased prolificacy (Anderson et al., 1985; Motto and Moll, 1983; Nakaseko and Gotoh, 1976; Otegui, 1995) this same 'recipe' approach for both Jubilee and SS42 is further questionable.

[1] In 1996, SS42 and Jubilee accounted for over 95% of the sweet corn processed at Gisborne.

The potential for increasing yield with density is demonstrated by studies with sweet corn achieving yield increases of 3-12 t/ha over the range of 25,000 to 110,000 plants per hectare (Andrew and Weis, 1974; Bailey, 1941; Bowers, 1943; Mack, 1972[2]; Moss and Mack, 1979; Roberts et al., 1980a; Warren and Kelly, 1963; Watson and Davis, 1938). For maize[3], grain yield increases of 0.5-3 t/ha have been observed over a similar density range (Anderson, 1986; Downey, 1971; Dungan et al., 1958; Giesbrecht, 1969; Milbourn et al., 1978; Rutger, 1971; Sims et al., 1998). Mack (1972) and Moss and Mack (1979) suggested ear yield of Jubilee was maximised around 110,000 plants per hectare. However, studies with other cultivars indicate that considerably lower densities of 45-75,000 plants per hectare maximise yield (Dubetz and Wilson, 1969; Fery and Janick, 1971; Freyman et al., 1972; Jorgenson, 1966; Nichols, 1974; Rogers and Lomman, 1988; Shoemaker and Walkof, 1941; Warren, 1963). Not only do such reports raise the question whether 55,000 plants per hectare maximises yield of SS42 and Jubilee, but also whether SS42 and Jubilee respond to density in a similar manner.

As sweet corn and maize partition more N to the grain than any other nutrient derived from the soil (Marschner, 1986; Steele et al., 1982) N is the mineral element most likely to limit plant growth (Dwyer et al., 1995; Ebelhar et al., 1987; Wienhold et al., 1995) and yield (Anderson et al., 1985; Downey, 1971). Smith (1984) reported that yield of sweet corn 'Deep Gold' and 'Northern Belle' increased 35% as N rate increased from 0 to 112 kg/ha. The frequency of such yield increases in the literature (e.g., Blackmer and Sanchez, 1988; Chancy and Kamprath, 1982a, 1982b; Eckert and Martin, 1994; Fox, 1973; Fox et al., 1986; Moll et al., 1987; Oikeh et al., 1998; Sander and Moline, 1980) suggests that soil N fertility is an important yield determinant. However, N fertiliser represents one of the largest input costs for commercial sweet corn production. Therefore, every attempt should be made to maximise the efficiency with which it is used. Steele and Cooper (1980) reason that there are four main factors which should be considered when developing a fertilizer regime: the amount of nutrient required by the crop, the amount of nutrient removed in the harvested component, the ability of the soil to provide the

[2] Care is needed when interpreting this paper as densities quoted are incorrect. As a result of using these incorrect densities, yields per hectare are also incorrect. Further discussion uses corrected figures.

[3] As sweet corn and maize belong to the same species (*Zea mays* L.) and are differentiated only on the basis of endosperm characters, their responses are likely to be similar (Brooking and McPherson, 1989).

nutrient, and the efficiency with which fertilizer is used by the crop. Unfortunately, many fertiliser recommendations in New Zealand frequently fail to achieve this goal, often as a consequence of subjective information. Recommendations based on previous experience, the number of years a field has been continuously cropped, information from field trials, and overseas work often result in either too much or too little fertiliser being applied. If insufficient N is applied, yields will be restricted, whereas excessive application, apart from causing unnecessary cost to the grower, may result in increased leaching of N through the soil profile (Bigeriego et al., 1979; Fox et al., 1989). In particular, excessive application may lead to nitrate pollution of groundwater (Stanford, 1973), a problem especially noted in intensive cropping (Gardner et al., 1990; Gordon et al., 1993; Kimble et al., 1972; Lory et al., 1995b; Olson, 1977; Parr, 1973). Only by accurately predicting the N requirements of the crop and the N supplying capability of the soil can N fertilisers be used more effectively and the adverse effects minimised (Anderson et al., 1985; Karlen et al., 1998; Lory et al., 1995a; Vanotti and Bundy, 1994a).

Together, N nutrition and plant population dictate yield. Stone et al. (1998) suggested that because yield is related to the total amount of radiation intercepted by the crop canopy, increased yield with population results from both a reduced time to canopy closure and a greater maximum leaf area index. With inadequate N nutrition, canopy closure and the achievement of maximum leaf area may be delayed (Sinclair and Muchow, 1995; Stone et al., 1998). Inadequate N nutrition may also decrease leaf photosynthetic capacity (Sinclair and Muchow, 1995) and therefore the remobilisation of N to reproductive structures (Sinclair and Horie, 1989).

Although yields may also be increased with irrigation (e.g., Andrew and Groskopp, 1963; Brown, 1986; Eck, 1984; Mackay and Eaves, 1962; Vittum et al., 1959), growers of sweet corn in Gisborne generally do not consider that the expenditure is warranted (Davis, pers. comm.). This reflects the level of rainfall and the water holding capacity of soils around Gisborne which generally provide sufficient moisture to sustain good yields of sweet corn. Further, large volumes of irrigation water are not easily obtained in many parts of the region. Where water is available, it is typically used on crops of higher value than sweet corn. Thus, it can be assumed that the majority of sweet corn grown in Gisborne will be grown without irrigation in the foreseeable future (Davis, pers. comm.).

Even if an optimum density and N nutrition regime are identified for sweet corn production in Gisborne, the relief this offers the industry may only be short-lived. Such limited relief is because increased yields and decreased input costs would unlikely generate the 20% increase in profitability necessary to ensure the viability of the industry long-term. To generate higher yields beyond manipulating density and N nutrition regimes requires that physiological barriers limiting yield be identified and overcome. Identifying and overcoming such barriers is fundamental to increasing yield as evidenced by the higher yield and yield potentials of modern hybrids (e.g., Crosbie, 1982; Russell, 1985). Identifying barriers limiting yield may also provide opportunities to both minimise N application (Magdoff et al., 1984) and increase the efficiency with which fertiliser N is translated into kernel DM (i.e., N use efficiency or NUSE; Beauchamp et al., 1976; Moll et al., 1982a; Steenvoorden, 1989). These issues are particularly important if concerns about nitrate pollution of water supplies are to be addressed. Therefore, knowledge of mechanisms limiting yield is vital for not only developing superior sweet corn and maize hybrids but also improving management practices (Tsai et al., 1984).

Both Jubilee and SS42 are endosperm mutants, expressing the *sugary-1* (*su1*) and *shrunken-2* (*sh2*) mutations, respectively. *Shrunken-2* mutants are deficient in the activity of *ADP-glucose pyrophosphorylase* (Boyer and Hannah, 1994; Chourey, 1981; Dickinson and Preiss, 1969; Giroux and Hannah, 1994; Tsai and Nelson, 1966), the enzyme which is the rate-limiting step in starch biosynthesis (Hannah et al., 1993; Preiss et al., 1991). Thus kernels of *sh2* mutants contain only 20% of the starch of wild types (i.e., non-mutants; Boyer and Shannon, 1984, 1987; Nelson, 1980) and sucrose concentrations many times higher (Laughnan, 1953; Lee and Tsai, 1985; Tracy, 1997). *Sugary-1* mutants on the other hand, change both the types and proportions of polysaccharides stored in the endosperm (Boyer and Hannah, 1994; Boyer and Shannon, 1984), accumulating a highly branched form of starch known as phytoglycogen (Marshall, 1987; Nelson, 1980; Nelson and Pan, 1995). Sucrose concentrations are also enhanced as a consequence of the *su1* mutation, generally being 2-3 times higher than wild types (Garwood et al., 1976; Jennings and McComb, 1969; Wann et al., 1971; Wong et al., 1994). However, in addition to the *sh2* and *su1* mutations resulting in increased sucrose concentrations in kernels, DM accumulation in kernels of these mutants is also profoundly reduced. Compared to wild types, kernels of *su1* and *sh2* mutants accumulate 23-42% and 42-62% less DM, respectively

(Dalby and Tsai, 1975; Doehlert and Kuo, 1994; Glover et al., 1975; Lee and Tsai, 1985; Misra et al., 1972, 1975a; Tsai et al., 1978a, 1978b; Wilson, 1992). These workers suggest that the lower DM accumulation results from reduced levels of zein - the primary N storage protein in kernels (Tsai et al., 1980, 1983). Using plants heterozygous for the *opaque-2* (*o2*) mutation and wild type alleles, Tsai et al. (1980) demonstrated with $^{14}CO_2$ labelling that sucrose movement into kernels was strongly associated with zein accumulation. They found that there was little difference in radioactivity between *o2* kernels and kernels of the wild type prior to zein accumulation. However, as kernels developed, levels of zein in the wild type increased, being associated with similar increases in radioactivity. In contrast, lower zein accumulation in kernels of the *o2* mutant corresponded with significantly lower radioactivity. Moreover, when zein synthesis in the *o2* mutant terminated, sucrose movement into kernels was severely reduced (Russelle et al., 1983; Tsai et al., 1978a, 1980).

Although reduced zein synthesis through *sh2* and *su1* mutations may be associated with lower grain yield compared with wild types, lower grain yields may also be attributed to differences in the plant's ability to partition N to kernels for zein synthesis. As N fertility increases, zein becomes increasingly abundant in the endosperm (Lyznik and Tsai, 1989; Rendig and Broadbent, 1979; Schneider et al., 1952; Tsai et al., 1980, 1984; Wolfson and Shearer, 1981). Therefore, N sufficiency during the growing season is important not only for structural and metabolic functions (e.g., photosynthesis (Boote et al., 1978; Heichel, 1971; Osman and Milthorpe, 1971)), but also because it affects grain fill kinetics (Tsai et al., 1986, 1990). Hence, if endogenous N levels are low, or insufficient N is partitioned to kernels, both zein synthesis and photosynthesis may severely restrict yield (Hageman, 1979; Keeney, 1970; Tsai et al., 1991). It has been demonstrated that source strength for supplying newly assimilated N is commonly limiting in maize (Below et al., 1981, 1984; Cliquet et al., 1990b; Hanway, 1962a, 1962b; Reed et al., 1988; Swank et al., 1982; Tollenaar, 1977), so determining why this occurs and identifying ways to increase the uptake of N would appear fundamental to increasing yield. On the other hand, these workers also report that the reproductive sink capacity commonly limits maize grain yield, suggesting that the photosynthetic capacity is generally in excess of ear needs. Again, identifying if, and how, this occurs in sweet corn may provide a basis for increasing yield (Koch et al., 1982).

The high degree of association amongst zein synthesis, N nutrition, and DM partitioning to kernels indicates the importance of this system as a yield determinant in both sweet corn and maize. Hence, understanding the physiology of N and DM partitioning to kernels is paramount to identifying strategies to increase yield and NUSE. Therefore, with the goal of increasing yield, reducing input costs, or both, the broad objectives for this study were:

1. To identify densities which maximise yield of Jubilee and SS42.
2. To provide recommendations for the better management of N inputs.
3. To further elucidate the physiology of N and DM partitioning to kernels.

Experiments to meet these objectives were designed and undertaken over a two year period (1995-1996) near Gisborne (longitude 178°, latitude 38.7°), New Zealand.

Chapter 2

Effects of density and nitrogen rate on yield and yield components of sweet corn

2.1 Introduction

Identifying an optimum planting density is prerequisite for maximising yield of any crop. Although the weight of both primary and secondary ears of sweet corn decrease with density (Dolan and Christopher, 1952; Moss and Mack, 1979; Pickett, 1944; Watson and Davis, 1938), yield per unit area increases until an optimum is reached. Many workers have described this yield-density relationship as asymptotic (Fery and Janick, 1971; Freyman et al., 1972; Holliday, 1960), although others (Adelana and Milbourn, 1972a; Bunting, 1973; Hashemi-Dezfouli and Herbert, 1992; Karlen and Camp, 1985) have suggested the relationship might be better described as a flat topped parabola.

Densities which maximise yield of Jubilee and SS42 in Gisborne are undefined. While studies with Jubilee in the USA (Mack, 1972; Moss and Mack, 1979) have suggested that yield is maximised at densities greater than 110,000 plants per hectare, such densities are considerably higher than the 45-75,000 plants per hectare range suggested in other sweet corn studies (Dubetz and Wilson, 1969; Fery and Janick, 1971; Freyman et al., 1972; Jorgenson, 1966; Nichols, 1974; Rogers and Lomman, 1988; Shoemaker and Walkof, 1941; Warren, 1963). Moreover, 110,000 plants per hectare is over 40,000 plants per hectare greater than suggested by Douglas et al. (1971) to maximise grain yield of maize in New Zealand.

Optimum densities vary between studies because of variations in row spacing (Alessi and Power, 1974), the use of irrigation (Freyman et al., 1972), prolificacy (Anderson et al., 1985; Motto and Moll, 1983), or environmental conditions (e.g., temperature (Tollenaar et al, 1979)). It is well established that higher temperatures result in more rapid leaf expansion and therefore the attainment of maximum leaf area index (Moss et al., 1961; Tollenaar et al, 1979; Warrington and Kanemasu, 1983.). As a consequence, the onset of interplant competition may be earlier than in cooler climate conditions resulting in lower optimum densities. Alternatively, different criteria for determining whether an ear (e.g., a small secondary ear) contributes to yield or not will influence the choice of an optimum density.

Although yield tends to increase with density, the use of high densities increases the risk of lodging (Lang et al., 1956; Milbourn et al., 1978). Not only does lodging physically damage plants (Yoshida, 1972; Zuber and Kang, 1978), but it makes harvesting difficult. Reduced stalk diameter and increased ear height contribute to a greater incidence of lodging at high densities (Colville and McGill, 1962; Rutger and Crowder, 1967). Enhanced N fertility also increases lodging (Below et al., 1984; Krantz and Chandler, 1951) as the resultant heavier ears place more mechanical stress on stems (Yoshida, 1972). While these variables almost certainly contribute to lodging, the preharvest weather conditions are the major influence (Milbourn et al., 1978). Severe wind storms in Krantz and Chandler's (1951) study caused up to 93% of plants to lodge. Although no studies in New Zealand reporting high incidences of lodging have been sighted, lodging is well-known in commercial practice in New Zealand. Jubilee is recognised internationally in the processing industry as being more susceptible to lodging compared to other hybrids in common use (Davis, pers. comm.). Hence, increased risk of lodging must be considered in any commercial decision to use high densities.

Yield of sweet corn on soils of low N fertility may increase with N fertiliser application, irrespective of density (Iragavarapu et al., 1997; Muchow and Sinclair, 1995; Roberts et al., 1980b; Sanchez et al., 1989; Sanmaneechai et al., 1984; Wienhold et al., 1995). Yield increases of 4-11 t/ha are possible (Balko and Russell, 1980b; Fox; 1973; Lang et al., 1956; Sanmaneechai et al., 1984; Steele et al., 1982) through increased weight and number of both primary and secondary ears (Anderson et al., 1985; Krantz and Chandler, 1954; Moll et al., 1987; Salardini et al., 1992; Wong et al., 1995). However, as density increases, interplant competition for N also increases (Donald, 1963) and as a consequence, the levels of N required for maximum yield also increase (Bray, 1954; Chipman and MacKay, 1960; Colyer and Kroth, 1968; Downey, 1971; Duncan, 1954; Lang et al., 1956). Thus, unless soil N fertility is high, yield at high densities may be severely limited (Duncan, 1954; Tanaka and Yamaguchi, 1972).

Many existing N fertilizer recommendations in New Zealand are based on grower experience and the number of years a field has been continuously cropped (Steele et al., 1982). Such a basis is unsatisfactory as it often leads to fertiliser being applied in excess of crop requirements (Fox et al., 1989; Steele et al., 1982), potentially leading to pollution of water supplies (Parr, 1973;

Russelle et al., 1981; Spalding and Exner, 1993; Stanford, 1973). Rather, recommendations should be based on the expected yield increase per unit of N applied (i.e., a yield response curve; Anderson and Nelson, 1975; Elias and Causton, 1976; Whitear, 1976). As the point of maximum yield on the response curve is approached, yield increase per unit of N decreases until further increases do not significantly increase yield (Howard and Tyler, 1989; Liegel and Walsh, 1976; Rabuffetti and Kamprath, 1977; Reddy and Reddy, 1993; Schlegel and Havlin, 1995; Thomas, 1956; Welch et al., 1971).

Soil tests also provide a valuable source of information when estimating fertiliser N requirements. They are particularly useful as soils differ both in the amount of residual N and quantity of N mineralized during a growing season (Bundy and Malone, 1988; Oberle and Keeney, 1990a, 1990b; Olsen et al., 1970; Schepers et al., 1986), both of which may be important sources of N (Roberts et al., 1980b; Stanford, 1973; Vanotti and Bundy, 1994a, 1994b). Indeed, soils with a history of high N fertilization may contain sufficient residual N to achieve maximum yield (Douglas et al., 1972; Roberts et al., 1980b; Steele and Cooper, 1980). Hence, levels of residual N are often estimated using a pre-plant soil nitrate test (Bundy and Malone, 1988; Roberts et al., 1980b; Stanford and Hanway, 1955; Stanford and Smith, 1972).

Most N recommendations and density studies focus on maximising ear yield. However, marketable yield is more important to growers of process sweet corn (Pickett, 1944). Marketable ear yield is the yield of ears remaining after discarding ears containing poorly developed kernels (i.e., ears of poor quality). The ears retained are referred to as 'marketable' (Moss and Mack, 1979; Nichols, 1974; Rogers and Lomman, 1988). As ears which do not meet marketability criteria are deducted from payments, marketable ear yield is most important to growers. However, as with ear yield, densities which maximise marketable ear yields vary considerably amongst studies. For example, Rogers and Lomman (1988) reported maximum marketable ear yield between 100,000 and 140,000 plants per hectare. Considerably lower optimum densities of 56,000 to 68,500 plants per hectare were reported by Nichols (1974) and Fery and Janick (1971).

Determining the influence of density or N nutrition on marketable yield is made difficult by the wide range of criteria in the literature used to define marketability. Ear lengths of 102 mm (Chipman and MacKay, 1960), 130 mm (Fery and Janick, 1971), or 178 mm (Warren, 1963) have been used to assess marketability, whereas others have used cob lengths of 100 mm (Smith, 1984), 170 mm (Heckman et al., 1995), or 200 mm (Nichols, 1974). Rogers and Lomman (1988) discarded cobs either ≤ 120 mm long or ≤ 250 g. While all these authors agree that cobs must carry consistently mature kernels, they do not justify the selection criteria. For example, Moss and Mack (1979) rejected cobs of Jubilee < 220 g and in doing so, admitted that some rejected cobs would have been processable. Clearly, the criteria used to determine marketability of cobs must take into account product specifications for the market(s) in question and, for process sweet corn, the processing practices and capabilities of the processor.

Marketable kernel yield (i.e., yield of kernels cut from the rachis - generally referred to as 'recovery' in the processing industry, e.g., Brooking and McPherson (1986)) and marketable cob yield are also important yield variables for processors as they reflect the saleable products. Tsai and Chung (1984) broadly defined a range of 60-180,000 plants per hectare as being optimum for marketable cob yield. A much narrower range of 76,100-109,800 plants per hectare was suggested by Moss and Mack (1979) for Jubilee. Such wide density ranges make it difficult to identify a density which maximises marketable cob yield.

When considering an optimum density for marketable cob yield, cob length becomes important. At Heinz Wattie's Australasia in Gisborne, only cobs with kernels consistently mature over 180 mm in length are used in producing 'whole cob corn' (Davis, pers. comm.). Over the range where marketable cob yield increases with density, cob length decreases (Bailey, 1941; Chipman and MacKay, 1960; Colville, 1961; Enzie, 1942; Freyman et al., 1972; Moss and Mack, 1979; Rutger and Crowder, 1967). For example, marketable cob yield increased 35% in Moss and Mack's (1979) study as density increased from 43,900 to 109,800 plants per hectare while mean length of primary cobs decreased 19 mm. Nitrogen nutrition is a further complicating factor as cob lengths increase with N fertiliser. Increases of 11% were reported in Smith's (1984) study, although lengths were unaffected in Wong et al.'s (1995) study, even with 310 kg N/ha applied.

As most secondary ears do not meet marketability criteria they are generally regarded as waste by processors. While it is generally accepted that weight and length of secondary ears decline with increasing density (Lang et al., 1956; McAllan and Phipps, 1977; Moss and Mack, 1979; Poneleit and Egli, 1979; Stickler, 1964), few studies have examined how their yield contribution changes with density. Of those that have (e.g., Moss and Mack, 1979; Tetio-Kagho and Gardner, 1988b), no attempts were made to model the relationship. Durieux et al. (1993) reported that secondary ears may contribute 25% of yield for plants grown at 43,000 plants per hectare, and hence may be an important contributor to marketable yields.

Manipulating density and N rate may provide increases in yield (marketable or otherwise) of SS42 and Jubilee approaching the yield potential for a given environment. Thereafter, yields will unlikely increase unless their yield potential is increased. Thus, if yield is to be increased beyond manipulating planting and fertiliser regimes, physiological barriers limiting yield must be identified. Identifying such barriers is vital if breeders are to select for the right attributes. Valuable information may be gained by studying the association between yield and yield components (e.g., primary and secondary ear weights, silk delay, stalk diameter, tillers per plant) under various states of crop stress.

The extent to which the secondary ear influences the weight of the primary ear for either Jubilee or SS42 is unknown. Ear priority for photoassimilate in maize is in the order of ear 1 > ear 2 > ear 3 (Tetio-Kagho and Gardner, 1988b; Tollenaar, 1977). Observed reductions in the size of the secondary ear may therefore be attributed to the dominance of the primary ear (Bauman, 1960; Durieux et al., 1993; Harris et al., 1976; Pinthus and Belcher, 1994; Prine, 1971). However, diverting photoassimilate to the secondary ear reduces that available for the primary ear, therefore placing them in direct competition (Eddowes, 1969; Haynes and Sayre, 1956). Such competition by the secondary ear was suggested by Hallauer (1974) to reduce the size of the primary ear. In contrast, Camberato (1987) and Durieux et al. (1993) observed that the presence of a secondary ear was actually accompanied by increased weight of the primary ear.

At high densities, silk delay can dramatically influence sink strength of ears, and thus be an important yield determinant. Silk delay, the time difference between silking of the primary ear

and anthesis (Collins, 1963; Edmeades and Daynard, 1979a), was described by Moss and Stinson (1961) as the most important variable affecting fertilization and grain formation. Delays as short as five days may reduce yield per plant (Edmeades and Daynard, 1979a), even causing barrenness (the failure to produce grain - Harris et al., 1976; Iremiren and Milbourn, 1980). Increasing density (Buren et al., 1974; Daynard and Muldoon, 1983; Downey, 1971; Edmeades and Daynard, 1979a; Modarres et al., 1998; Woolley et al., 1962) or N stress (Anderson et al., 1984b; Tanaka and Yamaguchi, 1972) may delay silking such that the supply of viable pollen is inadequate for full seed set (Hashemi-Dezfouli and Herbert, 1992; Moss and Stinson, 1961; Sass and Loeffel, 1959).

Tillers may also be an important yield determinant as they contribute photoassimilate to the stalk (Alofe and Schrader, 1975; Earley et al., 1971), which may in turn be transported to the ear (McAllan and Phipps, 1977). Both Alofe and Schrader (1975), using ^{14}C labelling, and Russelle et al. (1984) and Kovacs (1970) using ^{32}P labelling, concluded that a large, barren tiller could make a considerable contribution to the main plant. Reports of increased yield with tillers (Downey, 1972; Dungan, 1931; Lyon, 1905; Montgomery, 1909; Rosenquist, 1968) further suggest that tillers may be a source of photoassimilate. Despite such reports, other authors have regarded tillers as being unimportant, even suggesting that they reduce yield (e.g., Dungan et al., 1958; Tetio-Kagho and Gardner, 1988a; Wianko, 1911). These authors suggest that photoassimilate partitioned to developing tillers was wasted because as tillers become shaded under the increasing shade conditions of a closing canopy their photosynthetic rate declines (Kasperbauer and Karlen, 1986) and they may senesce (Dungan, 1946; Montgomery, 1909). It is likely that their contribution to yield declines with density because decreases in tiller number are associated with decreased stalk diameters (Downey, 1972; Dungan, 1931; Genter and Camper, 1973; Kasperbauer and Karlen, 1994; Moss and Mack, 1979; Rosenquist, 1968; Rutger and Crowder, 1967). However, increases in tiller number and stalk diameter with N (McClelland, 1928; Wu et al., 1993) suggest that N fertility may prolong the ability of tillers to contribute photoassimilate. Without a physiological basis for claiming tillers are 'unimportant', workers may be dismissing an important yield determinant.

With the goal of identifying optimum densities and N rates for sweet corn production in Gisborne, the first objective of this experiment was to quantify the relationship between density and N rate on yield of Jubilee and SS42. The second objective was to determine marketability criteria and to use these criteria to identify densities which maximise marketable yield of SS42 and Jubilee. The third objective was to examine the association between yield and yield components, and their response to density and N rate.

2.2 Materials and methods

This experiment was located near Gisborne, New Zealand (longitude 178°, latitude 38.7°) and commenced during spring 1995.

2.2.1 Soil characteristics

The soil type was a Kaiti clay loam (Pullar, 1962) with a cropping history of tomatoes and pasture. Sweet corn had been used as a rotational crop every 3-4 years. In October 1995 the field was ploughed and disced to 150 mm. Three weeks prior to sowing, nine soil samples (150 mm depth) were taken throughout the field. Ammonium- and nitrate-N were extracted from samples using 2M KCl, following the method of Keeney and Nelson (1982), and determined using an autoanalyser. Results are expressed on an air-dried basis (Table 2.1) and converted to kg/ha following the method of Lemcoff and Loomis (1986) (i.e., nutrient concentration (μg/g) × depth sampled (m) × bulk density[1] (g soil/cm^3) × 10). Excess soil was frozen (-18 C). During April 1996, mineralizable N (Table 2.1) of frozen samples was determined using anaerobic incubation for two weeks following the method of Craighead and Clark (1989). Chi-square analysis of the data for each nutrient indicated that no nutrient gradients were present in the field.

[1] Soil correction factor (g/ml) was substituted for bulk density.

Table 2.1. Summary of soil test results.

Nutrient	kg/ha[z]
Ammonium N	15.15 (1.79)
Nitrate N	73.39 (4.25)
Mineralizable N	170.4[y] (17.0)
Phosphorous	78.83 (6.99)
Sulphate	18.26 (1.24)
	meq/100 g
Potassium (exchangeable)	1.27 (0.11)
Calcium (exchangeable)	27.9 (0.75)
Magnesium (exchangeable)	3.28 (0.08)
Sodium (exchangeable)	0.20 (0.01)
Cation exchange capacity	40.7 (0.53)
pH	6.0 (0.10)
Organic matter (%)	5.25 (0.97)

[z] Brackets represent SE (n=9)
[y] Mean and SE of six observations

2.2.2 Experimental design

Constraints imposed by current production practices were incorporated into the design of the experiment to enable direct comparisons with current practices and to aid commercial adoption of any improvements suggested by the results. For example, as commercial sweet corn production in New Zealand is based exclusively on 760 mm row spacings, plant density treatments were established by varying the within row spacings only. Similarly, as urea (46% N) is the predominant N fertiliser used in Gisborne, a consequence of its low cost per unit of N (Davis, pers. comm.), it was used as the sole N source.

The experiment comprised a factorial set of treatments in a fully randomized split-plot design with four blocks. The main plot factor was N rate with density as the split plot factor. Nitrogen rates were 0, 74, 115, 172, or 230 kg/ha with densities of 40,710, 55,710, 68,980, 79,920, or 100,660 plants per hectare. The levels of both density and N rate were decided from machine settings and the ease with which the settings could be changed. To achieve these densities, seed was sown at intervals of 161, 236, 191, 165, or 131 mm, respectively, in rows 760 mm apart. At V2 (i.e., when the ligule of the second leaf was visible; Ritchie and Hanway, 1984), alternate seedlings in the 40,710 plants per hectare treatment (161 mm spacing) were removed.

Each plot was 12 rows wide and 11 m long with the outer three rows and 1.5 m ends of each plot serving as guard plants (Douglas et al., 1982). Blocks were separated by 6 m of plants and the experimental area was bounded on all four sides by 24 or more rows of sweet corn. To avoid cross-pollination between the *su1* and *sh2* genotypes, separate experiments were run for Jubilee and SS42 in adjacent areas of the same paddock, but separated by time of sowing.

2.2.3 Crop management

On November 8 the field was sprayed with 2.7 kg atrazine/ha and harrowed. Jubilee and SS42 were sown November 10 and November 29, respectively, to a depth of 25 mm using a John Deere four-row finger planter. Counter 20G® (terbufos) was applied at sowing at 1.0 kg a.i./ha to control Argentine stem weevil (*Listronotus bonariensis*). No fertilizers were included at planting. At V1 and V4 plants were sprayed with Decis® (deltamethrin) at 12.5 g a.i./ha to control cutworm (*Agrotis ipsilon*).

Weeds were controlled with 2.2 kg atrazine/ha applied two days before side-dressing at V4. Urea was applied at 0, 74, 115, 172, or 230 kg N/ha through coulters which placed it 50-100 mm either side of the plant rows and incorporated it to a depth of 50 mm. Control N treatments were also cultivated. Weeds remaining after side-dressing were removed manually.

2.2.4 Growing degree days, rainfall distribution, and incident radiation during ontogeny

Meteorological data were recorded 12 km from the experimental site at a National Institute of Water and Atmospheric Research Ltd (NIWA) station. From planting to harvest Jubilee and SS42 accumulated 1252 and 1204 growing degree days (GDD; base 6 C; Brooking and McPherson, 1989), respectively (Fig. 2.1a). During this period, 229 and 298 mm of rain fell for Jubilee and SS42, respectively (Fig. 2.1b). Incident radiation during the experiment totalled 2065 $MJ \cdot m^{-2}$ for Jubilee and 1850 $MJ \cdot m^{-2}$ for SS42.

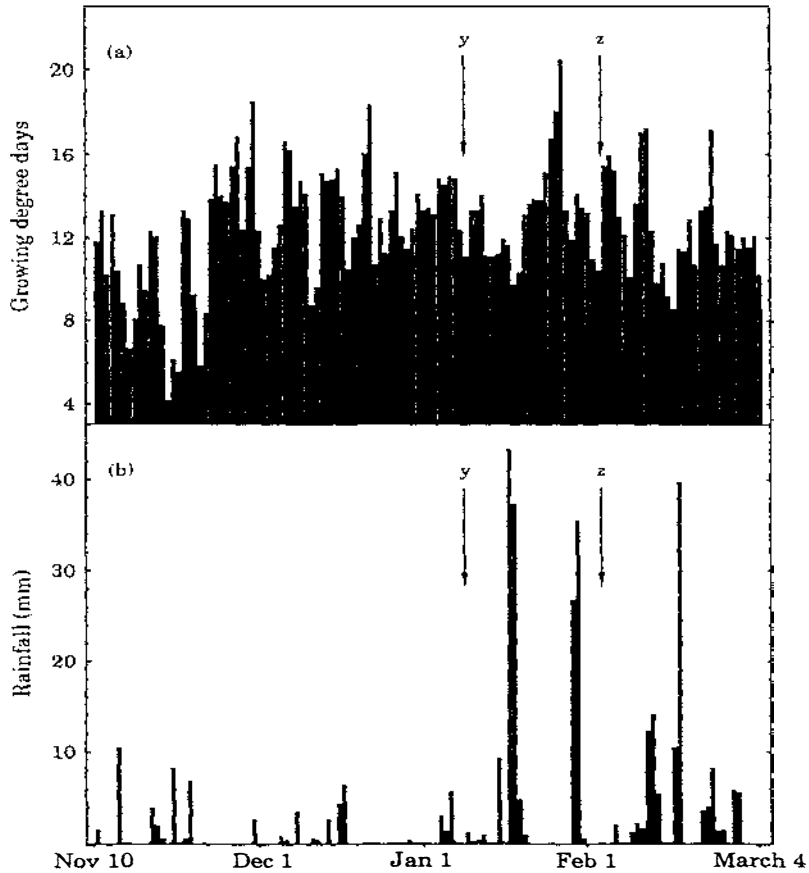

Fig. 2.1. Distribution of (a) growing degree days and (b) rainfall during the cropping period. Arrows *y* and *z* indicate the date at which 50% of plants of Jubilee and SS42, respectively, had 'silked'; January 7 and February 5, respectively.

2.2.5 Pre- and post-harvest measurements

At V4, 25 plants in each plot were randomly selected and labelled. Labelling at this early stage avoided possible bias in plant selection at later ontogenetic stages. At R1, the dates of anthesis of the primary tassel and silking for both primary and secondary ears and the number of ears which 'silked' were recorded for each plant. Anthesis was defined as the date at which 50% of male florets on the primary tassel had opened, with the first appearance of silks from the tip of the prophyll signalling silking (Edmeades, 1972). Flowering variables were recorded daily between 4.30 and 8.30 pm. Two days prior to harvest, tiller number, lodging, and stalk diameter were recorded for each plant. Stalk diameter was measured between the root crown and the first node. A plant was defined as having lodged if its stem was angled $\geq 45^{\circ}$ from vertical.

The seed moisture content (SMC) of primary ears from randomly selected plots was assessed daily for the six days leading up to harvest. Jubilee and SS42 were harvested when SMCs of primary ears were 72% (February 16) and 76% (March 4), respectively; the typical SMC for these hybrids when harvested for processing. Before hand harvesting ears were labelled according to position on the plant (i.e., primary, secondary, tertiary, or tiller). Harvested ears were graded as either harvestable or non-harvestable; a harvestable ear having a maximum diameter greater than 40 mm or length greater than 150 mm (i.e., the size of mechanically harvested cobs; Davis, pers. comm.). Non-harvestable ears were discarded. Plants for which the primary ear was discarded were classified as barren. Those plants on which the secondary ear was discarded were classified as secondary ear barren. Harvestable ears were sorted into groups of primary or secondary ears. Shanks were cut to 30 mm, and loose husk leaves discarded. This procedure not only standardized shank lengths, but simulated mechanical harvesting (Fig. 2.2). Each ear was then weighed, husked, reweighed, and the cob measured for length. Length was measured from the butt of the cob to the tip. Kernels were cut from rachis using a Food Manufacturing Corporation corn cutter (model SC-120) and rachis (Fig. 2.3) weights recorded. Once each group had been processed, the bulk kernel sample was weighed and a 50 cm^3 sample removed for SMC. Samples for SMC were prepared by pulping kernels for 30 seconds at high speed using a Waring blender. The SMC of a 3 g subsample was then determined using a Sartorius Infra-Red Analyser (model YTCO1L).

Fig. 2.2. Comparison of hand harvested (top), mechanically harvested (middle), and standardized ears (bottom).

Fig. 2.3. Rachis after kernel removal.

2.2.6 Data analysis

Treatment effects on the means for each plot were analysed using ANOVA with regression analysis used to model trends. Models for regression analysis were selected based on biological relevance, significance of coefficients at the 5% level, and reduction in residual sums of squares (RSS). The assumptions underlying regression analysis (Mead et al., 1993) were checked using plots of studentised residuals against fitted values, normal probability plots, and Durbin-Watson statistics (data not presented).

Cultivars were not included in the experiment design due to being unable to standardise results for the different yield variables. For example, to compare marketable ear yield would require standardising for husk and rachis moisture contents which were unknown. Any comparison of cultivars in this experiment is therefore qualitative only.

All data in this and ensuing chapters were analysed using the Statistical Analysis System (SAS; SAS Institute, 1989). All results are discussed as being significant at the 5% level unless otherwise stated.

Adjusting data for significant block effects

Data were adjusted using indicator variables to fit a single regression line to data where block effects were significant (Colwell, 1994). Coefficients for indicator variables from this model were then added to the original means after reversing the sign of the coefficient. The model was re-run using adjusted data but without the indicator variables. Checks were made on RSS to ensure they remained unchanged in both models. In using indicator variables in this manner, data are adjusted against a reference block. That is, the coefficient for the indicator variable indicates how much higher or lower the yields from other blocks are compared to the reference block. To avoid 'over adjusting' the data, the reference block upon which data were adjusted excluded the highest and lowest yielding blocks.

Non-linear regression

Many of the density × yield relationships were modelled using an exponential term to represent an asymptotic tendency (Mead et al., 1993; Equations 2.1 and 2.2). Equation 2.3 is an extension of Equation 2.1 to allow a lower asymptote (Ratkowsky, 1990). Where an asymptote was not evident, either the reciprocal model (Equation 2.4; Ratkowsky, 1990; Willey and Heath, 1969) or the similar Gunary model (Equation 2.5; Gunary, 1970) were used, both of which allow relative maxima (Ratkowsky, 1990). The logistic model (Equation 2.6) was used to model sigmoidal responses having a lower asymptote of zero and a finite upper asymptote (Ratkowsky, 1990). Adding a constant to this model allowed a non-zero lower asymptote to be specified (Equation 2.7).

$$y = a(1-e^{-kx}) \tag{2.1}$$

$$y = ae^{-kx} \tag{2.2}$$

$$y = b-a(1-e^{-kx}) \tag{2.3}$$

$$y = \frac{x}{(a+bx+cx^2)} \tag{2.4}$$

$$y = \frac{x}{(a+bx+c\sqrt{x})} \tag{2.5}$$

$$y = \frac{a}{(1+e^{-b+cx})} \tag{2.6}$$

$$y = \frac{a}{(1+e^{-b+cx})} + d \qquad (2.7)$$

To account for non-constant variance, models were weighted by the inverse of the SE of the mean for each density (Chatterjee and Price, 1991). Coefficients of determination for these models were calculated using Equation 2.8.

$$R^2_{adj} = 1 - \left(\frac{n-1}{n-p} \times \frac{RSS}{TSS} \right) \qquad (2.8)$$

where R^2_{adj} is the adjusted coefficient of determination; n is the total degrees of freedom; p is the number of parameters in the model; RSS and TSS are the residual and total sums of squares for the model, respectively.

Independent variables in functions of ensuing graphs are expressed as plants per m^2. For clarity in graphs where significant N effects were recorded, data were pooled across blocks. In these instances, pooling was conducted after analysis.

Chi-square analysis

Count data were generated when determining whether an ear was harvestable or not (i.e., barrenness; Section 2.2.5). Chi-square analysis was used to determine whether barrenness was dependent on density, N rate, or both. The chi-square statistic tests the hypothesis that the parameter estimate is zero (i.e., no linear dependence; Ott and Mendenhall, 1990). For ease of discussion, data are presented as percentages.

Logistic regression

Logistic regression was used to investigate the relationship between whether a cob was marketable or not and the explanatory variables of cob weight and length. Assumptions

underlying logistic regression (e.g., homogeneous variation; Hosmer and Lemeshow, 1989) were checked for each model.

Probability estimates

All harvestable ears were processed, regardless of quality. It was noted, however, that some cobs carried pale and poorly formed kernels. Kernels recovered from such cobs were generally poorly cut and would often jam in the 'cutter'. Normally, such cobs would be discarded during processing. Preliminary data analysis indicated that cobs giving recoveries $\leq$ 70 g would have been discarded. Modelling the relationship between kernel recovery and cob or ear weight using simple linear regression analysis enabled the cob or ear weight expected to give a recovery of $\leq$ 70 g to be estimated. These estimates were then used as criteria for determining marketable yield of kernels, cobs, and ears.

In estimating the probability that ears, cobs, or kernel recoveries would be marketable, z-scores were calculated (Equation 2.9).

$$z^* = \frac{\bar{x} - \mu_0}{\sigma_{\bar{x}}} \qquad (2.9)$$

Where z^* is the z-score; $\bar{x}$ is the sample mean; μ_0 is a specified value; $\sigma_{\bar{x}}$ is the sample standard deviation.

The z-score statistic is normally distributed with mean zero and unit variance (Ott and Mendenhall, 1990). Thus, a significance level for the z-score can be derived from the normal probability density function. The significance level is equivalent to the probability that the sample mean is greater than the specified value.

Path analysis

Path analysis is a form of structured multiple regression analysis which can be used to investigate relationships among standardized variables (MacKay, 1995). The advantage of such an analysis is that the effect of one variable on another can be isolated from influences of other variables. By calculating the sign and significance of path coefficients, the direct effect of each variable on another is revealed following removal of the indirect effects exerted by other variables (Li, 1975; Wright, 1921). The greater the magnitude of the path coefficient, the greater its direct effect.

Path analysis has been used to evaluate yield components in many agronomic crops (e.g., Dewey and Lu, 1959; McGiffen et al., 1994; Pandey and Torrie, 1973; Shasha's et al., 1973), but is infrequently used in plant research (Hicklenton, 1990; Karlsson et al., 1988). The reasons for this are unclear, but may reflect the absence of path analysis routines in statistical software packages (MacKay, 1995).

In this study, path analysis provided the opportunity to examine a possible structural relationship between ear weights and variables influencing their weights (e.g., stalk diameter, tiller number, silk delay). A structure may offer a plausible interpretation of the relationships among these variables.

The path coefficients are equivalent to standardized partial regression coefficients. Thus, raw data were standardized to zero mean and unit variance, and multiple linear regressions, consistent with the postulated path diagrams, performed. As estimates of regression analysis are distorted if excessive collinearity exits among the independent variables in the model, appropriate measures of collinearity (e.g., variance inflation factors; Myers, 1990) were checked for each model.

Harvestable ear weight (Section 2.2.5) was used as the response variable in multiple regression models used for path analysis as using this variable avoided the problem of insufficient data for secondary ears at high densities. Thus, rather than treating a non-harvestable ear as a missing

value, it was treated as zero harvestable weight. Plants where data was missing for other variables used in multiple regression were deleted before calculating correlation coefficients.

Canonical discriminant analysis

By reducing the dimensionality of data sets, canonical discriminant analysis (CDA) identifies and summarises important differences among treatments, while recognising the complex relationships among many variables (Cruz-Castillo et al., 1994). In finding the linear combination of variables contributing to differences amongst treatments, CDA maximally separates groups of individuals while keeping variation within groups as small as possible.

Data for CDA were not standardized as the outcome is unaffected by the scale of individual variables (Manly, 1986). However, because curvilinear or nonlinear relationships between two variables will not be reflected in the results of CDA unless suitable transformations are first performed (Mathew et al., 1994), the need for such transformations was checked by plotting each variable pair as recommended by MacKay (1995).

As with regression analysis, cases with missing data are ignored in CDA. Thus, to avoid a shortage of data at high densities, harvestable ear weight (Section 2.2.5) was used with non-harvestable ears treated as zero harvestable ear weight.

2.3 Results

2.3.1 Analysis of SS42 harvest data

Kernel loss during processing was less than 0.5 g (SE 0.04) per cob and was independent of treatment. Seed moisture contents of kernels from primary and secondary ears were 76.9% (SE 0.86) and 79.1% (SE 0.97), respectively, and were also independent of treatment.

2.3.1.1 Barrenness

Barrenness, determined by the number of non-harvestable primary ears, increased with density (Table 2.2). At 40,710 plants per hectare, 1.5% of plants were barren, rising to 16% at 100,660 plants per hectare.

Table 2.2. Influence of density on the proportions of harvestable and non-harvestable primary ears of SS42.

	Plants per hectare					
	40,710	55,710	68,980	79,920	100,660	Total
Non-harvestable ears (%)	1.5	2.7	6.4	8.6	16.1	35.3
Harvestable ears (%)	98.5	97.3	93.6	91.4	83.9	464.7
Total	100.0	100.0	100.0	100.0	100.0	500.0

$\chi^2 = 94^{***}$

$^{NS, *, **, ***}$ Nonsignificant or significant χ^2 test at $P \leq 0.05, 0.01, 0.001$, respectively.

Nitrogen rate did not influence the proportion of barren plants. Similarly, the combination of density and N rate did not influence the level of barrenness.

All barren plants were also secondary ear barren. Thus, as with primary ears, the proportion of plants barren for the secondary ear also increased with density (Table 2.3). However, not only were more plants secondary ear barren, but the proportion which were barren increased more rapidly with density (cf. Tables 2.2 and 2.3). At 40,710 plants per hectare, over 39% of plants were secondary ear barren, in contrast to the 1.5% primary ear barren. By 100,660 plants per hectare, primary ear barrenness had increased to 16%, far less than the 96% recorded for secondary ears.

Table 2.3. Influence of density on the proportions of harvestable and non-harvestable secondary ears of SS42.

	Plants per hectare					
	40,710	55,710	68,980	79,920	100,660	Total
Non-harvestable ears (%)	39.4	60.6	78.7	93.1	96.1	367.9
Harvestable ears (%)	60.6	39.4	21.3	6.9	3.9	132.1
Total	100.0	100.0	100.0	100.0	100.0	500.0

$\chi^2 = 540^{***}$

$^{NS, *, **, ***}$ Nonsignificant or significant χ^2 test at $P \leq 0.05, 0.01, 0.001$, respectively.

As with primary ears, N rate did not influence the proportion of plants barren for the secondary ear. The proportion of plants with a harvestable secondary ear was not influenced by the combined effects of density and N rate.

2.3.1.2 Harvestable ear yield

Total harvestable ear yield increased as density increased to 70,000 plants per hectare, but began to plateau at higher densities (Fig. 2.4a). Although highest yield of 24.14 (SE 1.47) tonnes was recorded at 100,660 plants per hectare, it was not significantly different to the 23.33 (SE 1.53) tonnes at 68,980 plants per hectare. Yield at 40,710 plants per hectare, on the other hand, was 19.45 (SE 1.42) tonnes and significantly lower (2.94 tonnes) than at 100,660 plants per hectare.

As total yield began to plateau, the yield of primary and secondary ears approached maximal and zero yield, respectively (Figs. 2.4b and 2.4c). Thus, primary ear yield of 22.25 (SE 1.41) tonnes at 79,920 plants per hectare was similar to the 24.32 (SE 1.33) tonnes recorded at 100,660 plants per hectare. Significant increases in primary ear yield were, however, achieved with each increase in density up to 79,920 plants per hectare. Yield of secondary ears, on the other hand, declined significantly with each increase in density between 55,710 and 100,660 plants per hectare. Thus at 100,660 plants per hectare, total yield comprised about 24.32 (SE 1.33) tonnes

of primary and 0.11 (SE 0.18) tonnes of secondary ears. In contrast, yield at 40,710 plants per hectare comprised about 15.27 (SE 1.34) and 5.09 tonnes (SE 0.42), respectively.

As yield data were based on harvestable weights for the 25 plants in each plot, the calculated means may have included plants whose contribution to harvestable weight was nil. In other words, some of the 25 plants may have been barren for the primary ear, secondary ear, or both (Tables 2.2 and 2.3). Hence, inferences regarding the distribution of ear weights from ear yields (Figs. 2.4a and 2.4b) may be misleading. To enable kernel recoveries, ear weights, and cob weights to be determined, non-harvestable ears were treated as missing values.

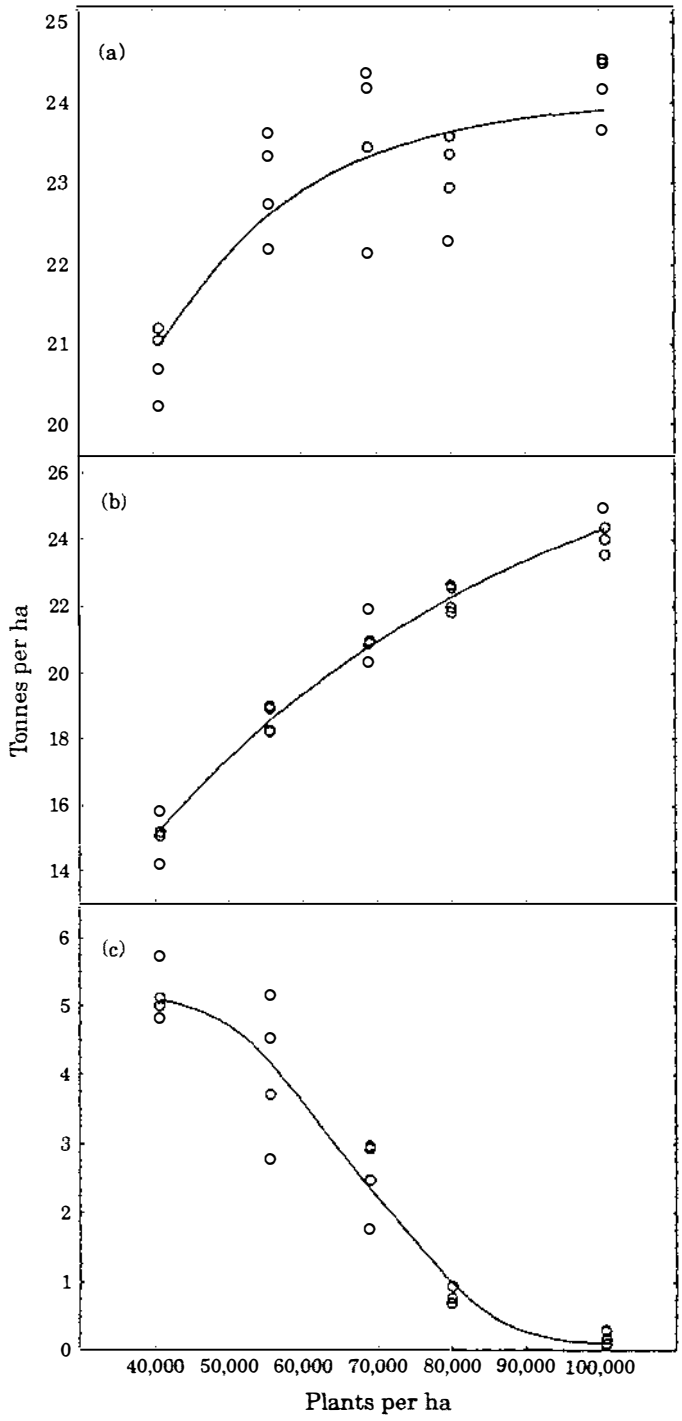

Fig. 2.4. Harvestable ear yield of SS42 as affected by density for (a) total, (b) primary, and (c) secondary ears. Data are the means for each density and block, pooled across N rates. Data in (a) and (b) were adjusted for significant block effects. Fitted function for (a) is $Y=24.06(1-e^{-0.50X})$ ($R^2_{adj}=0.73$). Fitted function for (b) is $Y=28.73(1-e^{-0.19X})$ ($R^2_{adj}=0.97$). Fitted function for (c) is $Y=5.36/(1+e^{-7.59+1.14X})$ ($R^2_{adj}=0.95$).

2.3.1.3 Kernel recoveries

Kernel recovery from primary cobs decreased from 184 g (SE 14.4) to 135 g (SE 14.4) per cob as density increased from 40,710 to 100,660 plants per hectare (Fig. 2.5a). Despite this 27% decline, recoveries, even for the 100,660 plants per hectare treatment, were still 65 g above the 70 g rejection level determined in Section 2.2.6. The associated probability that a recovery (SD 52.6)[2] from this treatment would be ≤ 70 g, was 0.10. Hence, an estimated 10% of primary cobs would have been discarded at 100,660 plants per hectare. In contrast, fewer than 1.2% of cobs for the 40,710 plants per hectare treatment (SD 50.5) would have been discarded.

A significant density × N rate interaction was detected for recoveries from secondary ears. A major contributor to the significant interaction was the 74 kg N/ha treatment as this treatment had lower recoveries than the control at both the highest and lowest densities, but recoveries almost as great as the 230 kg N/ha treatment at intermediate densities (Fig. 2.5b). However, recoveries from the 74 kg N/ha treatment were not significantly different from other N treatments, regardless of density. Irrespective of density, highest recoveries were achieved at 230 kg N/ha and were significantly higher (about 19%) than the control. Other N treatments gave recoveries similar to the control and 230 kg N/ha treatments. Although recoveries increased with N fertiliser, recoveries declined 68% as density increased from 40,710 to 100,660 plants per hectare. The highest mean recovery was 121 g (SE 18.8) per cob recorded for the 40,710 plants per hectare and 230 kg N/ha treatment. The lowest mean recovery was 9 g (SE 8.7) for the 100,660 plants per hectare and 74 kg N/ha treatment.

Where 230 kg N/ha was applied, only plants grown at densities less than 75,520 plants per hectare had 50% or more secondary cobs with recoveries ≥ 70 g (Fig. 2.5b). At 40,710 plants per hectare and 230 kg N, 25% of secondary cobs (SD 52.8) would have been rejected, far less than the 81% for the 74 kg N/ha treatment at 100,660 plants per hectare which had a recovery of only 9 g (SD 50.1).

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[2] Standard deviations refer to the distribution of kernel recoveries at the density, N rate, or both, under discussion.

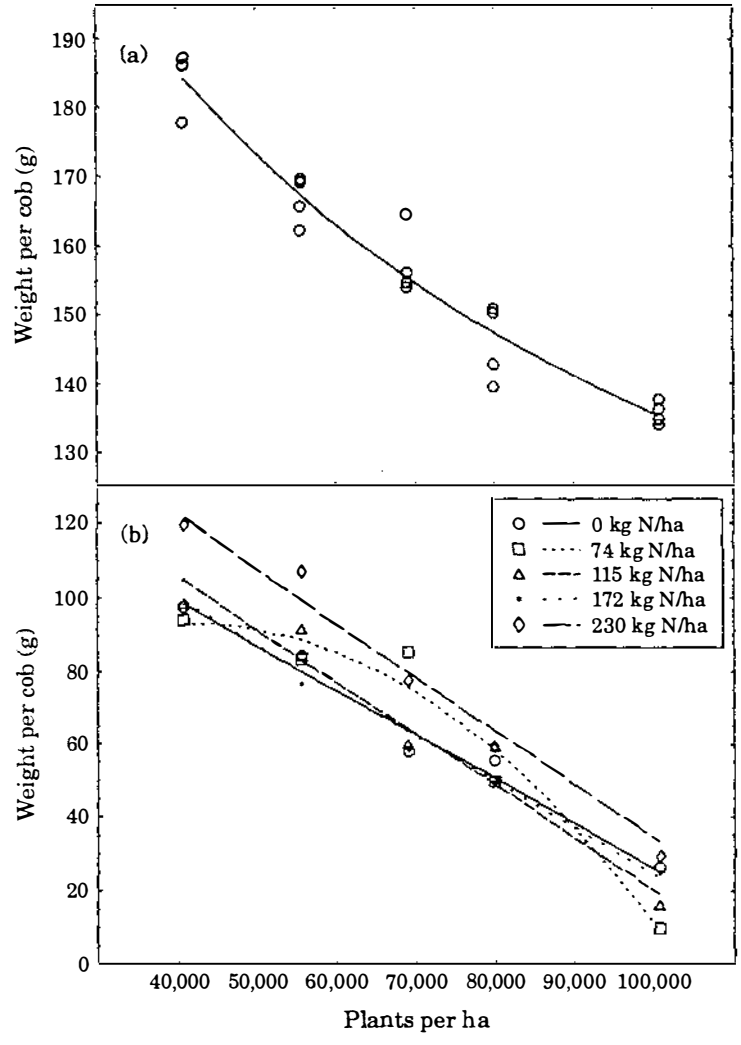

Fig. 2.5. Kernel recoveries for SS42 as affected by density and N rate for (a) primary and (b) secondary ears. Data in (a) are the means for each density and block, pooled across N rates. Data in (b) are the means for each density and N rate. Fitted function for (a) is $Y=257.12-152.16(1-e^{-0.16X})$ ($R^2_{adj}=0.95$). Fitted functions for (b): 0 kg N/ha, $Y=148.14-12.22X$ ($r^2=0.65$); 74 kg N/ha, $Y=49.30+20.77X-2.46X^2$ ($R^2_{adj}=0.69$); 115 kg N/ha, $Y=162.88-14.29X$ ($r^2=0.70$); 172 kg N/ha, $Y=150.43-12.61X$ ($r^2=0.79$); 230 kg N/ha, $Y=181.09-14.71X$ ($r^2=0.81$).

2.3.1.4 Harvested ear and cob weights

Increasing density from 40,710 to 100,660 plants per hectare resulted in the average weight of both primary ears and cobs decreasing about 23% (Figs. 2.6a and 2.7a). Primary ear weight declined from 376 g (SE 21.8) to 288 g (SE 21.9) as density increased from 40,710 to 100,660 plants per hectare, while weight of primary cobs declined from 326 g (SE 19.8) to 255 g (SE 19.9). Although weights declined 11% between 68,980 and 100,660 plants per hectare, this decline was not statistically significant for either ears or cobs.

Consistent with kernel recoveries from secondary ears (Fig. 2.5b), a significant density × N rate interaction was recorded for weight of secondary ears and cobs. At the highest and lowest densities, heaviest ears were recorded with 230 kg N/ha. However, at intermediate densities the 74 and 172 kg N/ha treatments gave heaviest ears and cobs (Figs. 2.6b and 2.7b). Although at intermediate densities all N rates gave significantly heavier ears than the control, only the 230 kg N/ha treatment gave significantly heavier ears than the control at lowest densities. At 100,660 plants per hectare, all N treatments gave similar ear weights. Differences amongst N treatments for cob weight at any density were also not significant. Heaviest secondary cobs were recorded at 40,710 plants per hectare with 230 kg N/ha (i.e., 249 g (SE 24.0)) and lowest at 100,660 plants per hectare with 115 kg N/ha (i.e., 37 g (SE 42.3)).

The predicted weight of primary and secondary ears yielding recoveries ≤ 70 g was ≤ 187 g (SE 14.5) and ≤ 182 g (SE 44.7), respectively. Similarly, primary cobs ≤ 164 g (SE 12.3), and secondary cobs, ≤ 151 g (SE 44.8) were estimated to have given a recovery ≤ 70 g. Applying these marketability criteria to the distribution of ear weights at each density gave rejection rates similar to those for kernel recoveries, and to avoid repetition are not reported.

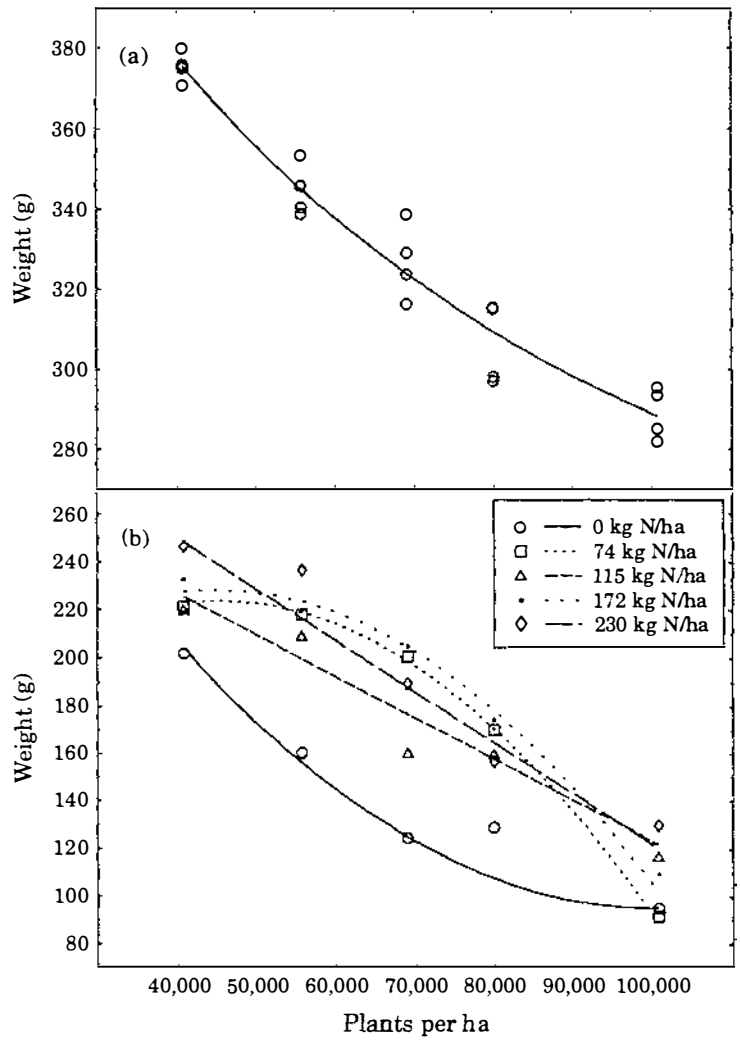

Fig. 2.6. Ear weights of SS42 as affected by density and N rate for (a) primary and (b) secondary ears. Data in (a) are the means for each density, pooled across N rates, and adjusted for significant block effects. Data in (b) are the means for each density and N rate. Fitted function for (a) is $Y=506.22-271.63(1-e^{-0.16X})$ ($R^2_{adj}=0.95$). Fitted functions for (b): 0 kg N/ha, $Y=406.39-62.29X+3.12X^2$ ($R^2_{adj}=0.76$); 74 kg N/ha, $Y=135.47+39.31X-4.37X^2$ ($R^2_{adj}=0.71$); 115 kg N/ha, $Y=296.25-17.62X$ ($r^2=0.86$); 172 kg N/ha, $Y=5.30+5.91X-60.04X^2$ ($R^2_{adj}=0.86$); 230 kg N/ha, $Y=335.68-21.40X$ ($r^2=0.87$).

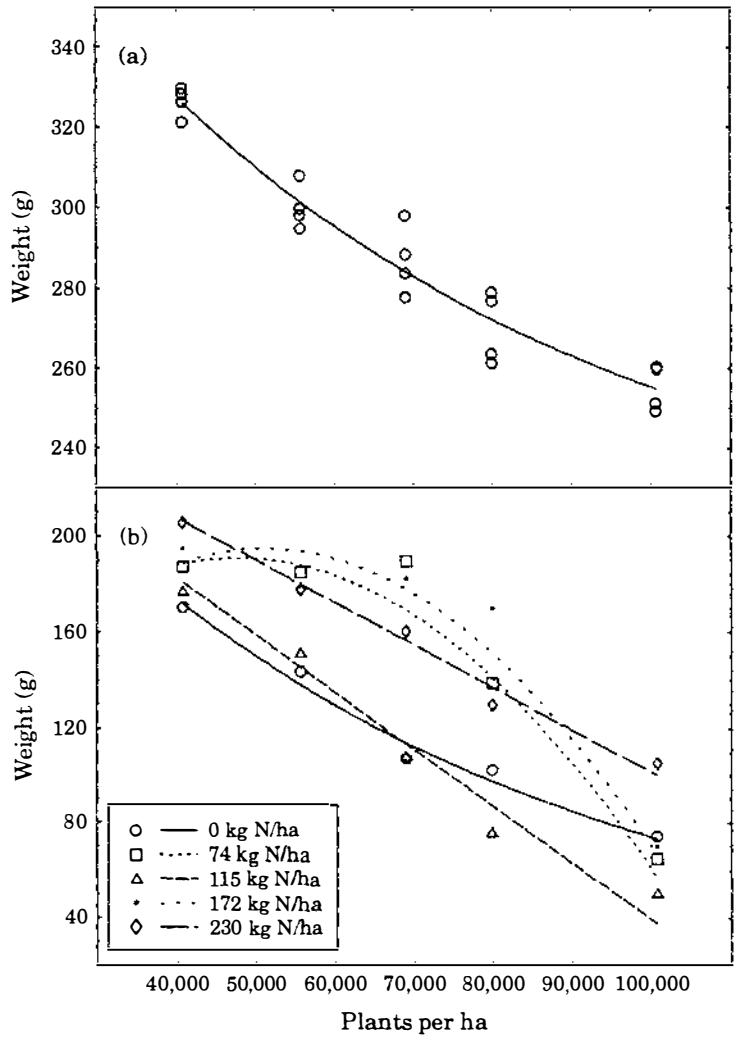

Fig. 2.7. Cob weights of SS42 as affected by density and N rate for (a) primary and (b) secondary ears. Data in (a) are the means for each density and block, pooled across N rates, and adjusted for significant block effects. Data in (b) are the means for each density and N rate. Fitted function for (a) is $Y=433.71-222.00(1-e^{-0.16X})$ ($R^2_{adj}=0.93$). Fitted functions for (b): 0 kg N/ha, $Y=317.05-306.51(1-e^{-0.16X})$ ($R^2_{adj}=0.80$); 74 kg N/ha, $Y=83.75+45.13X-4.75X^2$ ($R^2_{adj}=0.67$); 115 kg N/ha, $Y=278.59-23.96X$ ($r^2=0.74$); 172 kg N/ha, $Y=5.24+4.88X-55.46X^2$ ($R^2_{adj}=0.91$); 230 kg N/ha, $Y=278.61-17.71X$ ($r^2=0.82$).

Yield presented in Fig. 2.4 included ears which would normally be discarded during processing. As processors deduct such ears from payments to growers, analysis now focuses on treatment effects on marketable yield (i.e., yield of ears, cobs, and kernels that meet the marketability criteria determined in Sections 2.3.1.3 and 2.3.1.4).

2.3.1.5 Marketable ear yield

Marketable ear yield was maximised at 80,800 plants per hectare (Fig. 2.8a). The mean yield of 20.72 (SE 0.82) tonnes at this density was 2.54 tonnes greater than at 40,710 plants per hectare, but only 0.19 tonnes greater than at 100,660 plants per hectare. While yield of 17.41 (SE 0.78) tonnes at 55,710 plants per hectare was significantly higher than the 18.18 (SE 0.74) tonnes recorded at 40,710 plants per hectare, it was similar to that recorded at higher densities.

Maximum yield of marketable primary ears was not identified in this study (Fig. 2.8b). Nevertheless, this study found that marketable yield of primary ears increased 6.72 tonnes as density increased from 40,710 to 100,660 plants per hectare. Yield of 20.71 (SE 0.69) tonnes recorded at 100,660 plants per hectare was, however, statistically similar to that at 68,980 plants per hectare (i.e., 19.13 (SE 0.73) tonnes).

As marketable ear yield of primary ears approached a maximum, marketable yield of secondary ears asymptotically approached zero (Fig. 2.8c). Thus at 100,660 plants per hectare, total marketable yield comprised almost solely of primary ears. In contrast, yield at 40,710 plants per hectare comprised about 14.04 (SE 0.68) tonnes of primary, and 3.91 (SE 0.52) tonnes of secondary ears.

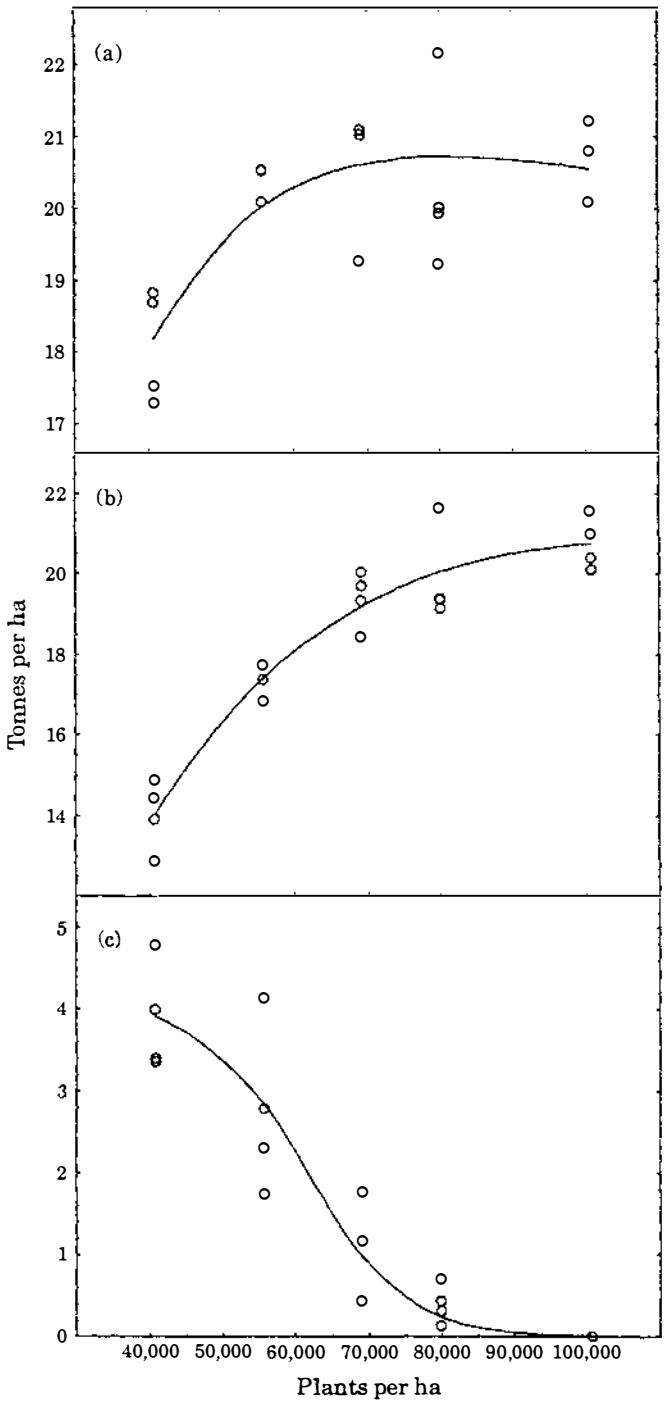

Fig. 2.8. Marketable ear yield of SS42 as affected by density for (a) total, (b) primary, and (c) secondary ears. Data are the means for each density and block, pooled across N rates. Data in (a) and (b) were adjusted for significant block effects. Fitted function for (a) is $Y=X/(0.325+0.09X-0.229X^{0.5})$ ($R^2_{adj}=0.60$). Fitted function for (b) is $Y=X/(0.59+0.10X-0.35X^{0.5})$ ($R^2_{adj}=0.93$). Fitted function for (c) is $Y=4.10/(1+e^{-9.10+1.49X})$ ($R^2_{adj}=0.92$).

2.3.1.6 Marketable kernel yield

Marketable kernel yield increased with density up to 77,430 plants per hectare before declining (Fig. 2.9a). Recovery of 10.09 (SE 0.42) tonnes at this density was significantly higher than the 8.82 (SE 0.39) tonnes recorded at 40,710 plants per hectare, but similar to the 9.94 (SE 0.39) tonnes recorded at 100,660 plants per hectare.

Like marketable ear yield results (Fig. 2.8), the density which maximised marketable kernel recovery from primary cobs was not identified in this study (Fig. 2.9b). Nevertheless, recovery from primary ears increased from 6.83 (SE 0.37) to 9.91 (SE 0.37) tonnes as density increased from 40,710 to 100,660 plants per hectare. However, yield of 9.27 (SE 0.39) tonnes at 69,980 plants per hectare was not significantly different to that at 100,660 plants per hectare.

Concomitant with the increase in marketable kernel yield from primary cobs with increasing density was the significant decline in yield from secondary cobs (cf. Figs. 2.9b and 2.9c). Marketable kernel yield from secondary cobs declined from 3.90 (SE 0.29) to 0.01 (SE 0.07) tonnes as density increased from 40,710 to 100,660 plants per hectare. Thus at 77,430 plants per hectare, total marketable kernel yield comprised about 9.58 (SE 0.40) and 0.18 (SE 0.13) tonnes of kernels derived from primary and secondary cobs, respectively.

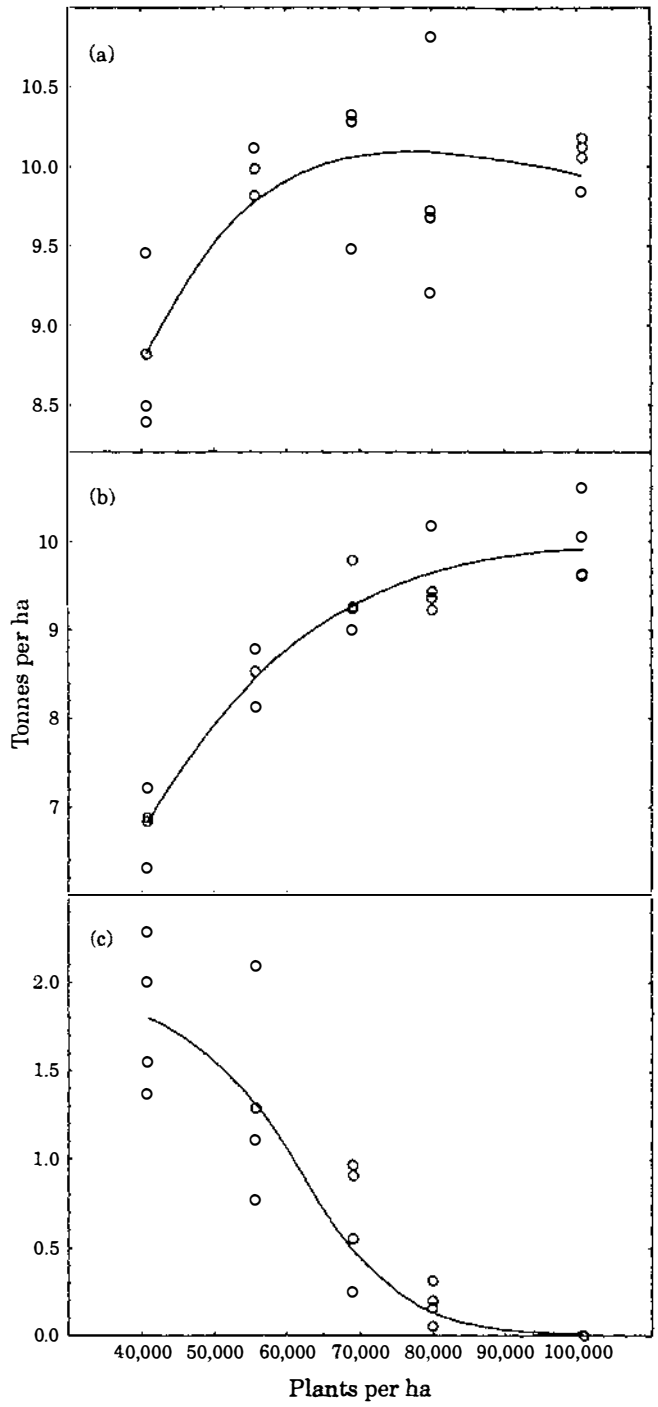

Fig. 2.9. Marketable kernel yield for SS42 as affected by density for (a) total, (b) primary, and (c) secondary ears. Data are the means for each block and density, pooled across N rates. Data in (a) and (b) were adjusted for significant block effects. Fitted function for (a) is $Y=X/(0.768+0.198X-0.552X^{0.5})$ ($R^2_{adj}=0.58$). Fitted function for (b) is $Y=X/(1.27+0.22X-0.78X^{0.5})$ ($R^2_{adj}=0.93$). Fitted function for (c) is $Y=1.90/(1+e^{-8.59+1.40X})$ ($R^2_{adj}=0.90$).

2.3.1.7 Marketable cob yield

Maximum cob yield of 18.58 (SE 0.61) tonnes was calculated at 70,580 plants per hectare (Fig. 2.10a). Although yield declined either side of this density, yield of 17.34 (SE 0.60) tonnes at 55,710 plants per hectare, or similarly, at higher densities was not significantly different to that at 70,580 plants per hectare. Marketable yield of primary cobs also increased with density, although unlike total yield, the maximum yield was not identified in this study (Fig. 2.10b). This trend was consistent with the response of marketable ear and kernel yields for primary cobs to density (Figs. 2.8b and 2.9b). Nonetheless, all three graphs indicate a maximum was being approached about 100,660 plants per hectare as the rate of yield increase with density began to slow. Thus, while increases in density up to 68,980 plants per hectare significantly increased yield of primary cobs, higher densities gave a yield similar to the 16.81 (SE 0.64) tonnes recorded at 68,980 plants per hectare. As marketable yield of primary cobs approached a maximum, yield of secondary cobs asymptotically approached zero yield (Fig. 2.10c). At 100,660 plants per hectare, secondary cobs contributed less than 0.02 (SE 0.09) tonnes to marketable cob yield, 2.92 (SE 0.47) tonnes less than at 40,710 plants per hectare.

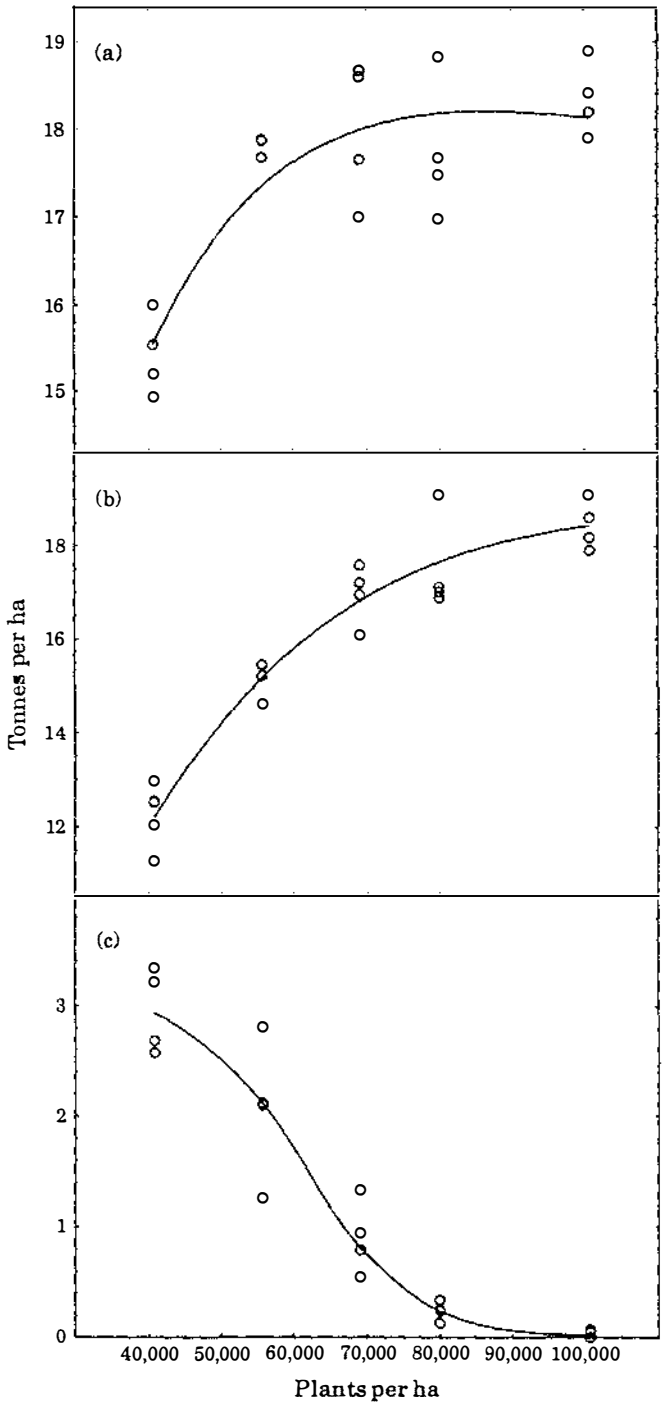

Fig. 2.10. Marketable cob yield of SS42 as affected by density for (a) total, (b) primary, and (c) secondary ears. Data are the means for each block and density, pooled across N rates. Data in (a) and (b) were adjusted for significant block effects. Fitted function for (a) is $Y=X/(0.385+0.099X-0.262X^{0.5})$ ($R^2_{adj}=0.72$). Fitted function for (b) is $Y=X/(0.64+0.106X-0.365X^{0.5})$ ($R^2_{adj}=0.93$). Fitted function for (c) is $Y=3.13/(1+e^{-8.21+1.34X})$ ($R^2_{adj}=0.95$).

2.3.2 Analysis of Jubilee harvest data

Kernel loss during processing was less than 0.5 g (SE 0.09) per cob irrespective of treatment. With no treatment effects on seed moisture contents of kernels detected, the pooled means were 71.0% (SE 1.08) and 73.4% (SE 1.57) for primary and secondary ears, respectively.

2.3.2.1 Barrenness

About 3% of plants were barren at 40,710 plants per hectare (Table 2.4). However, at 100,660 plants per hectare, this figure had increased to 15%, constituting a five-fold increase in barrenness. Unlike density, however, N rate did not influence barrenness. Similarly, there was no interaction between density and N rate for the proportion of plants barren.

Table 2.4. Influence of density on the proportions of harvestable and non-harvestable primary ears of Jubilee.

	Plants per hectare					
	40,710	55,710	69,980	79,920	100,660	Total
Non-harvestable ears (%)	3.4	6.3	7.1	11.9	15.0	43.7
Harvestable ears (%)	96.6	93.7	92.9	88.1	85.0	456.3
Total	100.0	100.0	100.0	100.0	100.0	500.0

$\chi^2 = 48^{***}$

$^{NS, *, **, ***}$ Nonsignificant or significant χ^2 test at $P \leq 0.05, 0.01, 0.001$, respectively.

Although all barren plants were also secondary ear barren, increasing density had a greater effect on secondary ear barrenness than primary ear barrenness (cf. Tables 2.4 and 2.5). For example, 33% of plants were secondary ear barren at 40,710 plants per hectare, but only 3% were primary ear barren. However, at 100,660 plants per hectare the proportion secondary ear barren had increased to over 98%, whereas only 15% were primary ear barren.

Table 2.5. Influence of density on the proportions of harvestable and non-harvestable secondary ears of Jubilee.

	Plants per hectare					
	40,710	55,710	68,980	79,920	100,660	Total
Non-harvestable ears (%)	33.0	60.4	81.0	92.2	98.3	364.9
Harvestable ears (%)	67.0	39.6	19.0	7.8	1.7	135.1
Total	100.0	100.0	100.0	100.0	100.0	500.0

$\chi^2 = 652^{***}$

$^{NS, *, **, ***}$ Nonsignificant or significant χ^2 test at $P \leq 0.05, 0.01, 0.001$, respectively.

Secondary ear barrenness was also influenced by N rate. Compared to the control, 10% fewer plants were barren with 230 kg N/ha (Table 2.6). Despite both density and N rate influencing secondary ear barrenness, there was no interaction between the two.

Table 2.6. Influence of N rate on the proportions of harvestable and non-harvestable secondary ears of Jubilee.

	N rate (kg/ha)					
	0	74	115	172	230	Total
Non-harvestable ears (%)	77.6	76.4	77.2	67.8	67.6	366.6
Harvestable ears (%)	22.4	23.6	22.8	32.2	32.4	133.4
Total	100.0	100.0	100.0	100.0	100.0	500.0

$\chi^2 = 25^{***}$

$^{NS, *, **, ***}$ Nonsignificant or significant χ^2 test at $P \leq 0.05, 0.01, 0.001$, respectively.

2.3.2.2 Harvestable ear yield

Nitrogen fertiliser significantly increased ear yield but its effect was influenced by the planting density. With 230 kg N/ha, yield of 23.60-24.39 (SE 1.72) tonnes (depending on density) was recorded, 4.09 tonnes greater than the control (Fig. 2.11a). Highest yield (25.12 tonnes (SE 1.86)), however, was recorded with 172 kg N/ha at 100,660 plants per hectare. This yield was significantly higher (28%) than the lowest yielding treatment (i.e., 40,710 plants per hectare with no added N). Despite an apparent trend for yield differences between the control and other N treatments to increase with density, in particular the 74 and 115 kg N/ha treatments, differences amongst the three lowest N rates were not significant.

Yield of primary ears increased 7.16 tonnes between 40,710 and 100,660 plants per hectare (Fig. 2.11b). As yield increased with density, differences in yield between N rates increased. Whereas yields were similar among N rates at low and intermediate densities, significant differences among the N treatments were detected from 68,980 plants per hectare onwards. Thus at 100,660 plants per hectare, yield of 25.82 (SE 1.45) tonnes from the 172 kg N/ha treatment was significantly greater than the 21.76 (SE 1.68) tonnes with no added N.

Yield of secondary ears declined 6.7 tonnes as density increased from 40,710 to 100,660 plants per hectare (Fig. 2.11c). However, significant yield increases, particularly at lowest densities, were achieved with added N fertiliser. For example, at 40,710 plants per hectare, a significant increment in yield of 2.56 tonnes was achieved with 230 kg N/ha compared to the control. However, at 100,660 plants per hectare, the increase in yield of secondary ears (i.e., 0.08 tonnes) with additional N was negligible.

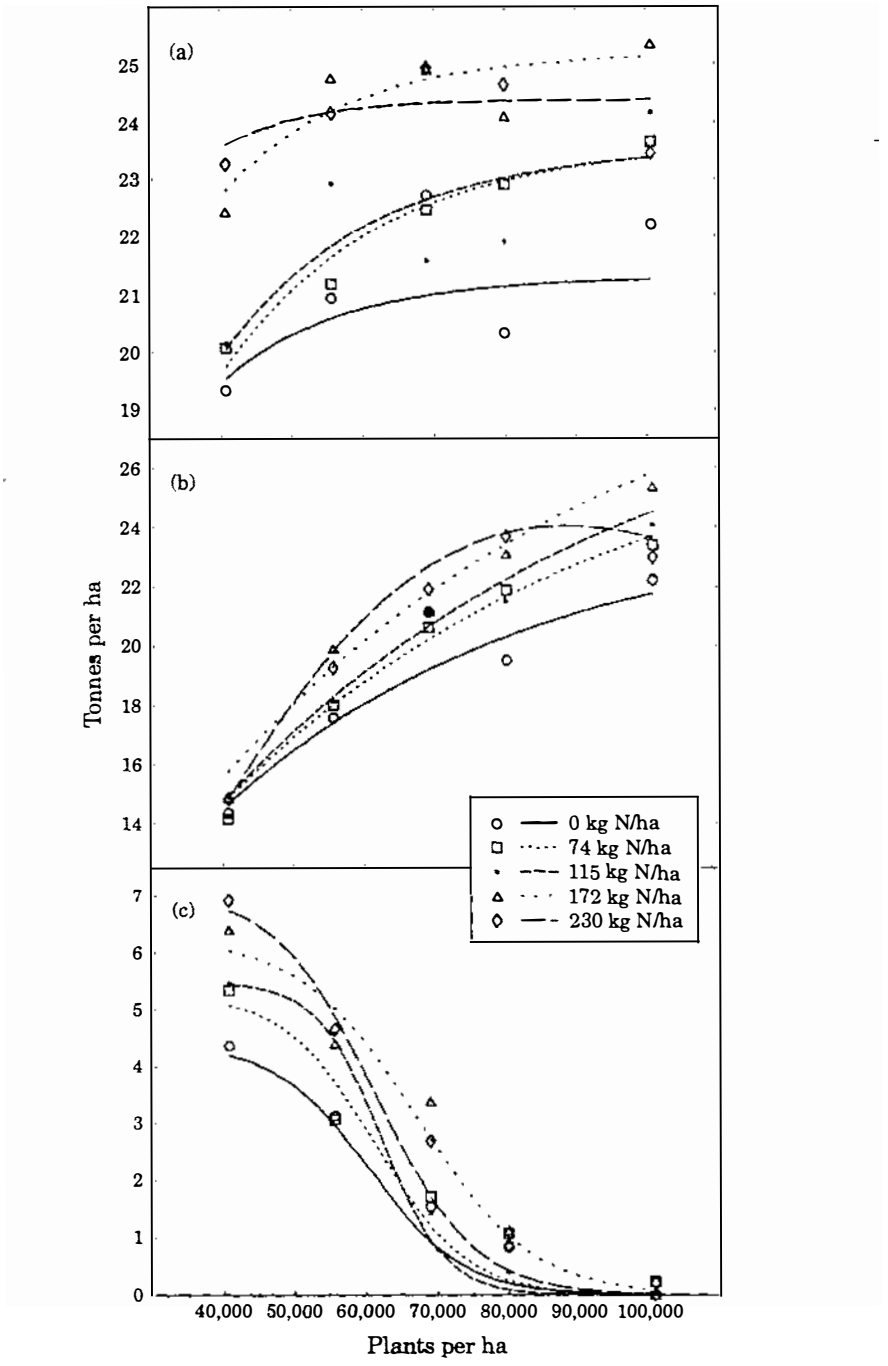

Fig. 2.11. Harvestable ear yield of Jubilee as affected by density for (a) total, (b) primary, and (c) secondary ears. Data are the means for each density and N rate. Fitted functions for (a): 0 kg N/ha, $Y=21.29(1-e^{-0.61X})$ ($R^2_{adj}=0.25$); 74 kg N/ha, $Y=23.66(1-e^{-0.44X})$ ($R^2_{adj}=0.24$); 115 kg N/ha, $Y=23.59(1-e^{-0.47X})$ ($R^2_{adj}=0.24$); 172 kg N/ha, $Y=25.19(1-e^{-0.58X})$ ($R^2_{adj}=0.20$); 230 kg N/ha, $Y=24.40(1-e^{-0.84X})$ ($R^2_{adj}=0.05$). Fitted functions for (b): 0 kg N/ha, $Y=24.16(1-e^{-0.23X})$ ($R^2_{adj}=0.90$); 74 kg N/ha, $Y=28.07(1-e^{-0.18X})$ ($R^2_{adj}=0.82$); 115 kg N/ha, $Y=29.95(1-e^{-0.17X})$ ($R^2_{adj}=0.80$); 172 kg N/ha, $Y=31.49(1-e^{-0.17X})$ ($R^2_{adj}=0.86$); 230 kg N/ha, $Y=X/(0.36-0.04X+0.005X^2)$ ($R^2_{adj}=0.86$). Fitted functions for (c): 0 kg N/ha, $Y=4.38/(1+e^{-9.36+1.55X})$ ($R^2_{adj}=0.72$); 74 kg N/ha, $Y=5.27/(1+e^{-9.73+1.59X})$ ($R^2_{adj}=0.82$); 115 kg N/ha, $Y=5.47/(1+e^{-14.19+2.28X})$ ($R^2_{adj}=0.90$); 172 kg N/ha, $Y=6.25/(1+e^{-8.38+1.25X})$ ($R^2_{adj}=0.93$); 230 kg N/ha, $Y=7.07/(1+e^{-8.96+1.46X})$ ($R^2_{adj}=0.90$).

2.3.2.3 Kernel recoveries

As with SS42, cobs giving kernel recoveries ≤ 70 g would have been discarded during processing due to unacceptable quality. Primary ears ≤ 187 g (SE 17.7), and secondary ears ≤ 195 g (SE 14.2), were estimated to give recoveries ≤ 70 g. Similarly, primary cobs ≤ 157 g (SE 14.0), and secondary cobs ≤ 155 g (SE 11.5), would have been rejected. These criteria were used in this and the next section for calculating the probability that a recovery, ear, or cob would be rejected at the processing stage.

Kernel recovery from primary cobs declined from 187 g (SE 5.5) to 127 g (SE 5.5) as density increased from 40,710 to 100,660 plants per hectare (Fig. 2.12a). Except for the 40,710 and 50,710 plants per hectare treatments, each increase in density significantly decreased kernel recoveries. Despite a 32% decline in recoveries over the density range, recoveries, even at 100,660 plants per hectare (SD 40.4)[3] were still 57 g above the 70 g the cutoff point for being marketable. Thus an estimated 7.5% of primary cobs grown at 100,660 plants per hectare would have discarded during processing. In contrast, fewer than 0.1% of cobs grown at 40,710 plants per hectare would have been rejected (SD 38.0).

Kernel recovery from secondary cobs decreased 81% as density increased from 40,710 to 100,660 plants per hectare (Fig. 2.12b). However, the rate of decline in kernel recoveries slowed as density increased. Thus, although recoveries of 53 g (SE 12.5) were recorded at 68,980 plants per hectare, recoveries of 20 g (SE 11.7) at 100,660 plants per hectare were not significantly different.

Only densities less than 57,400 plants per hectare had at least 50% of secondary cobs providing recoveries of acceptable quality for processing. Even at 40,710 plants per hectare, recoveries (SD 51.0) were only 31 g above the 70 g level for rejection. Hence, an estimated 30% of secondary cobs would have been discarded, three-fold fewer than at 100,660 plants per hectare (SD 28.1).

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[3] Standard deviations refer to the distribution of kernel recoveries at the density under discussion.

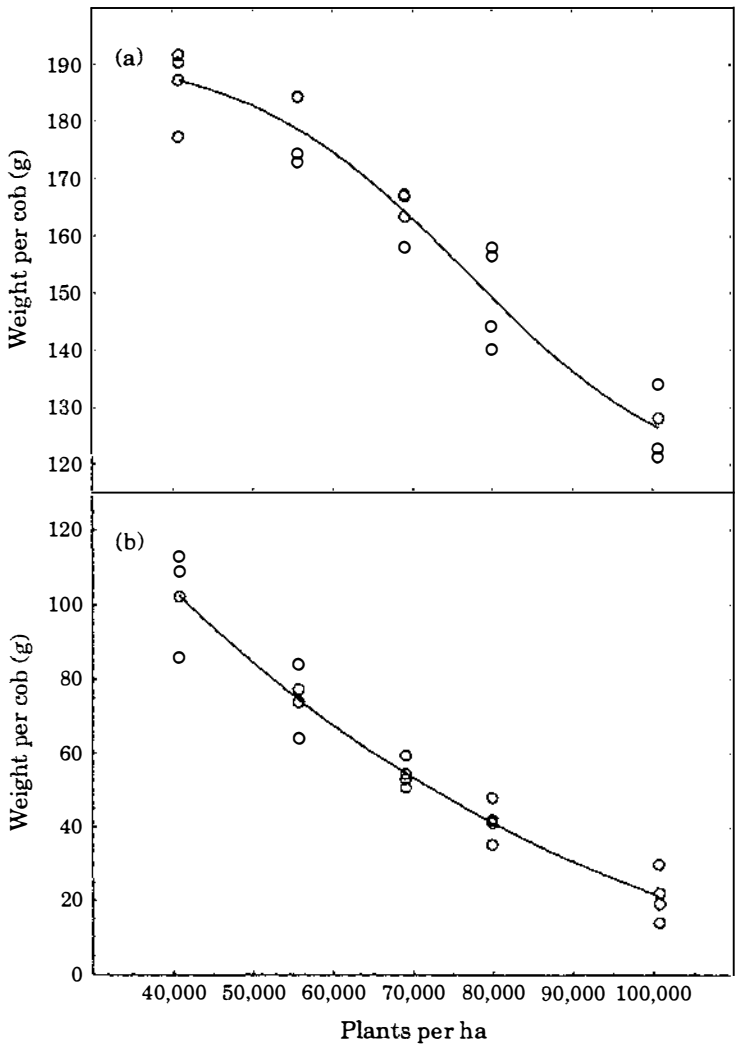

Fig. 2.12. Kernel recoveries for Jubilee as affected by density for (a) primary and (b) secondary ears. Data are the means for each density and block, pooled across N rates, and adjusted for significant block effects. Fitted function for (a) is $Y=114.32+78.48/(1+e^{-5.49+0.71X})$ ($R^2_{adj}=0.94$). Fitted function for (b) is $Y=221.79-252.66(1-e^{-0.16X})$ ($R^2_{adj}=0.94$).

2.3.2.4 Harvested ear and cob weights

There was a significant density x N rate interaction for weight of primary ears. At 40,710 plants per hectare, 115 kg N/ha produced significantly heavier ears than either the 172 or 230 kg N/ha rates (Fig. 2.13a). However, at intermediate and higher densities, ear weights were similar among the N treatments. Nevertheless, ears produced at 40,710 plants per hectare with 115 kg N were significantly heavier (35%) than the 250 g (SE 18.8) recorded for the 'poorest' regime (i.e., 100,660 plants per hectare with no added N).

Unlike primary ears, weight of secondary ears was not influenced by N rate. However, weights were influenced by density, decreasing 54% as density increased from 40,710 to 100,660 plants per hectare (Fig. 2.13b). Hence, at 100,660 plants per hectare, secondary ears weighed 110 g (SE 15.3), 127 g less than the 237 g (SE 15.0) recorded at 40,710 plants per hectare. While decreases in weight of secondary cobs were significant for each increase in density up to 68,980 plants per hectare, cob weights did not decline significantly with further increases in density.

Weight of cobs also declined significantly with increasing density. Weight of primary cobs decreased from 302 g (SE 6.7) to 226 g (SE 6.6) as density increased from 40,710 to 100,660 plants per hectare (Fig. 2.14a). Weight of secondary cobs declined from 188 g (SE 13.3) to 82 g (SE 13.6) over this density range (Fig. 2.14b).

Similar proportions of ears and cobs did not meet marketability criteria (Section 2.3.2.3) as for kernel recoveries. Hence, to avoid repetition, they are not reported here.

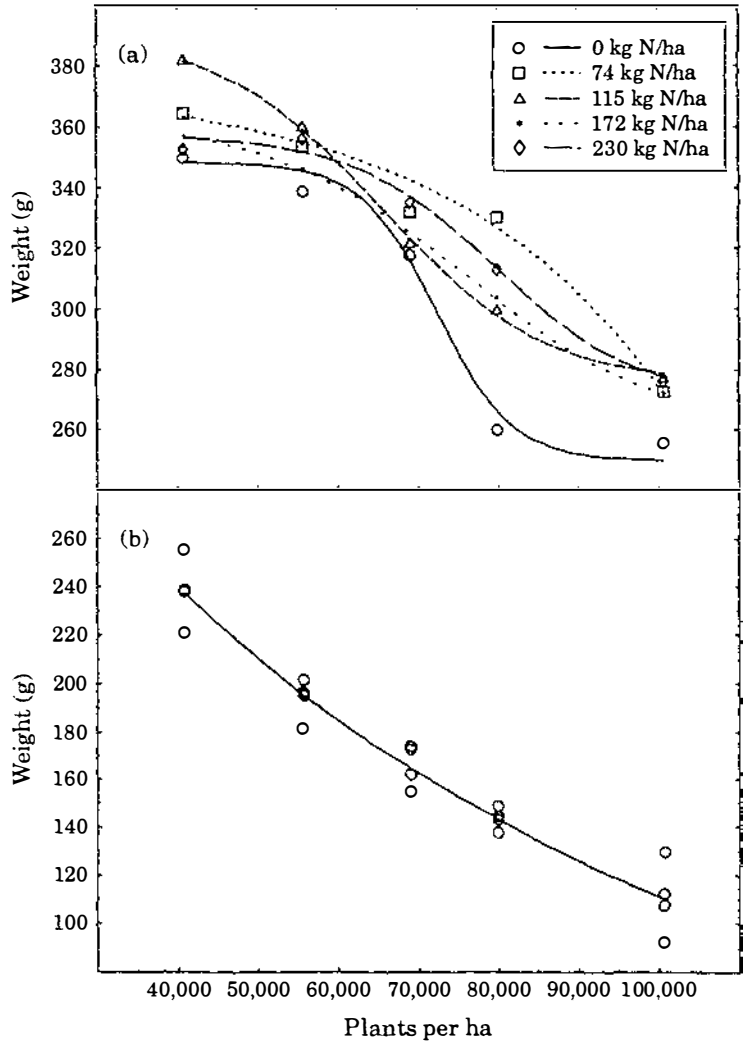

Fig. 2.13. Ear weights of Jubilee as affected by density and N rate for (a) primary and (b) secondary ears. Data in (a) are the means for each density and N rate, adjusted for significant block effects. Data in (b) are the means for each density and block, pooled across N rates. Fitted functions for (a): 0 kg N/ha, $Y=249.65+98.84/(1+e^{-15.28+2.11X})$ ($R^2_{adj}=0.84$); 74 kg N/ha, $Y=374.82-2.59e^{0.37X}$ ($R^2_{adj}=0.76$); 115 kg N/ha, $Y=275.59+114.66/(1+e^{-6.57+1.80X})$ ($R^2_{adj}=0.98$); 172 kg N/ha, $Y=259.83+103.20/(1+e^{-6.09+0.80X})$ ($R^2_{adj}=0.86$); 230 kg N/ha, $Y=269.95+87.61/(1+e^{-8.86+1.11X})$ ($R^2_{adj}=0.80$). Fitted function for (b) is $Y=404.121-397.907(1-e^{-0.133X})$ ($R^2_{adj}=0.95$).

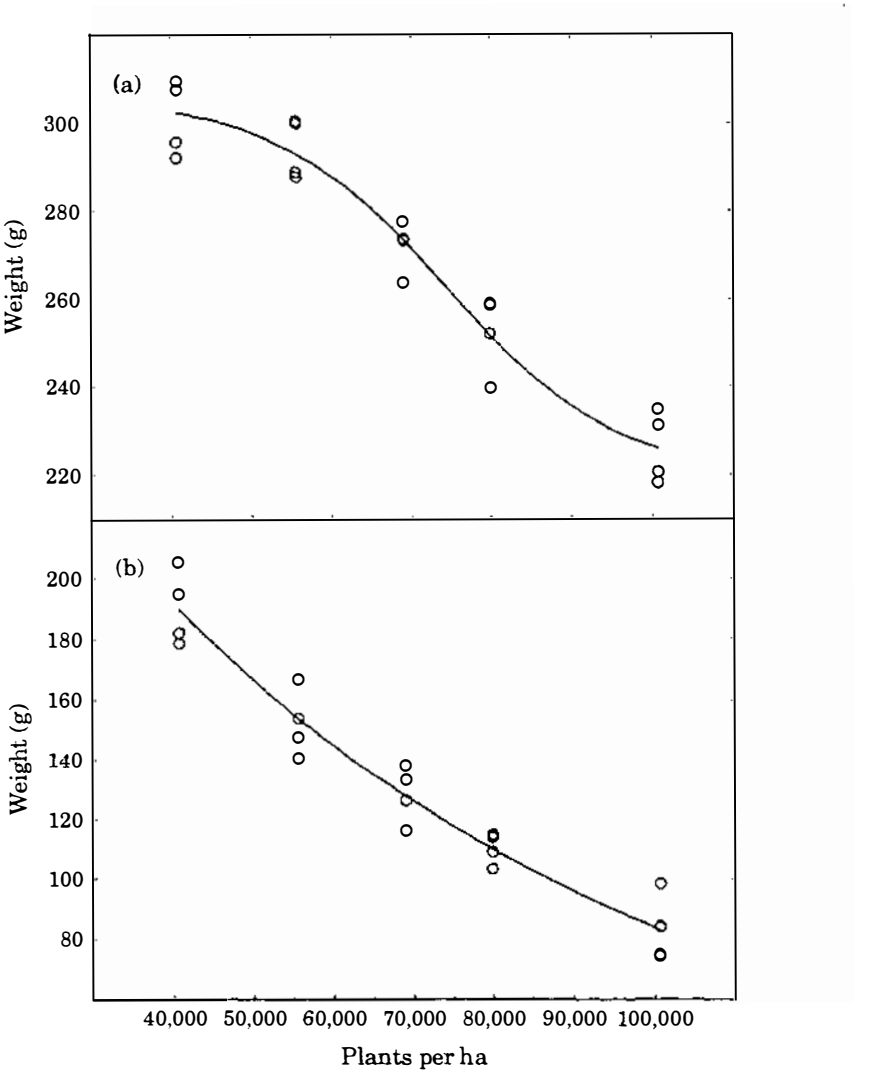

Fig. 2.14. Weight of Jubilee cobs as affected by density and N rate for (a) primary and (b) secondary ears. Data in (a) and (b) are the means for each density and block, pooled across N rates, and adjusted for significant block effects. Fitted function for (a) is $Y=218.70+87.50/(1+e^{-6.84+0.92X})$ ($R^2_{adj}=0.94$). Fitted function for (b) is $Y=339.81-331.17(1-e^{-0.15X})$ ($R^2_{adj}=0.94$).

2.3.2.5 Marketable ear yield

The density which maximised marketable ear yield was not identified in this study (Fig. 2.15a). Nevertheless, at 100,660 plants per hectare yield was 19.77 (SE 0.88) tonnes, 12% greater than the 17.40 (SE 0.85) tonnes recorded at 40,700 plants per hectare. Yield at 55,710 plants per hectare was not significantly different from that at 100,660 plants per hectare.

A density of 92,200 plants per hectare maximised marketable yield of primary ears (Fig. 2.15b). Yield of 20.05 tonnes at this density was significantly greater than the 18.53 (SE 0.95) tonnes recorded at 68,980 plants per hectare, but similar to that recorded at higher densities.

Varying response to N rates contributed to a significant density × N rate interaction for marketable yield of secondary ears. At intermediate densities the 115 kg N/ha treatment gave highest yield, while the 172 kg N/ha treatment gave greatest yield at highest densities (Fig. 2.15c). Despite these varying trends, differences among the N treatments were significant only at 40,710 plants per hectare. At this density, yield with 230 kg N/ha was 6.10 (SE 0.64) tonnes, 42% greater than the 2.55 (SE 0.74) tonnes recorded for the control. This difference declined with density, however, consistent with the asymptotic approach of secondary ears to zero yield. At 100,660 plants per hectare, the largest yield difference among N treatments was 0.03 tonnes, a difference which was not statistically significant.

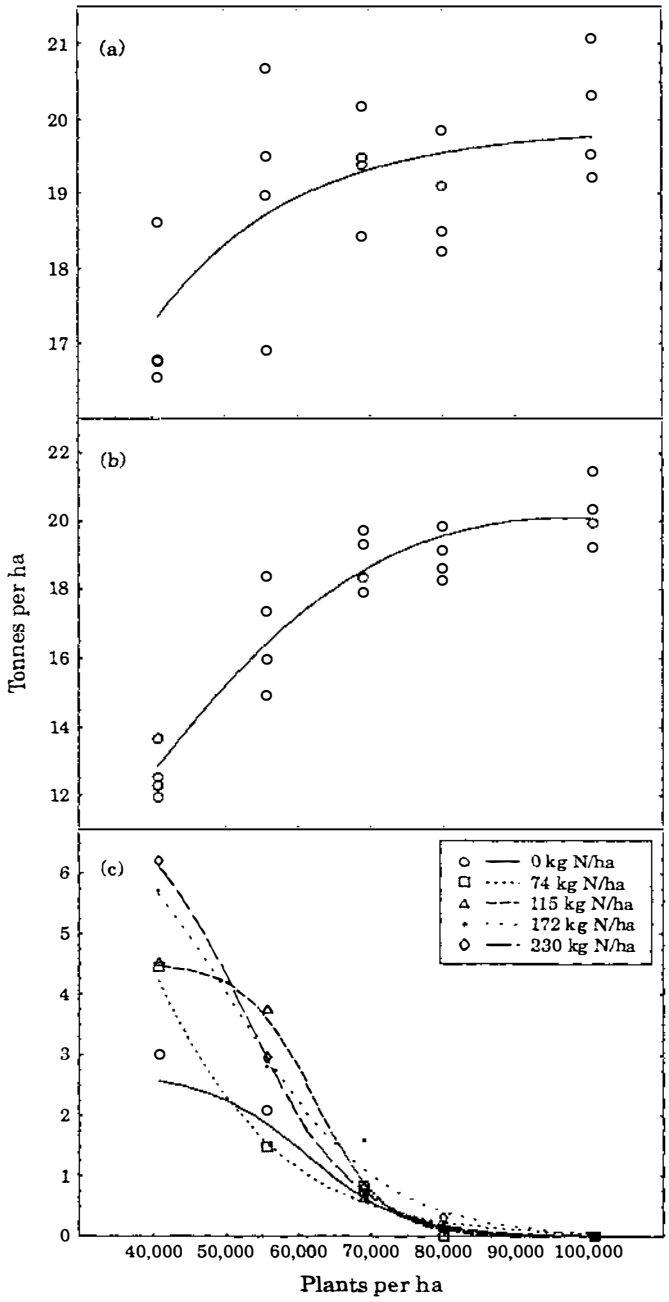

Fig. 2.15. Marketable ear yield of Jubilee as affected by density for (a) total, (b) primary, and (c) secondary ears. Data in (a) and (b) are the means for each density, pooled across N rates and adjusted for significant block effects. Data in (c) are the means for each density and N rate. Fitted function for (a) is $Y=19.89(1-e^{-0.51X})$ ($R^2_{adj}=0.44$). Fitted function for (b) is $Y=X/(0.34-0.02X+0.004X^2)$ ($R^2_{adj}=0.89$). Fitted functions for (c): 0 kg N/ha, $Y=2.68/(1+e^{-9.12+1.49X})$ ($R^2_{adj}=0.55$); 74 kg N/ha, $Y=16.15/(1+e^{-2.24+0.80X})$ ($R^2_{adj}=0.80$); 115 kg N/ha, $Y=4.50/(1+e^{-13.89+2.10X})$ ($R^2_{adj}=0.78$); 172 kg N/ha, $Y=7.71/(1+e^{-5.02+0.99X})$ ($R^2_{adj}=0.89$); 230 kg N/ha, $Y=7.32/(1+e^{-7.07+1.34X})$ ($R^2_{adj}=0.91$).

2.3.2.6 Marketable kernel yield

Marketable kernel yield peaked at about 75,180 plants per hectare (Fig. 2.16a). Kernel recovery of 9.35 (SE 0.50) tonnes at this density was significantly higher than the 8.23 (SE 0.46) tonnes recorded at 40,710 plants per hectare. Yield at 55,710 plants per hectare or greater, however, was similar to that at 75,180 plants per hectare.

Marketable kernel yield from primary ears followed a similar trend to that of total yield (cf. Figs. 2.16a and 2.16b), although yield was maximised at the higher density of 86,650 plants per hectare. Nonetheless, recoveries at 86,650 plants per hectare were only 0.11 tonnes greater than at 75,180 plants per hectare, a difference which was not statistically significant. Similarly, yield of 9.39 (SE 0.52) tonnes was also similar to that at 75,180 plants per hectare, but significantly higher than the 6.54 (SE 0.49) tonnes recorded at 40,710 plants per hectare.

Unlike total recovery or that from primary cobs, recoveries from secondary cobs were influenced by N rate. At 40,710 plants per hectare, yield was significantly higher than the control at N rates $\geq$ 172 kg/ha (Fig. 2.16c). However, as density increased, the yield difference among N rates declined, with less than 0.08 tonnes separating the N treatments at 100,660 plants per hectare. At 55,710 plants per hectare and above, all N rates resulted in similar kernel yields. Total marketable kernel yield at 75,180 plants per hectare therefore comprised about 9.99 (SE 0.53) tonnes derived from primary and about 0.18 (SE 0.23) tonnes derived from secondary cobs. In comparison, total yield at 40,710 plants per hectare comprised about 6.68 (SE 0.49) tonnes of kernels from primary and about 2.70 (SE 0.38) tonnes from secondary cobs. The density $\times$ N rate interaction for marketable kernel yield from secondary ears was not significant.

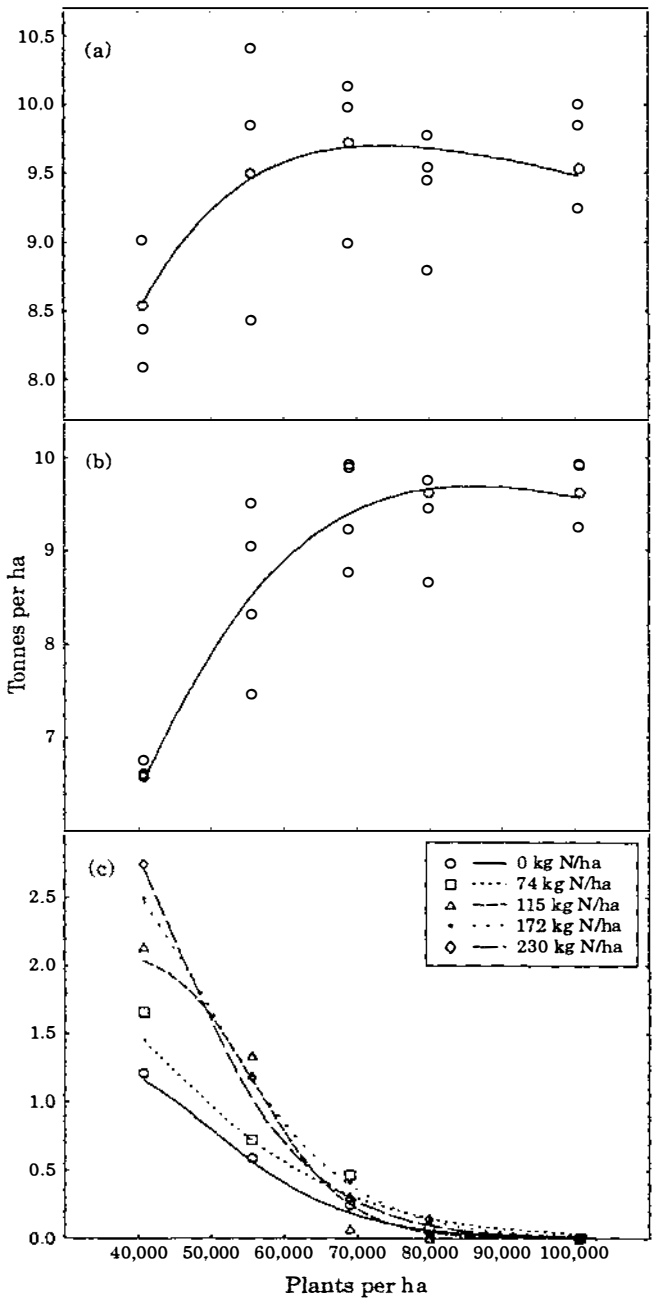

Fig. 2.16. Marketable kernel yield of Jubilee as affected by density for (a) total, (b) primary, and (c) secondary ears. Data in (a) and (b) are the means for each density and block, pooled across N rates, and adjusted for significant block effects. Data in (c) are the means for each density and N rate. Fitted function for (a) is $Y=X/(0.844+0.218X-0.622X^{0.5})$ ($R^2_{adj}=0.39$). Fitted function for (b) is $Y=X/(2.085+0.346X-1.422X^{0.5})$ ($R^2_{adj}=0.85$). Fitted functions for (c): 0 kg N/ha, $Y=1.59/(1+e^{-5.38+1.07X})$ ($R^2_{adj}=0.58$); 74 kg N/ha, $Y=2.91/(1+e^{-3.03+0.74X})$ ($R^2_{adj}=0.51$); 115 kg N/ha, $Y=2.19/(1+e^{-9.29+1.64X})$ ($R^2_{adj}=0.59$); 172 kg N/ha, $Y=3.48/(1+e^{-5.15+1.05X})$ ($R^2_{adj}=0.77$); 230 kg N/ha, $Y=4.66/(1+e^{-4.68+1.07X})$ ($R^2_{adj}=0.80$).

2.3.2.7 Marketable cob yield

Maximum marketable cob yield of 16.71 (SE 1.08) tonnes was estimated at 69,390 plants per hectare (Fig. 2.17a). Although yield at this density was 0.32 and 0.50 tonnes higher than at either 55,710 or 100,660 plants per hectare, respectively, these differences were not significant. However, this yield was significantly higher (11%) than the 14.86 (SE 0.99) tonnes recorded at 40,710 plants per hectare. A considerably higher density of 91,650 plants per hectare maximised marketable yield of primary cobs. Yield of 16.56 tonnes at this density was only 0.14 tonnes greater than at 69,390 plants per hectare, but 1.78 tonnes greater than at 40,710 plants per hectare (Fig. 2.17b). While yield at 40,170 plants per hectare was significantly less than that at 91,650 plants per hectare, yield at 100,660 plants per hectare was not. Similarly, yield at 68,980 plants per hectare was similar to that at 91,650 plants per hectare.

The approach of primary cobs to maximum yield coincided with significant reductions in yield of secondary cobs. As density increased from 40,710 to 100,660 plants per hectare, marketable yield of secondary cobs declined from 4.57 (SE 0.25) to only 0.06 tonnes (SE 0.11) (Fig. 2.17c). Thus, at 69,390 plants per hectare, total yield comprised about 15.56 (SE 1.08) tonnes of primary and 1.39 (SE 0.26) tonnes of secondary cobs.

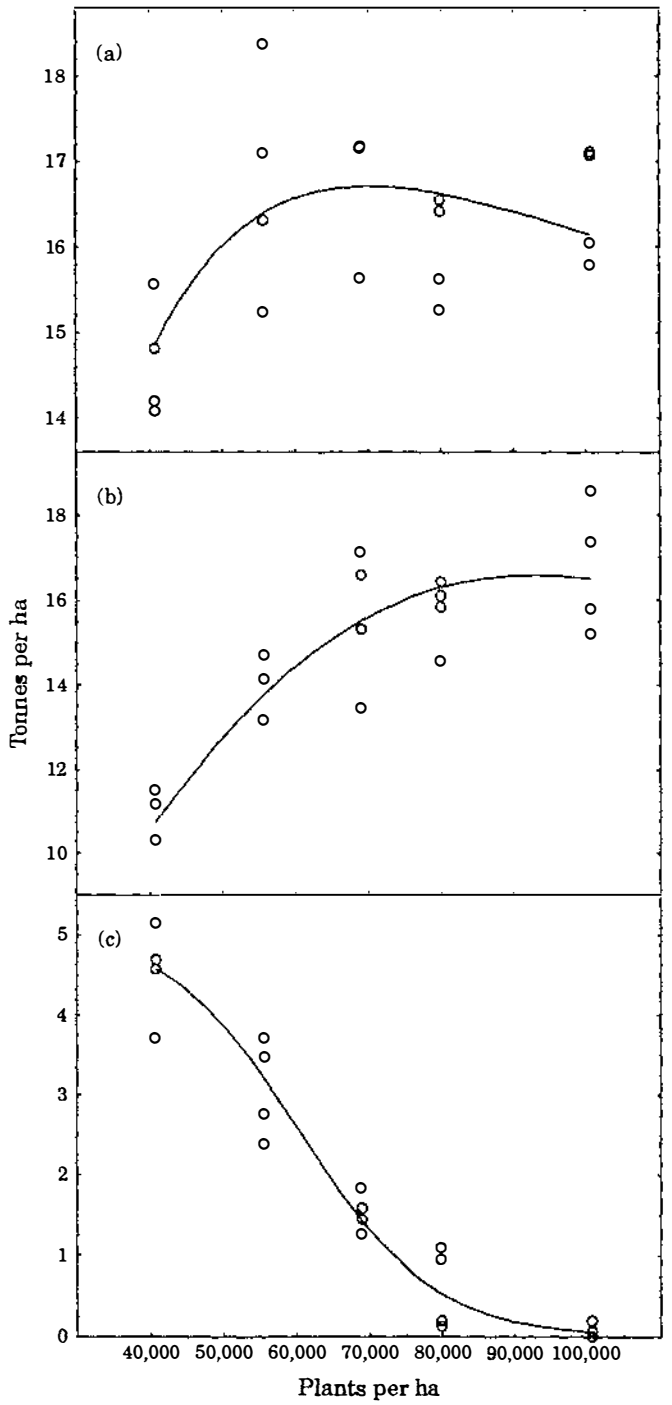

Fig. 2.17. Marketable cob yield of Jubilee as affected by density for (a) total, (b) primary, and (c) secondary ears. Data are the means for each density and block, pooled across N rates. Data in (a) and (b) were adjusted for significant block effects. Fitted function for (a) is $Y=X/(0.537+0.136X-0.405X^{0.5})$ ($R^2_{adj}=0.43$). Fitted function for (b) is $Y=X/(0.42-0.03X^{+0.005X^2})$ ($R^2_{adj}=0.82$). Fitted function for (c) is $Y=5.10/(1+e^{-6.64+1.10X})$ ($R^2_{adj}=0.95$).

2.3.2.8 Cob lengths of SS42 and Jubilee

Increasing density from 40,710 to 100,660 plants per hectare significantly reduced primary cob length of SS42 and Jubilee by 14 and 16 mm, respectively (Figs. 2.18 and 2.19a). The length of secondary cobs of Jubilee declined from 187 mm (SE 18) to 170 mm (SE 22) as density increased from 40,710 to 100,660 plants per hectare (Fig. 2.19b). Length of secondary cobs of SS42, on the other hand, was not influenced by density, averaging 186 mm (SE 13). Depending on cultivar, primary cobs were up to 16% longer than secondary cobs at 40,710 plants per hectare. Primary cobs of SS42 were about 15 mm longer than those of Jubilee at this density.

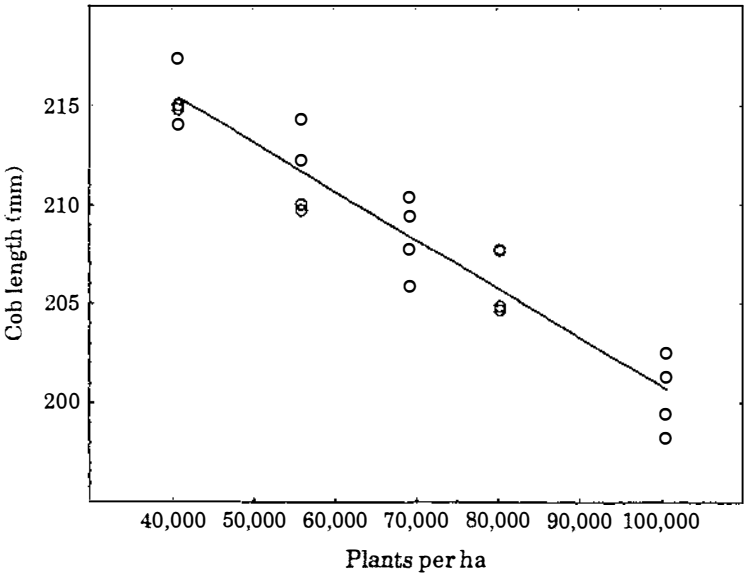

Fig. 2.18. Effect of density on length of primary cobs of SS42. Data are the means for each block and density, pooled across N rates, and adjusted for significant block effects. Fitted function is $Y=225.5-2.40X$ ($r^2=0.91$).

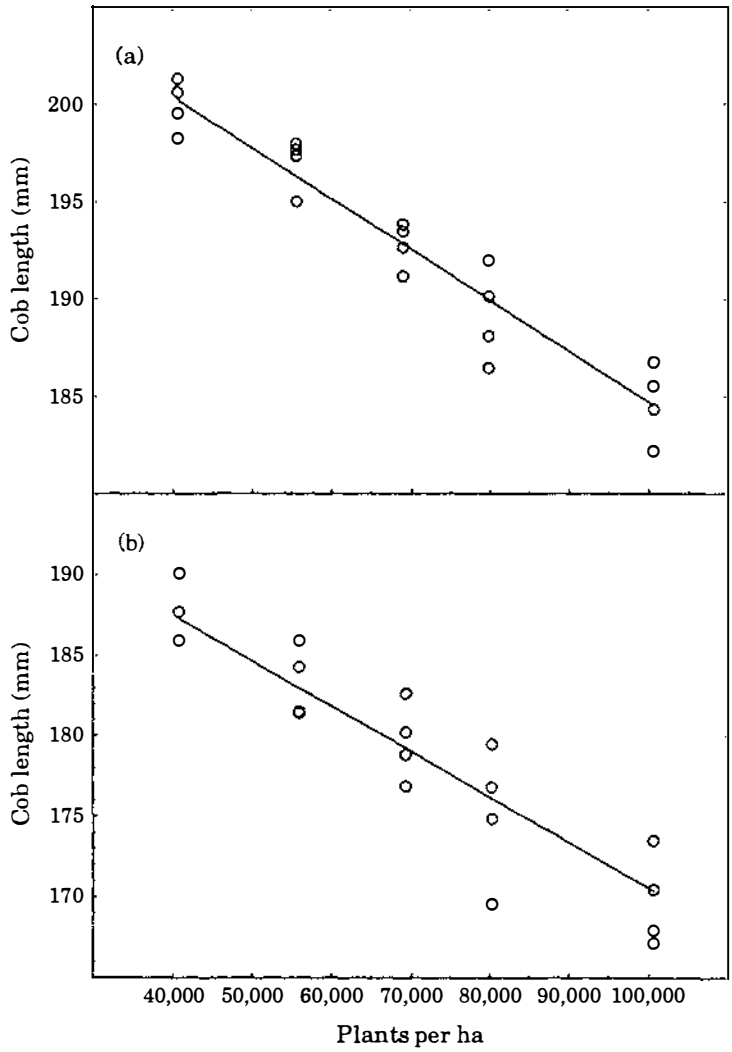

Fig. 2.19. Effect of density on lengths of (a) primary and (b) secondary cobs of Jubilee. Data are the means for each density and block, pooled across N rates, and adjusted for significant block effects. Fitted function for (a) is Y=210.08-2.61X (r^2=0.93). Fitted function for (b) is Y=198.8-2.82X (r^2=0.73).

2.3.3 Analysis of pre-harvest variables

2.3.3.1 Flowering components

Silk delay for both SS42 and Jubilee was significantly influenced by density. At 40,710 plants per hectare, silking of primary ears was delayed 1.1 (SE 0.26) and 2.0 (SE 0.18) days beyond anthesis for SS42 and Jubilee, respectively (Fig. 2.20a and 2.21a). As density increased from 40,710 to 100,660 plants per hectare silk delay increased a further 1.2-1.4 days (depending on cultivar). Longer delays were recorded for secondary ears. At 40,710 plants per hectare, silking of secondary ears of SS42 was delayed 3.5 (SE 0.47) days, 2.4 days longer than for primary ears (Fig. 2.20). Similarly, silking of secondary ears of Jubilee was delayed 3.7-5.5 (SE 1.99) days (depending on N rate), 1.5-2.7 days longer than primary ears (Fig. 2.21). A t 100,660 plants per hectare, however, silking of secondary ears of SS42 and Jubilee was delayed 6.7 (SE 0.44) and 8.0-13.4 (SE 1.96) days, respectively. Compared to primary ears of SS42 and Jubilee, this was a delay 4.3 and 4.6-10.4 days longer, respectively.

Silk delay for secondary ears of Jubilee was reduced by the addition of N, particularly at high densities (Fig. 2.21b). At 100,660 plants per hectare, 74 kg N/ha reduced silk delay by four days compared to the control. The density × N rate interaction was not significant.

Time to 50% anthesis, recorded as 70 (SE 0.32) and 76 (SE 0.28) days after planting for Jubilee and SS42, respectively, was not influenced by density, N rate, or their combination.

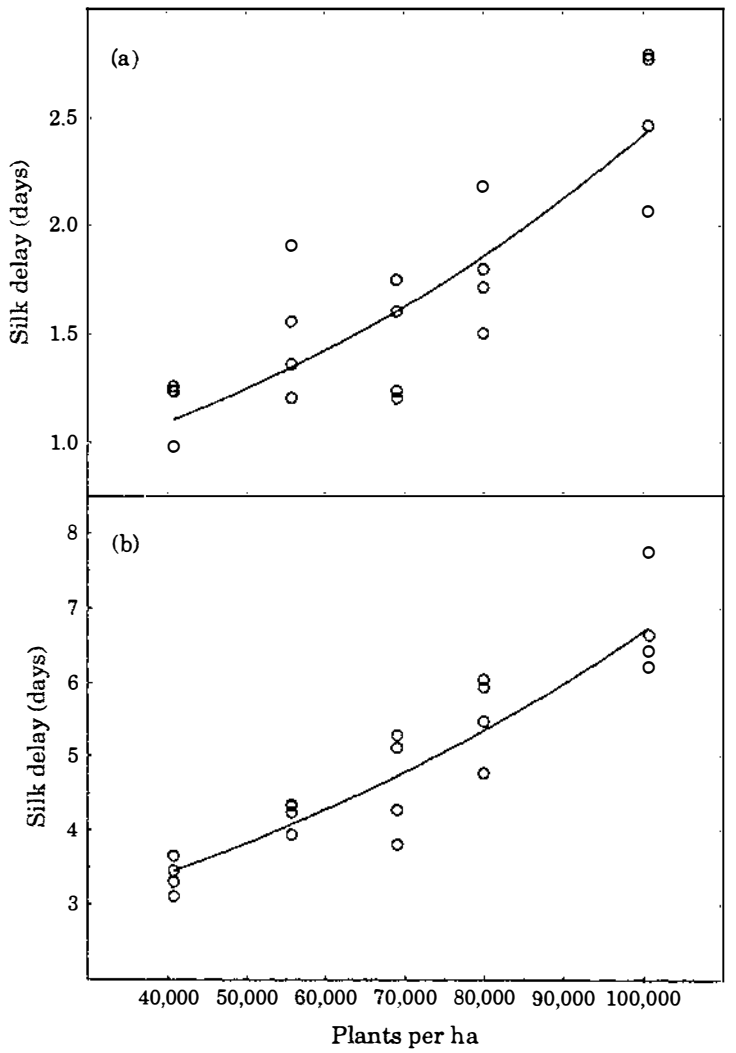

Fig. 2.20. Effect of density on silk delay for (a) primary and (b) secondary ears of SS42. Data are the means for each density and block, pooled across N rates. Fitted function for (a) is $Y=0.64e^{0.13X}$ ($R^2_{adj}=0.70$). Fitted function for (b) is $Y=2.19e^{0.11X}$ ($R^2_{adj}=0.87$).

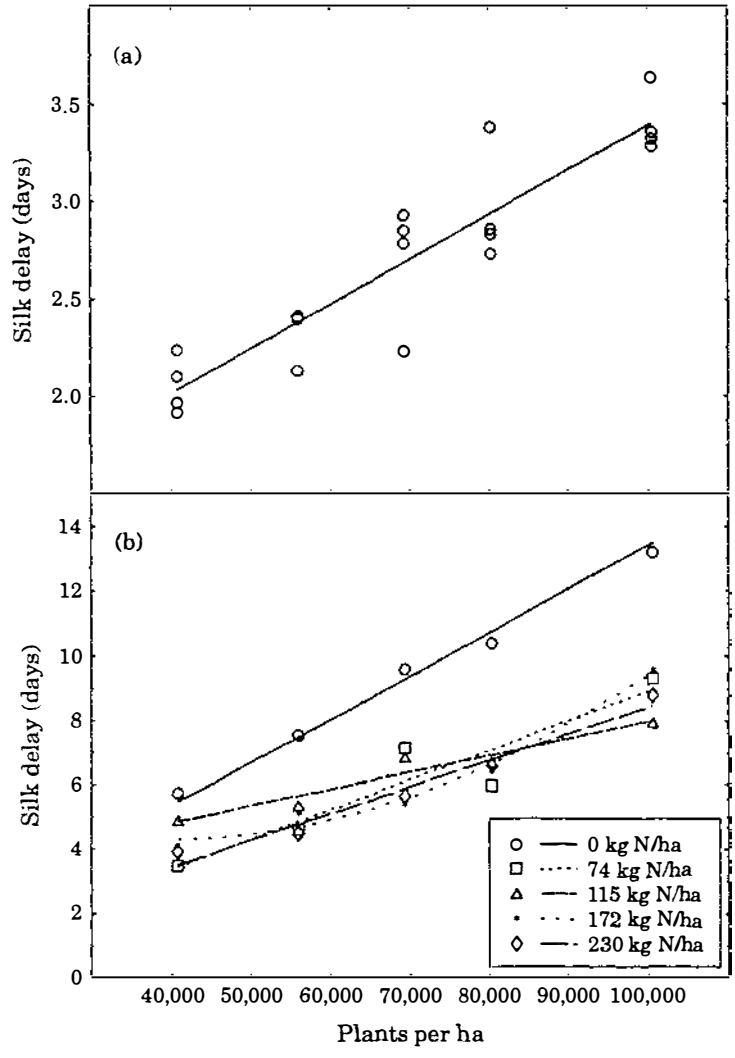

Fig. 2.21. Effect of density and N rate on silk delay for (a) primary and (b) secondary ears of Jubilee. Data are the means for each density and block, pooled across N rates, and adjusted for significant block effects. Fitted function for (a) is $Y=1.10+0.23X$ ($r^2=0.85$). Fitted functions for (b): 0 kg N/ha, $Y=-0.01+1.30X$ ($r^2=0.64$); 74 kg N/ha, $Y=-0.34+0.93X$ ($r^2=0.73$); 115 kg N/ha, $Y=2.65+0.53X$ ($r^2=0.72$); 172 kg N/ha, $Y=6.29-1.05X+0.14X^2$ ($R^2_{adj}=0.78$); 230 kg N/ha, $Y=0.12+0.83X$ ($r^2=0.78$).

2.3.3.2 Ears per plant

Although the number of ears which silked for Jubilee significantly increased with N fertiliser, ear numbers declined with density. At 40,710 plants per hectare, plants of Jubilee carried 2.3-2.6 (SE 0.30) ears (Fig. 2.22a). However, at 100,660 plants per hectare, the number of ears had declined to 1.4-1.8 (SE 0.19) per plant (depending on N rate). Ear numbers for SS42 similarly declined, decreasing from 2.7 (SE 0.07) to 1.7 (SE 0.07) per plant as density increased from 40,710 to 100,660 plants per hectare (Fig. 2.22b). In this instance the decline was not influenced by N rate.

2.3.3.3 Tillers per plant

At 40,710 plants per hectare Jubilee produced about 2.5 (SE 0.17) tillers, 1.4 more per plant than SS42 (SE 0.09) (Fig. 2.23). However, as density increased, the number of tillers per plant declined significantly, until at 100,660 plants per hectare, both cultivars produced about 0.4 tillers per plant (SE 0.18 and 0.08 for Jubilee and SS42, respectively).

2.3.3.4 Stalk diameter

Stalk diameter of Jubilee decreased from 24.6 mm (SE 0.52) to 20.1 mm (SE 0.51) as density increased from 40,710 to 100,660 plants per hectare (Fig. 2.24). A significant decline was also recorded for SS42, with stalk diameters decreasing from 20.1 mm (SE 0.44) to 17.0 mm (SE 0.41) over this density range. Irrespective of density, stalk diameters of Jubilee were 15 to 20% greater than those of SS42.

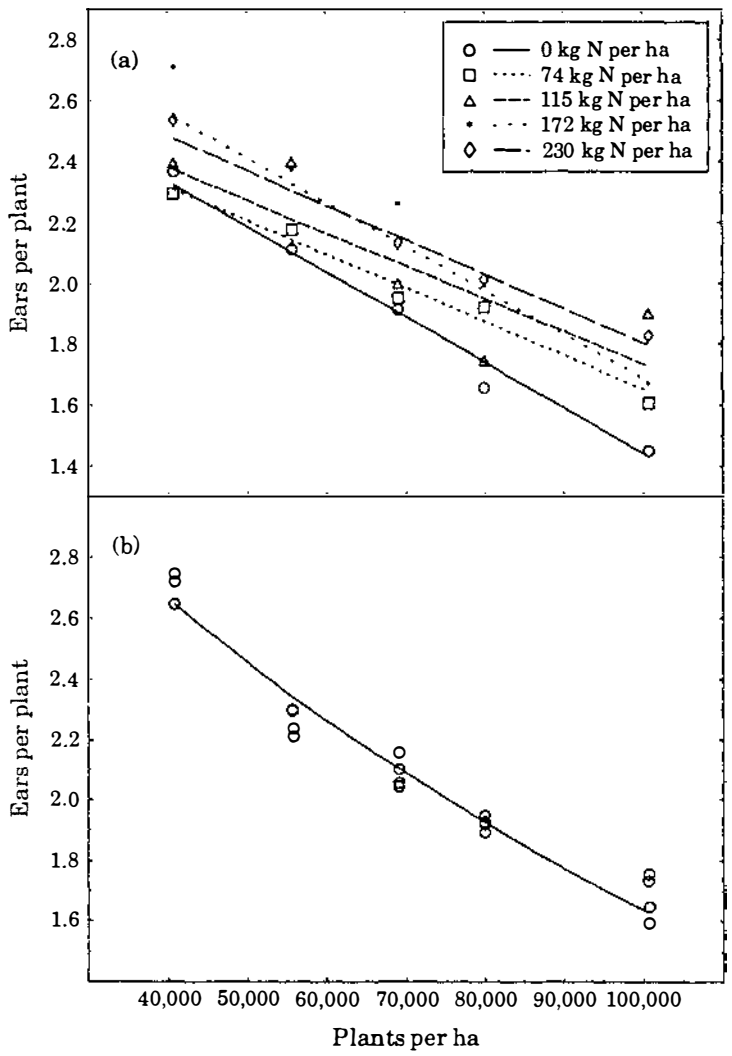

Fig. 2.22. Effect of density and N rate on the number of ears per plant for (a) Jubilee and (b) SS42. Data in (a) are the means for each N rate and density, adjusted for significant block effects. Data in (b) are the means for each density and block, pooled across N rates. Fitted functions for (a): 0 kg N/ha, Y=2.93-0.15X (r^2=0.51); 74 kg N/ha, Y=2.77-0.11X (r^2=0.63); 115 kg N/ha, Y=2.81-0.11X (r^2=0.64); 172 kg N/ha, Y=3.13-0.14X (r^2=0.68); 230 kg N/ha, Y=2.94-0.11X (r^2=0.80). Fitted function for (b) is $Y=3.69e^{-0.08X}$ (R^2_{adj}=0.96).

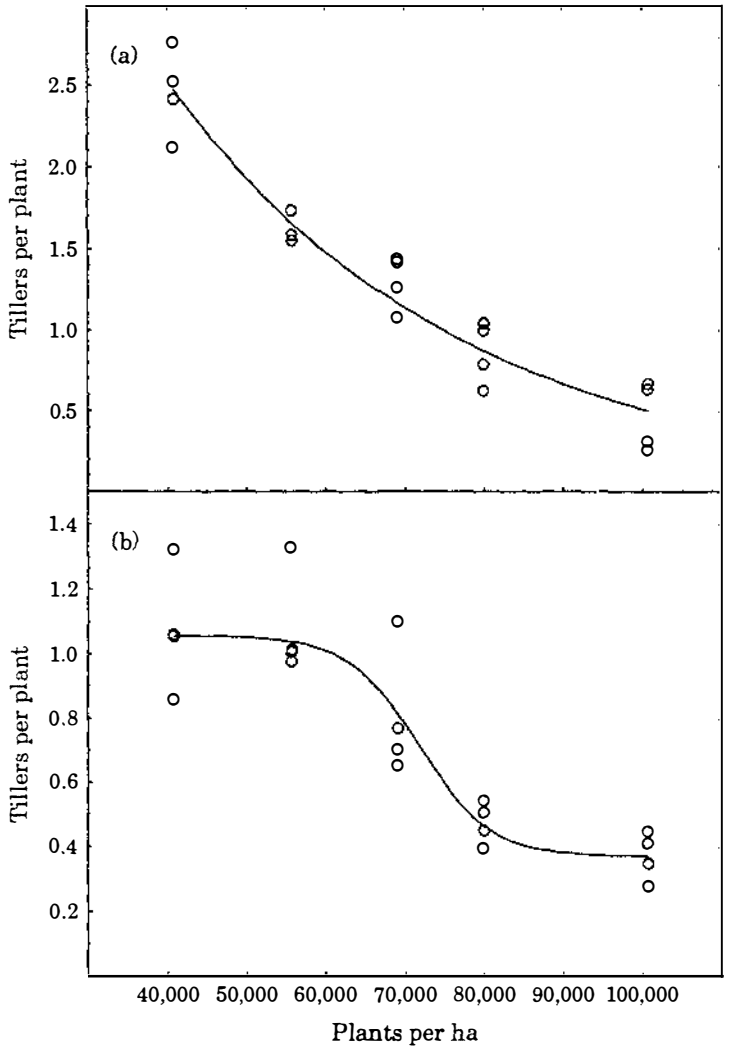

Fig. 2.23. Effect of density on tiller number per plant for (a) Jubilee and (b) SS42. Data are the means for each density and block, pooled across N rates, and adjusted for significant block effects. Fitted function for (a) is $Y=7.31e^{-0.27X}$ ($R^2_{adj}=0.94$). Fitted function for (b) is $Y=0.37+0.69/(1+e^{-15.94+2.22X})$ ($R^2_{adj}=0.81$).

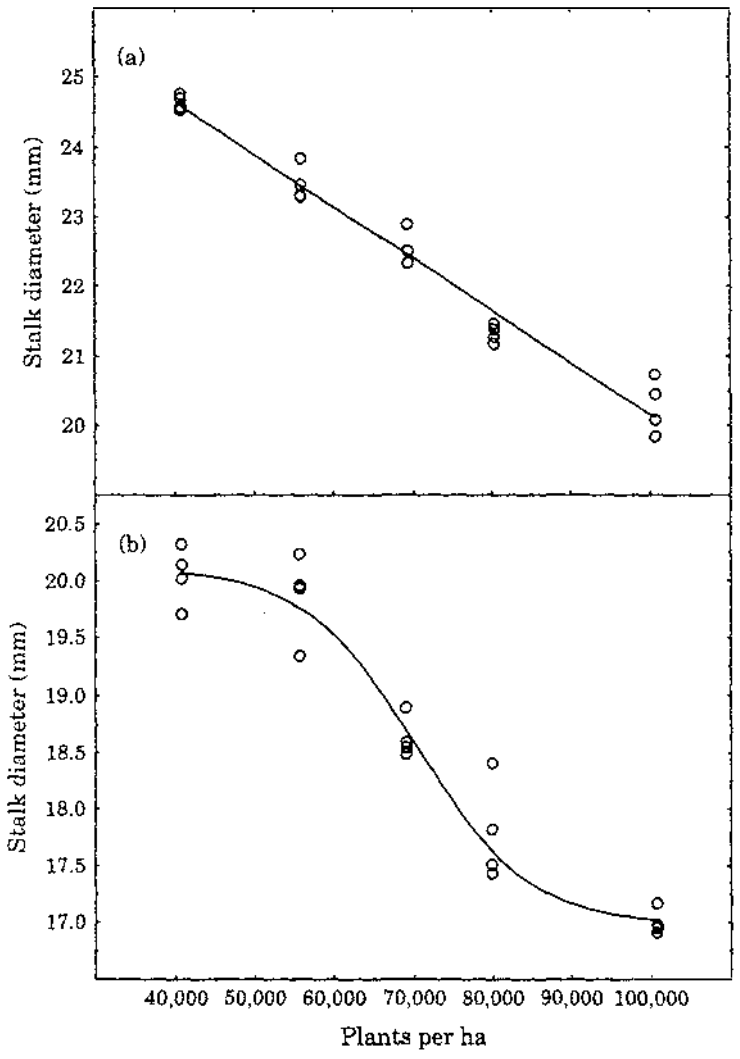

Fig. 2.24. Effect of density on stalk diameter for (a) Jubilee and (b) SS42. Data are the means for each density and block, pooled across N rates, and adjusted for significant block effects. Fitted function for (a) is Y=27.65-0.75X (r^2=0.98). Fitted function in (b) is $Y=16.98+3.14/(1+e^{-9.88+1.40X})$ (R^2_{adj}=0.96).

2.3.3.5 Lodging

Even at 100,660 plants per hectare, lodging was less than 2%. Although there were no incidences of lodging at the other densities the overall influence of density was not significant. Similarly, N rate did not influence the proportion of plants which lodged.

2.3.4 Path analysis

Path analysis provided insight into the relationships among variables influencing yield (tillers, silk delay, and stalk diameter) and kernel recovery from harvestable primary and secondary ears at both a low (40,710 plants per hectare) and a high density (100,660 plants per hectare). The model investigated indicated that both tillers (i.e., a possible photoassimilate source) and size of the stalk (i.e., a measure of the storage reserves of the plant; McAllan and Phipps, 1977) were important for determining kernel recoveries at low densities (Figs. 2.25 and 2.26). Size of the stalk appeared important for kernel recovery from primary ears with tillers suggested as being important for recovery from secondary ears. Thus, even though the correlation between stalk diameter and kernel recovery for secondary ears was high, this correlation was largely via an indirect effect of tillers (Table 2.7a).

Kernel recovery from primary ears of both Jubilee and SS42 at low densities was directly influenced by silk delay of the secondary ear (Figs. 2.25 and 2.26; Table 2.7b). Silk delay was also negatively associated with kernel recoveries from secondary ears. However, significant correlations between silk delay for the secondary ear and kernel recoveries for the secondary ear are misleading as recoveries were influenced more by the indirect effects of tiller number and stalk diameter than by silk delay itself (Table 2.7b). These indirect effects resulted from tillers and stalk diameter both being highly correlated with silk delay (Figs. 2.25 and 2.26). Silk delay for the primary ear, on the other hand, did not directly affect kernel recoveries from either ear.

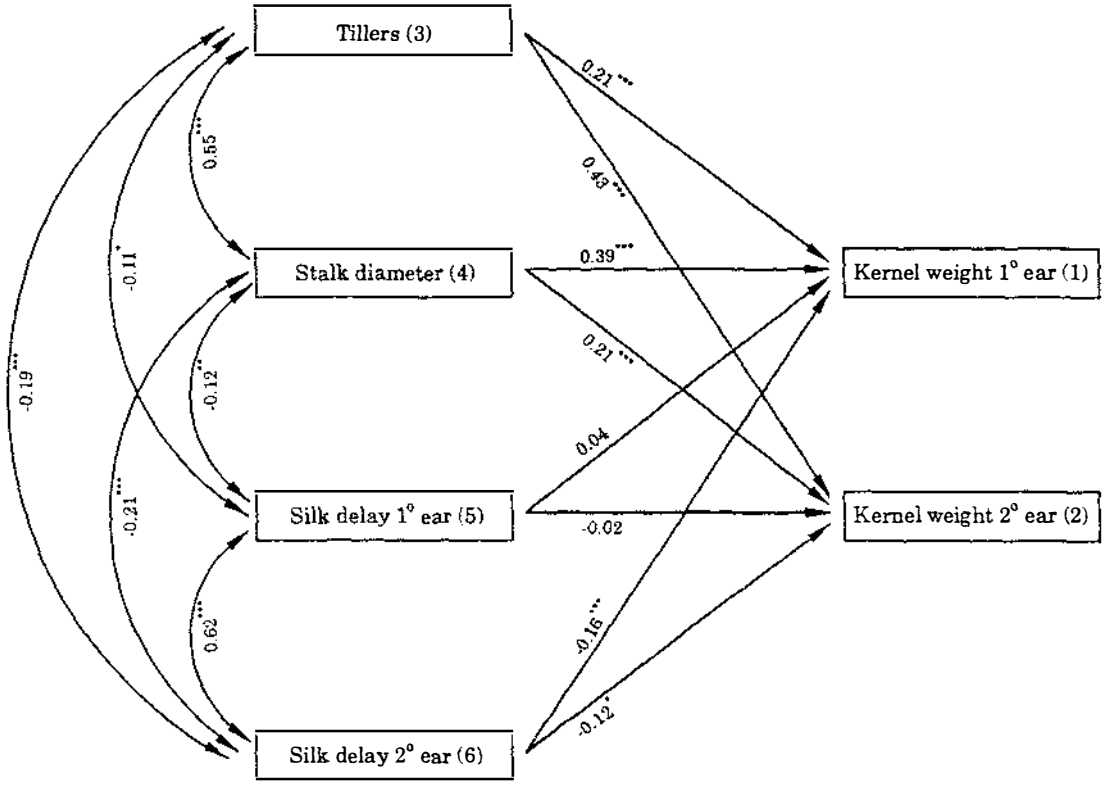

Fig. 2.25. Path analysis diagram of relationships among variables influencing yield (tillers, stalk diameter, and silk delay) and kernel recovery for SS42 grown at 40,710 plants per hectare. Curved lines represent correlations (r_{ij}) with straight lines representing path coefficients (P_{ij}). ^{NS,*,**,***} Nonsignificant or significant at $P \leq 0.05$, 0.01, or 0.001 respectively. n=470.

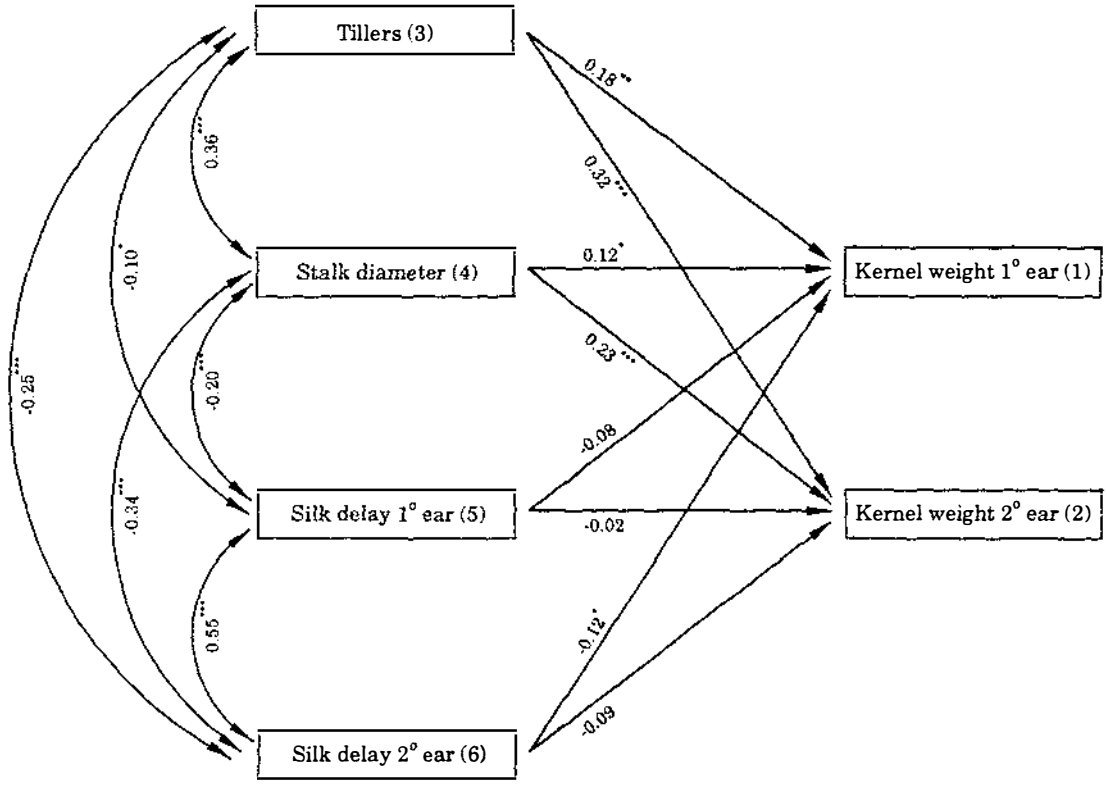

Fig. 2.26. Path analysis diagram of relationships among variables influencing yield (tillers, stalk diameter, and silk delay) and kernel recovery for Jubilee grown at 40,710 plants per hectare. Curved lines represent correlations (r_{ij}) with straight lines representing path coefficients (P_{ij}). $^{NS, *, **, ***}$ Nonsignificant or significant at $P \leq 0.05$, 0.01, or 0.001 respectively. n=407.

Table 2.7a. Path analysis of the effects of physiological components on kernel recoveries of SS42 and Jubilee grown at either 40,710 or 100,660 plants per hectare. Coefficients used to calculate influences (r_{ij}·P_{ij}) are from Figs. 2.25-2.28. Significance levels are presented for the direct effects and simple correlations only.

Pathways and designation of effect	SS42; 40,710 pph[z,y]	SS42; 100,660 pph[x]	Jubilee; 40,710 pph[w]	Jubilee; 100,660 pph[v]
	influence (r_{ij}·P_{ij})			
Tillers vs. kernel recovery from the primary ear				
Direct, P_{31}	0.21***	0.09*	0.18**	0.21***
Indirect via stalk diameter, $r_{34}P_{41}$	0.21	0.32	0.04	0.09
Indirect via silk delay (1° ear), $r_{35}P_{51}$	0.00	0.06	0.01	0.08
Indirect via silk delay (2° ear), $r_{36}P_{61}$	-0.02	0.02	0.03	0.01
Total correlation	0.45**	0.49***	0.26***	0.39***
Tillers vs. kernel recovery from the secondary ear				
Direct, P_{32}	0.43***	0.17**	0.32***	0.05
Indirect via stalk diameter, $r_{34}P_{42}$	0.11	-0.01	0.08	0.03
Indirect via silk delay (1° ear), $r_{35}P_{52}$	0.00	0.01	0.00	-0.01
Indirect via silk delay (2° ear), $r_{36}P_{62}$	0.02	0.01	0.02	0.02
Total correlation	0.57***	0.18**	0.43***	0.09
Stalk diameter vs. kernel recovery from the primary ear				
Direct, P_{41}	0.39***	0.53***	0.12*	0.21***
Indirect via tillers, $r_{43}P_{31}$	0.11	0.06	0.06	0.10
Indirect via silk delay (1° ear), $r_{45}P_{51}$	-0.01	0.11	0.02	0.14
Indirect via silk delay (2° ear), $r_{46}P_{61}$	0.03	0.03	0.04	0.01
Total correlation	0.53***	0.72***	0.24***	0.45***
Stalk diameter vs. kernel recovery from the secondary ear				
Direct, P_{42}	0.21***	-0.02	0.23***	0.07
Indirect via tillers, $r_{43}P_{32}$	0.24	0.10	0.12	0.02
Indirect via silk delay (1° ear), $r_{45}P_{52}$	0.00	0.01	-0.01	-0.01
Indirect via silk delay (2° ear), $r_{46}P_{62}$	0.03	0.01	0.03	0.03
Total correlation	0.47***	0.11*	0.38***	0.10*

^{NS,*,**,***} Nonsignificant or significant at $P \leq 0.05$, 0.01, or 0.001 respectively

^{z} Plants per hectare; ^{y} n=470; ^{x} n=461; ^{w} n=407; ^{v} n=434

Table 2.7b. Path analysis of the effects of physiological components on kernel recoveries of SS42 and Jubilee grown at either 40,710 or 100,660 plants per hectare. Coefficients used to calculate influences (r_{ij}·P_{ij}) are from Figs. 2.25-2.28. Significance levels are presented for the direct effects and simple correlations only.

Pathways and designation of effect	SS42; 40,710 pph[z,y]	SS42; 100,660 pph[z,x]	Jubilee; 40,710 pph[z,w]	Jubilee; 100,660 pph[z,v]
	influence (r_{ij}·P_{ij})			
Silk delay (1°ear) vs. kernel recovery from the primary ear				
Direct, P_{51}	0.04	-0.25***	-0.08	-0.33***
Indirect via stalk diameter, $r_{54}P_{41}$	-0.05	-0.23	-0.02	-0.09
Indirect via tillers, $r_{53}P_{31}$	-0.02	-0.02	-0.02	-0.05
Indirect via silk delay (2° ear), $r_{56}P_{61}$	-0.10	-0.04	-0.07	-0.01
Total correlation	-0.13**	-0.54***	-0.19***	-0.48***
Silk delay (1°ear) vs. kernel recovery from the secondary ear				
Direct, P_{52}	-0.02	-0.03	-0.02	0.03
Indirect via stalk diameter, $r_{54}P_{42}$	-0.03	0.01	-0.05	-0.03
Indirect via tillers, $r_{53}P_{32}$	-0.05	-0.04	-0.03	-0.01
Indirect via silk delay (2° ear), $r_{56}P_{62}$	-0.07	-0.01	-0.05	-0.03
Total correlation	-0.17**	-0.07	-0.15*	-0.04
Silk delay (2° ear) vs. kernel recovery from the primary ear				
Direct, P_{61}	-0.16*	-0.07*	-0.12*	-0.03
Indirect via stalk diameter, $r_{64}P_{41}$	-0.08	-0.20	-0.04	-0.09
Indirect via tillers, $r_{63}P_{31}$	-0.04	-0.03	-0.04	-0.06
Indirect via silk delay (1° ear), $r_{65}P_{51}$	0.03	-0.12	-0.04	-0.14
Total correlation	-0.25***	-0.43***	-0.25***	-0.32***
Silk delay (2° ear) vs. kernel recovery from the secondary ear				
Direct, P_{62}	-0.12*	-0.02	-0.09	-0.06
Indirect via stalk diameter, $r_{64}P_{42}$	-0.04	0.01	-0.08	-0.03
Indirect via tillers, $r_{63}P_{32}$	-0.08	-0.06	-0.08	-0.01
Indirect via silk delay (1° ear), $r_{65}P_{52}$	-0.01	-0.02	-0.01	0.01
Total correlation	-0.26***	-0.08	-0.26***	-0.09

NS, *, **, *** Nonsignificant or significant at $P \leq 0.05$, 0.01, or 0.001 respectively

[z] Plants per hectare; [y] n=470; [x] n=461; [w] n=407; [v] n=434

Increasing density to 100,660 plants per hectare changed the influence of the variables on kernel recoveries. With fewer secondary ears being harvestable (Tables 2.3 and 2.5) tillers and stalk diameter influenced kernel recoveries from secondary ears less at the higher density (cf. Figs. 2.25 and 2.27, 2.26 and 2.28) as evidenced by a decline in the magnitude of correlation coefficients (Table 2.7a). However, there were high negative correlations between silk delay for the secondary ear and kernel recovery for the primary ear (Table 2.7b). In this instance, the influence was via indirect effects of stalk diameter and silk delay for the primary ear rather than a direct effect. This suggests that silk delay for the secondary ear at 100,660 plants per hectare had little influence on kernel recoveries.

The size of the stalk influenced kernel recoveries from primary ears more at the high density than at the low density as indicated by an increase in the magnitude of the correlation coefficient (Table 2.7a). With the increase in density being associated with longer silk delays for the primary ear (Figs. 2.20a and 2.21a), kernel recoveries for the primary ear at the high density were negatively influenced by their silk delay (Figs. 2.27 and 2.28). This influence resulted in silk delay for the primary ear comprising a large indirect effect in the correlation between stalk diameter and kernel recoveries for the primary ear (Table 2.7a). Consistent with this, stalk diameter also comprised a large indirect effect for the correlation between silk delay for primary ears and their kernel recoveries (Table 2.7b).

SS42 and Jubilee differed in the importance of tillers on kernel recoveries for the primary ear at 100,660 plants per hectare. Whereas their importance appeared to decline with density for SS42, their importance appeared to increase for Jubilee (Table 2.7a). A higher correlation between stalk diameter and tillers for SS42 than Jubilee (cf. Figs. 2.27 and 2.28) contributed to this result. Hence, tillers exerted a greater direct influence on recoveries for Jubilee than SS42.

Path analysis of the influence of N rate on kernel recoveries was not conducted due to limited response to N rate revealed in univariate analysis (Sections 2.3.1-2.3.3).

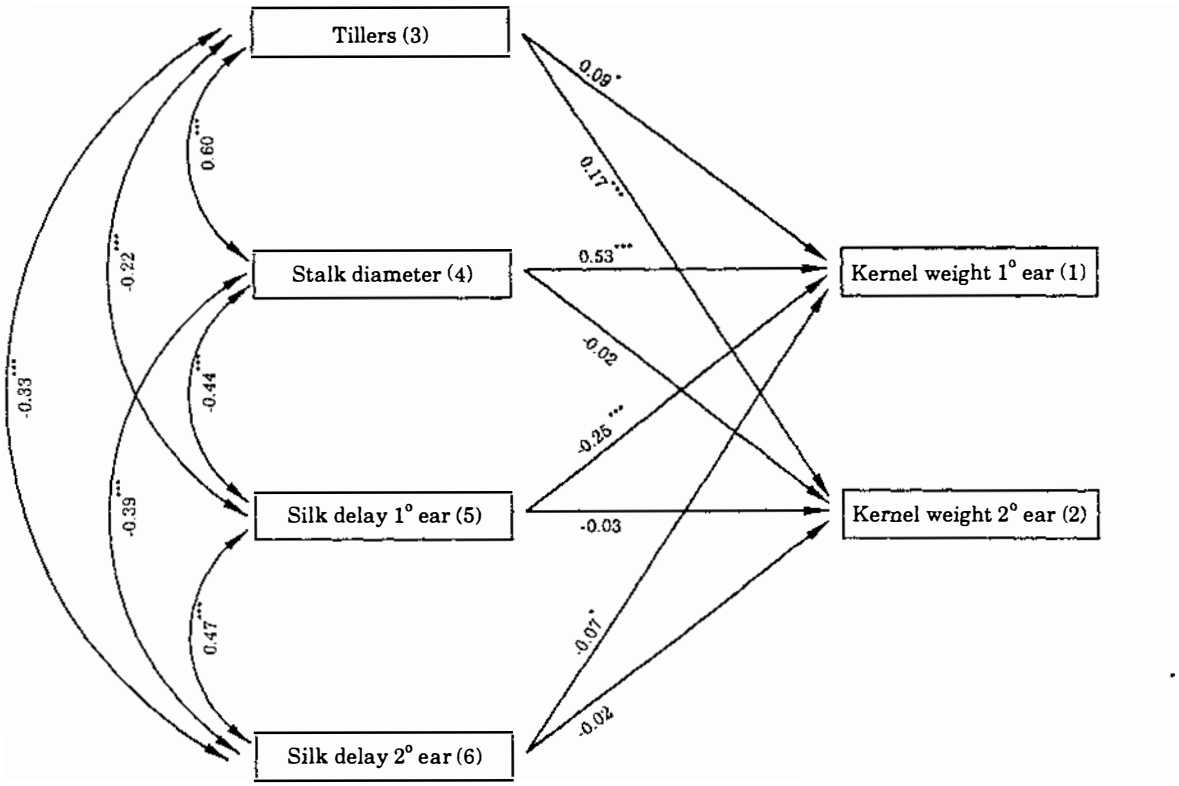

Fig. 2.27. Path analysis diagram of relationships among variables influencing yield (tillers, stalk diameter, and silk delay) and kernel recovery for SS42 grown at 100,660 plants per hectare. Curved lines represent correlations (r_{ij}) with straight lines representing path coefficients (P_{ij}). $^{NS, *, **, ***}$ Nonsignificant or significant at $P \leq 0.05$, 0.01, or 0.001 respectively. n=461.

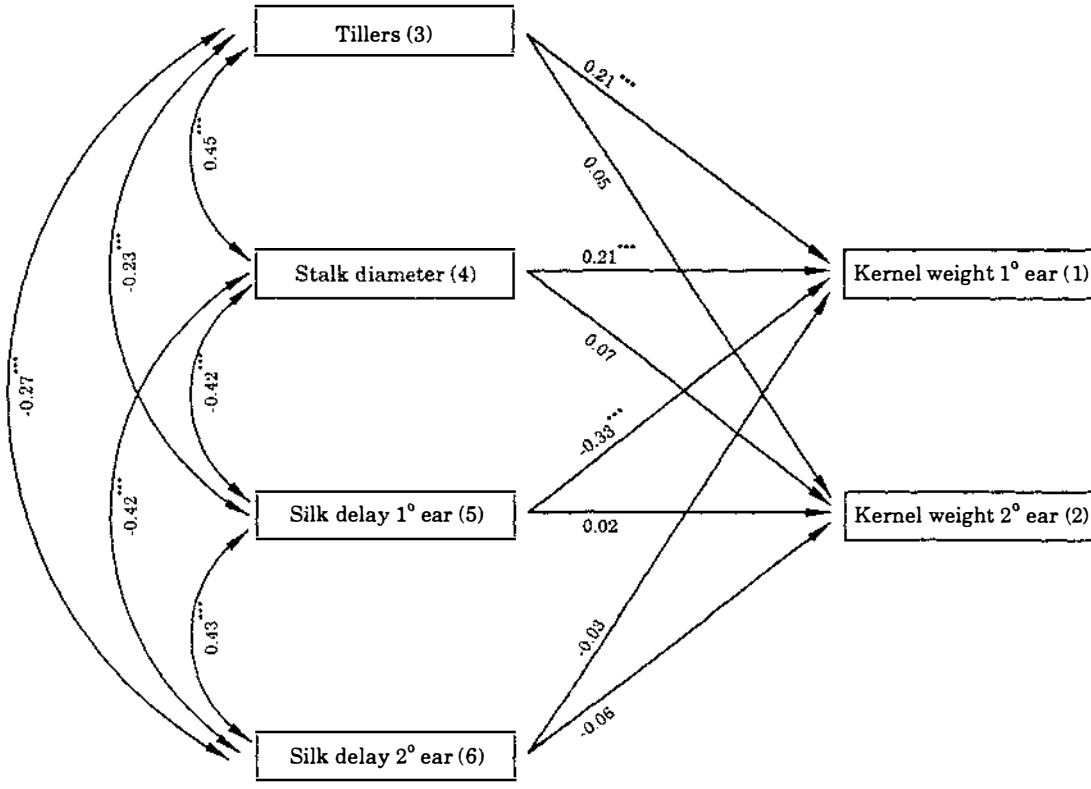

Fig. 2.28. Path analysis diagram of relationships among variables influencing yield (tillers, stalk diameter, and silk delay) and kernel recovery for Jubilee grown at 100,660 plants per hectare. Curved lines represent correlations (r_{ij}) with straight lines representing path coefficients (P_{ij}). $^{NS, *, **, ***}$ Nonsignificant or significant at $P \leq 0.05$, 0.01, or 0.001 respectively. n=434.

2.3.5 Canonical discriminant analysis

As there were few significant density × N rate interactions in univariate analysis, data for canonical discriminant analysis were pooled across N rates when examining the between-density variation. Similarly, data were pooled across densities when investigating the variables contributing to separation of N treatments.

As CDFs greater than two did not explain a significant proportion of the between-density variation for either cultivar, they were not further examined. Similarly, separation of N rates was not examined as canonical coefficients were not significant at the 5% level. This result was consistent with the limited response to N presented in univariate analysis (Sections 2.3.1-2.3.3).

The first canonical discriminant function (CDF_1) explained 90.0% and 91.2% of the between-density variation for SS42 and Jubilee, respectively, with a further 7.4% and 7.3% explained by CDF_2 (Table 2.8). The first CDF for SS42 discriminated largely on the number of ears per plant, kernel recovery from the secondary ear, stalk diameter, and length of the secondary cob. One explanation for this function is that a functional relationship may exist between the stalk diameter (i.e., a measure of the storage reserves of the plant) and the ability to support growth and development of a secondary ear. CDF_2 for SS42 discriminated on kernel recovery from the secondary ear, the number of tillers, and length of the primary cob. A negative loading for kernel recovery for the secondary ear and a positive loading for the number of tillers may suggest that secondary ears compete with tillers for nutrients (e.g., photoassimilate). The positive loading for length of the primary cob may reflect the closer proximity to a photoassimilate supply as compared to the secondary ear (Edmeades et al., 1979; Fairey and Daynard, 1978a, 1978b; Palmer et al., 1973).

CDF_1 for Jubilee discriminated largely on secondary ear components (i.e., cob length, kernel recovery, and silk delay) and possible sources of nutrients (i.e., number of tillers and stalk diameter) (Table 2.8). Separating on these two groups suggests that nutrient supplies influence the size and development of secondary ears. Separation of CDF_2 was dominated by negative loadings for both stalk diameter and kernel recovery from the primary ear and a positive loading

for kernel recovery for the secondary ear. Such separation suggests that the stalk is an important storage reserve for kernels. In particular, the positive loading for kernel recovery from the secondary ear with negative loadings for stalk diameter suggests that the size of secondary ear is dependent on an adequate supply of nutrients from the stem. However, both the primary and secondary ear appear to compete for the nutrient supply.

Separation of densities between CDF_1 and CDF_2 for Jubilee and SS42 is presented in Fig. 2.29.

Table 2.8. Standardized canonical coefficients between the first and second canonical discriminant functions (CDFs) on five densities for SS42 and Jubilee.

	SS42		Jubilee	
Variable	CDF_1	CDF_2	CDF_1	CDF_2
Number of tillers	-0.07	0.76	0.37	0.13
Stalk diameter	0.33	0.37	0.45	-0.67
Number of ears	0.42	-0.46	-0.22	0.13
Kernel weight[z] (1° ear)	0.02	-0.24	0.04	-0.95
Kernel weight[z] (2° ear)	0.37	-0.80	0.31	0.84
Primary cob length[z]	0.08	0.59	0.06	0.40
Secondary cob length[z]	0.34	0.27	0.42	-0.16
Primary ear silk delay	-0.14	-0.27	0.22	0.04
Secondary ear silk delay	-0.03	-0.08	0.35	-0.14
λ_i	10.29^{***}	0.85^{***}	8.12^{***}	0.65^{***}
Percent total variance	90.0	7.4	91.2	7.3
Density (plants per hectare)	---------- *ANOVA means* ----------			
40,710	5.03	1.03	4.55	-0.82
55,710	1.84	-1.31	1.43	0.81
68,980	-0.70	-0.71	-0.56	0.90
79,920	-2.40	0.03	-2.08	0.08
100,660	-3.68	0.89	-3.34	-0.97
SEOD (n=100)	0.22^{***}	0.23^{***}	0.12^{***}	0.22^{***}

[z] Harvestable ears only

λ_i: eigenvalue of the ith canonical discriminant function

$^{NS, *, **, ***}$ Nonsignificant or significant F test at $P \leq 0.05$, 0.01, 0.001, respectively

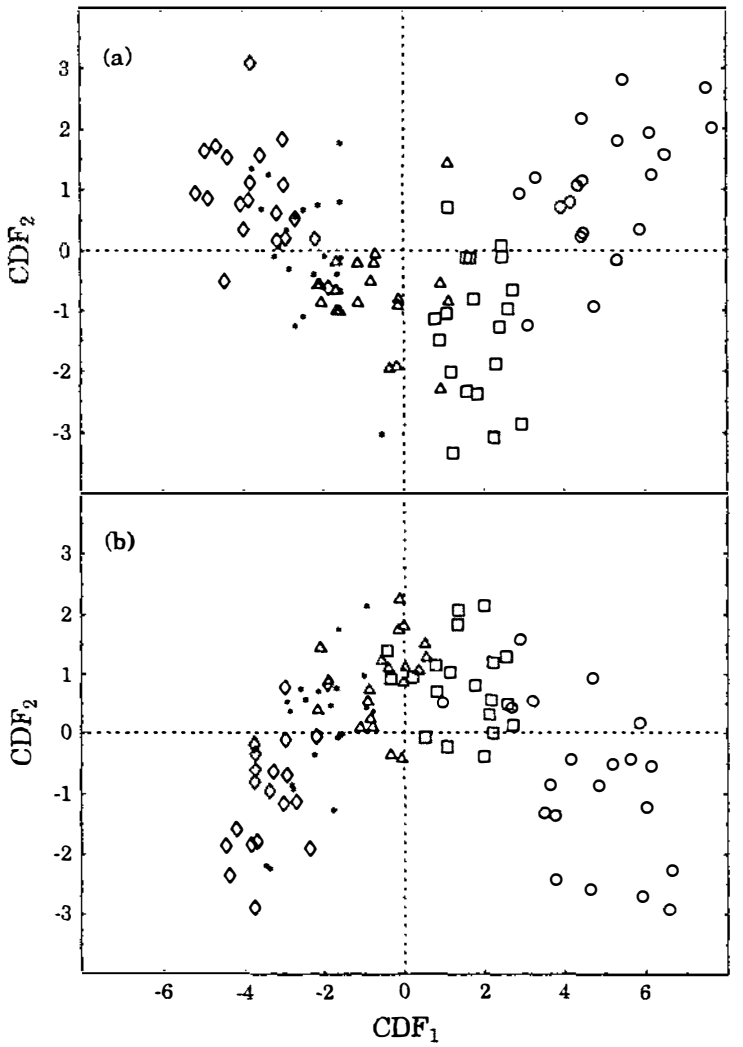

Fig. 2.29. Plots of canonical discriminant functions for (a) SS42 and (b) Jubilee at: 40,710 (○); 55,710 (□); 69,280 (△); 80,270 (*); and 100,660 plants per hectare (◇).

2.4 Discussion

Marketable kernel yield of Jubilee and SS42 was maximised in this study at 75,180 and 77,430 plants per hectare, respectively (Figs. 2.9a and 2.16a). Compared to 40,710 plants per hectare (the lowest density investigated), this represents a yield increase of 1.12-1.27 t/ha (depending on cultivar). However, compared to the density used by growers in Gisborne (i.e., 55,000 plants per hectare), this is a yield increase of only 0.26-0.35 t/ha. As yield at 55,000 plants per hectare was similar to that at each of the optimum densities it seems that growers are planting within the range for maximum yield. Moreover, maximum marketable cob yield occurred at 70,580 and 69,390 plants per hectare for SS42 and Jubilee, respectively (Figs. 2.10a and 2.17a) and was similar to that at 55,000 plants per hectare. This result further indicates that growers are planting within the density range for maximum yield.

To conclude that these densities are optimum requires data from more than one season. It is possible that with the lower radiation incidence for later sown crops (i.e., those crops receiving more heat units per day) that optimum densities may differ from those found in the current study. Density has a large influence on radiation interception (Stone et al., 1998); an important yield determinant as crop growth rate is closely related to the amount of radiation intercepted by the crop canopy (Maddonni and Otegui, 1996; Muchow et al., 1990).

The optimum density range for marketable cob yield (i.e., 55,000 to 100,000 plants per hectare) was not only lower, but followed a different trend than reported by Moss and Mack (1979). In their study, marketable cob yield of Jubilee increased to 76,100 plants per hectare, before plateauing to 109,800 plants per hectare, and then declining with further increases in density. Although yield of Jubilee also increased to 70,580 plants per hectare in the current study, yield declined beyond this optimum (Fig. 2.17a). These differences may result from differences in criteria for defining a marketable cob. Whereas primary and secondary cobs $\leq$ 164 and $\leq$ 151 g, respectively, were rejected in the current study, Moss and Mack (1979) rejected cobs < 220 g. As weight of primary cobs decline less rapidly with density than secondary cobs (cf. Figs. 2.14a and 2.14b), more secondary cobs are rejected as density increases, particularly if marketability criteria are strict. With almost all secondary cobs discarded in Moss and Mack's (1979) study,

the plateau phase for yield continued until primary cobs failed to meet marketability criteria. At this point the plateau phase ended, and marketable cob yield declined. A shorter plateau phase in the current study is therefore consistent with marketable cob yield comprising more secondary ears.

Clearly, marketability criteria influence the perception of yield. If criteria are too strict, cobs that may be otherwise processable, will be discarded (e.g., Moss and Mack, 1979). Relying on such criteria may result in planting regimes which do not maximise marketable yield. Thus criteria must be of sufficient rigour to minimise waste, yet not compromise quality. Unlike other studies (Chipman and MacKay, 1960; Fery and Janick, 1971; Heckman et al., 1995; Nichols, 1974; Smith, 1984; Warren, 1963), marketability criteria in the current study were based on weight rather than length measurements. Logistic regression analysis revealed that cob length was a poor predictor of whether a cob was marketable or not (data not presented). Moreover, the statistical relationship between cob length and kernel recovery (upon which many reported criteria are based) was not strong, with cob or ear weight being better predictors of marketability. Use of length measurements to determine marketability may actually compromise the goal of marketability criteria. Where criteria have not taken into account the unfilled tip length (i.e., the length of the cob over which kernels are considered not 'marketable'; e.g., Fig. 2.30), fewer cobs would be discarded. Hence, densities defined from such criteria may not identify maximum yield. Nevertheless, for producing 'whole cob corn', cob length will be a useful criterion even though it is not reliable for kernel yield prediction.

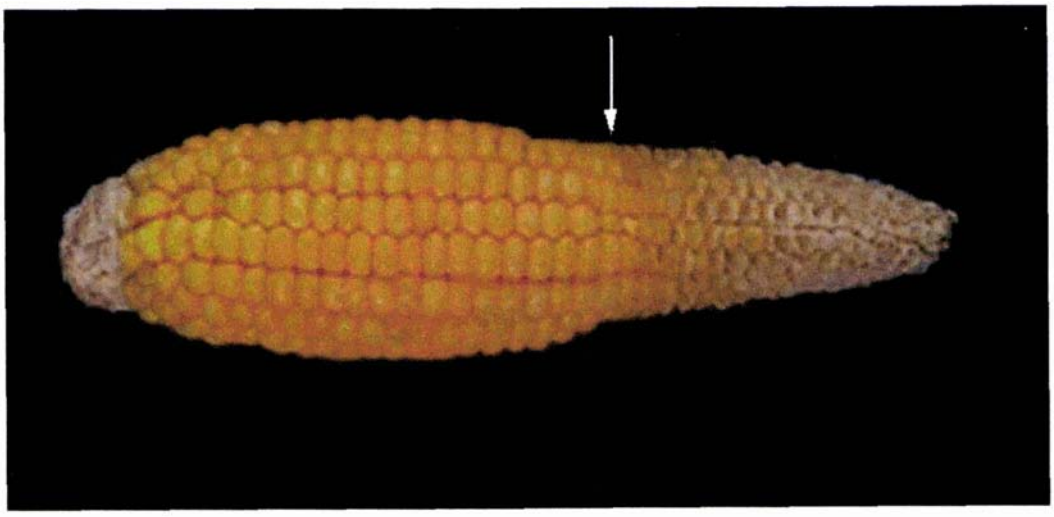

Fig. 2.30. A secondary cob demonstrating a large 'unfilled tip.' Kernels to the right of the arrow are not marketable.

The decline in cob length (Figs. 2.18 and 2.19) with density was consistent with other similar studies (Colville, 1961; Freyman et al., 1972; Moss and Mack, 1979; Rutger and Crowder, 1967). However, the lack of measures of tip fill in the current study means it is not possible to conclude that all cobs were suitable for producing frozen whole cob corn. Thus, even though the mean length of primary cobs produced at 100,660 plants per hectare (Figs. 2.18 and 2.19a) were greater than the 180 mm limit for whole cob corn (Davis, pers. comm.), their suitability for whole cob corn is unknown. Similarly, the suitability of secondary cobs of SS42 (Section 2.3.2.8), and those of Jubilee produced at densities less than 66,670 plants per hectare (Fig. 2.19b), was not quantified. It is possible that they were unsuitable as the unfilled tiplength increases with density (Camberato et al., 1989; Edmeades et al., 1993; Reddy and Daynard, 1983).

Although other studies have investigated the influence of density, N rate, or both on kernel recoveries (e.g., Freyman et al., 1972; Vittum et al., 1959; Wong et al., 1995), few have reported on marketable kernel yield. Lana (1956) reported recoveries[4] of 3.18–4.61 t/ha. This yield,

[4] Assumes USDA standards (Warren, 1963) were used as no account of what determined marketability was given.

however, is only half that recorded in the current study. Even with USDA standards being more strict than marketability criteria in the current study (Section 2.3.1.3), differences in criteria alone cannot account for the large gap in yield between the two studies. As plants in the current study carried at least 2.1 ears at 58,080 plants per hectare (Fig. 2.22), while those in Lanà's (1956) study carried only 0.8-1.0, hybrid prolificacy may explain the difference. Secondary ears contributed about 1.5 tonnes (i.e., about 15%) to marketable kernel yield at 50,080 plants per hectare (Figs. 2.9c and 2.16c). Such a large contribution is consistent with Durieux et al.'s (1993) study and supports Bauman's (1960) and Prine's (1971) suggestion that prolificacy provides a yield advantage over less prolific cultivars.

Processors would benefit from the use of densities of 69-77,000 plants per hectare (Figs. 2.9a, 2.10a, 2.16a, and 2.17a) as marketable cob and kernels yields are higher within this range than with 55,700 plants per hectare. Processors may further benefit from the higher density as fewer secondary cobs would be processed. This is advantageous because with kernels from secondary cobs generally having a higher SMC than primary cobs (about 2%) (Sections 2.3.1 and 2.3.2) and generally giving lower recoveries (Figs. 2.5 and 2.12), the consistency of the saleable product should be improved. However, to achieve this greater consistency would require 5-6% more cobs to be processed than at 55,700 plants per hectare (Tables 2.2-2.5). Whether this additional processing cost outweighs the benefit depends on the processing cost structure.

As growers are paid on the basis of marketable ear yield, it is necessary to compare the density range which maximises this with that which maximises marketable cob and kernel yields. For SS42, marketable ear yield was maximised at a density similar to that for marketable cob and kernel yields (cf. Figs. 2.8a-2.10a and 2.15a-2.17a). However, marketable ear yield of Jubilee was highest with 100,660 plants per hectare (Fig. 2.15a). With yield at this density statistically similar to that with 77,000 plants per hectare suggests that growers would not be disadvantaged by using the lower density. Moreover, the lower density offers the advantage of a lower potential for lodging (Bunting, 1973; Milbourn et al., 1978; Rutger and Crowder, 1967). Nevertheless, these results indicate that growers will benefit 0.74-0.79 tonnes (depending on cultivar) by increasing densities from 55,000 to 77,000 plants per hectare (Figs. 2.8a and 2.15a). While the additional cost of seed may largely negate the increase in yield, processors may encourage

growers to use the higher density through higher payments if they are to realise the advantage of a more consistent saleable product.

The approach of harvestable ear yield to an asymptotic maximum with density (Figs. 2.4a and 2.11a) was consistent with relationships reported in other studies (Fery and Janick, 1971; Freyman et al., 1972; Holliday, 1960; Moss and Mack, 1979; Mack 1972). Despite similar trends, the yield response to density in Mack's (1972) study with Jubilee was greater than in the current study. Whereas yield of Jubilee increased, at most, 16% as density increased from 40,710 to 100,660 plants per hectare (Fig. 2.11a), Mack (1972) reported a yield increase of 32-37% (depending on year). Although these differences may result from differences in the environments in which the crops were grown, cultural differences may explain the comparatively lower response. For example, the greater response in Mack's (1972) study may be due to irrigation being used. Water stress, particularly at high densities (Allison, 1969; Karlen et al., 1987), may dramatically reduce yield (Dale and Shaw, 1965). Alternatively, the lower response may have been due to small ears in the current study being discarded (Section 2.2.5).

Yield of secondary ears in the current study asymptotically approached zero as density increased (Figs. 2.4c and 2.11c). Such an approach was consistent with a decline in both their weight (Figs. 2.6b and 2.13b) and number (Tables 2.3 and 2.5). While weight and number of primary ears also declined with density (Figs. 2.6a and 2.13a; Tables 2.2 and 2.4), the decline was less dramatic than for secondary ears. Other studies have similarly noted the greater 'sensitivity' of the secondary ear over the primary ear (Bailey, 1941; Dolan and Christopher, 1952; Freyman et al., 1972; Mack, 1972; Pickett, 1944; Salardini et al., 1992; Vittum et al., 1959). Thus, in contrast to yield of secondary ears, yield of primary ears increased with density (Figs. 2.4 and 2.11). This trend was attributable to the number of primary ears increasing proportionately more rapidly with density than their decline in weight (cf. Tables 2.2, 2.4 and Figs. 2.6a, 2.13a). A plateauing in yield, however, indicates that the rate of decline in ear weight is directly proportional to the rate of increase in density. Presumably, as density increases further, the rate of decline in weight will eventually become greater than the increase in number and yield will decline as postulated by Downey (1971).

While yield (marketable or otherwise) was clearly responsive to density, yield and yield components of SS42 and to a lesser extent, Jubilee, were generally unresponsive to N fertiliser (Sections 2.3.1 and 2.3.2). Where responses were recorded, they often did not follow a consistent pattern with incremental increases in N rate. Muchow and Sinclair (1995) attributed a limited response to N rate of maize to high levels of mineralizable N. In the current study, mineralizable N contributed about 170 kg N/ha (Table 2.1) to the potentially available N in the soil. A further 89 kg N/ha was available from N present in the soil at planting (i.e., residual N). Therefore, the lack of response to N may have resulted from the 259 kg N/ha present in the soil during ontogeny, to which, additional N was applied. This result is consistent with Tsai et al.'s (1992) suggestion that grain yield would not increase with N fertiliser when levels of soil available N were greater than 175 kg/ha.

Numerous studies with sweet corn and maize have also reported either limited or no response to applied N (e.g., Adriaanse and Human, 1992; Bundy and Andraski, 1993; Bundy and Carter, 1988; Dickson, 1968; Fox and Piekielek, 1988; Gardner et al., 1990; Hatlitligh et al., 1984; Lory et al., 1995a; Moss and Mack, 1979; Schmid et al., 1959). In New Zealand, Steele and Cooper (1980) observed that almost half of the Ministry of Agriculture and Fisheries maize trials have shown no yield response to fertilizer N. Asghari and Hanson (1984) reported significant effects of N fertiliser on grain yields in only one of four years of experiments while Alessi and Power (1965) reported a significant effect in only one out of six years. With limited response to N rate so common, these studies suggest that in the absence of information of available N levels, some growers may be applying fertiliser N in excess of crop requirements for maximum yield.

Despite apparently high levels of soil available N, some yield responses for Jubilee to N fertiliser were recorded (e.g., Figs. 2.11, 2.16). In contrast, yield of SS42 did not increase with N fertiliser. In the numerous studies which have reported cultivar differences in the response to N rate (Dalby and Tsai, 1975; Eghball and Maranville, 1991; Friedrich and Schrader, 1979; Pollmer et al., 1979; Reed and Hageman, 1980; Smith, 1934; Tsai et al., 1978b, 1992) a common explanation for such differences was a difference in sink strength of the cultivars. Dalby and Tsai (1975) and Tsai et al. (1978b) reported levels of zein - a measure of sink strength (Russelle et al., 1983; Tsai et al., 1978a, 1980) - to be 43-54% lower in the *sh2* mutant than in the *su1* mutant. As zein

synthesis dramatically responds to N supply (Frey, 1951; Keeney, 1970; Rendig and Broadbent, 1979; Sauberlich et al., 1953; Schneider et al., 1952; Tsai et al., 1978a, 1980, 1983), the demand for N by kernels of Jubilee was presumably greater. Higher demand for N may therefore explain why Jubilee responded to increased levels of applied N (e.g., Table 2.6) whereas SS42 did not. Similarly, inconsistent increases in yield above the control with incremental increases in N (e.g., Figs. 2.13a and 2.15c) may indicate that levels of zein were approaching maximum levels as suggested in Tsai et al.'s (1984) study. Further research would be required to test this hypothesis.

The limited response of SS42 to N fertiliser compared to Jubilee suggests that SS42 requires less N fertiliser than Jubilee for maximum yield, and hence, is more efficient at using N fertiliser. Although this suggestion requires further validation, confirming this finding could have important ramifications for the planting of sweet corn in Gisborne. The N fertility of a site might be used to determine the choice of cultivar and the fertiliser regime to be used for it. The advent of such a management program would reduce both fertiliser and application costs. As this is in accord with the broad objectives given in Chapter 1 (i.e., to increase grower profit through decreased input costs), the differential response of Jubilee and SS42 to N rate is an important finding of this study and warrants further research.

While yield (marketable or otherwise) per unit area increases with density, yield per plant decreases (Dolan and Christopher, 1952; Moss and Mack, 1979; Pickett, 1944; Watson and Davis, 1938). Reduced weight of primary and secondary ear components with density (Figs. 2.5-2.7 and 2.12-2.14) is consistent with the consequences of a decrease in photoassimilate supply (Tollenaar et al., 1992). Photoassimilate supply declines through a combination of decreased leaf area (Early et al., 1967; Edmeades and Daynard, 1979b; Stickler, 1964), shading (Andrade et al., 1993b; Dwyer et al., 1991; Early et al., 1967; Hashemi-Dezfouli and Herbert, 1992; Moss and Stinson, 1961; Reed et al., 1988), and interplant (Modarres et al., 1998; Otegui, 1997; Prine and Schroder, 1964) and intraplant competition (Scott et al., 1975; Willey and Holliday, 1971; Wilson and Allison, 1978a). The proportionately greater decline in weight of secondary ears compared with primary ears with increasing density (Figs. 2.6 and 2.13) suggests that secondary ears are less competitive for photoassimilate. This response may result from the dominance of

the primary ear over the secondary ear (Pinthus and Belcher, 1994; Tetio-Kagho and Gardner, 1988b; Tollenaar, 1977). Thus as density increases and photoassimilate supplies decline, growth rates of secondary ears slow (Eddowes, 1969; Haynes and Sayre, 1956; Pinthus and Belcher, 1994). The decline in the number of ears per plant with density (Fig. 2.22) may therefore be the result of secondary ear abortion due to photoassimilate shortages (Bauman, 1960; Collins, 1963; Early et al., 1967; Earley et al., 1966; Prine, 1971; Prine and Schroder, 1965).

Photoassimilate supply may also be reduced by N stress (Amory and Creswell, 1984; Hanway, 1962b; Muchow and Sinclair, 1994; Sinclair and Horie, 1989). Not only does N stress reduce the capacity for photoassimilate utilisation in growth but also for photoassimilation (Connor et al., 1993; Lemcoff and Loomis, 1994; Muchow and Davis, 1988; Novoa and Loomis, 1981; Uhart and Andrade, 1995b). As density increases, the increasingly limited photoassimilate supply appears to be manifested in reduced size of secondary ears (Figs. 2.6b and 2.13b; Pinthus and Belcher, 1994; Tetio-Kagho and Gardner, 1988b; Tollenaar, 1977). The yield response of secondary ears to N rate in the current study (Fig. 2.15c and 2.16c) was consistent with the hypothesis that N assists in maintaining the photosynthetic capacity of the plant (Gifford, 1974; Greef, 1994; Murata and Matsushima, 1975; Novoa and Loomis, 1981). As the photoassimilate supply declines with density, the magnitude of yield differences among N rates for secondary ears declines (Fig. 2.11c). Hence, the influence of N rate on yield of secondary ears at high densities is less than at low densities (Fig. 2.11c; Anderson et al., 1984b; Salardini et al., 1992). In contrast, yield differences among N treatments for primary ears increase with density (cf. Figs. 2.11b and 2.11c). This trend is consistent with photoassimilate supplies becoming so limited at low N rates and high densities that primary ear growth also becomes inhibited.

The ability of an ear to attract photoassimilate depends on its sink strength (Jones and Simmons, 1983; Tollenaar, 1977; Tsai, 1979a). Potential sink strength, however, may be reduced by long silk delay causing poor pollination and reduced kernel set (Harris et al., 1976; Hashemi-Dezfouli and Herbert, 1992; Lemcoff and Loomis, 1994). Silk delays in the current study increased significantly with density, increasing 1.2-1.4 days for primary ears and 3.2-3.5 days for secondary ears as density increased from 40,710 to 100,660 plants per hectare (Figs. 2.20 and 2.21). Delays for secondary ears were at least 1.5 days longer than for primary ears. Hence, a lower sink

strength of secondary ears may be attributed to an excessively long silk delay as indicated in Otegui and Bonhomme's (1998) study. As silk delay for secondary ears increased with density, their potential sink strength may have been further reduced.

Increasing silk delays (Figs. 2.20 and 2.21) and significantly fewer ears silking as density increased (Fig. 2.22) suggests that the photoassimilate supply may have been limiting by the R1 stage of growth (Edmeades et al., 1993). Edmeades et al. (1993) noted that silk delay reflects a change in the development rate of either the tassel or the ear. More specifically, Otegui (1997) demonstrated that delayed floral differentiation in the ear was responsible for silk delays. As floral differentiation is sensitive to photoassimilate supply (Otegui and Melón, 1997), photosynthetic rates and partitioning of photoassimilate to the ear at R1 strongly influence kernel set (Cox, 1996; Edmeades and Daynard, 1979b; Johnson et al., 1986; Otegui and Melón, 1997; Otegui et al., 1995; Prine, 1971; Tollenaar et al., 1992).

Floral differentiation is also sensitive to water stress (Boyle et al., 1991; Herrero and Johnson, 1981; Westgate and Boyer, 1986). As water stress increases with density (Dale and Shaw, 1965), it is possible that increases in silk delay with increasing density (Figs. 2.20 and 2.21) were due to increased water stress than to reduced photoassimilate supply. Support for this postulate is provided by the association between silk delay and rainfall. Whereas 154 mm of rain fell during the three weeks preceding R1 for SS42 (Fig. 2.1b), only 12 mm fell for Jubilee. Moisture stressed plants partition less photoassimilate to pistillate spikelets, thereby inhibiting silk elongation (Schussler and Westgate, 1991a, 1991b; Westgate and Boyer, 1986). A longer silk delay for Jubilee than SS42 (cf. Figs. 2.20a and 2.21a) may therefore, at least partly, be attributable to water stress. However, water stress alone cannot explain increased delays as silk delay for SS42 continued to increase with density. Therefore, factors other than moisture stress must influence silk delay.

Limited photoassimilate supplies causing long silk delays eventually lead to barrenness (Hashemi-Dezfouli and Herbert, 1992). In the current study, negative correlations were calculated between silk delay and barrenness for both SS42 ($r=-0.38$; $P<0.001$) and Jubilee ($r=-0.50$; $P<0.001$). The stronger association for Jubilee is consistent with a delay one day longer

than SS42 (cf. Figs 2.20a and 2.21a). Considerably longer delays for secondary ears (Figs. 2.20b and 2.21b) were also associated with barrenness, although not as strongly as for primary ears (r=-0.31; $P<0.001$ and r=-0.29; $P<0.001$ for SS42 and Jubilee, respectively). Such low correlations suggest that other variables, in addition to silk delay, influence barrenness. Nevertheless, these associations and those reported by other workers (Buren et al., 1974; El-Lakany and Russell, 1971; Hashemi-Dezfouli and Herbert, 1992; Karlen and Camp, 1985; Woolley et al., 1962) indicate that silk delay is associated with barrenness and may therefore be an important yield determinant.

Path analysis further revealed that silk delay was associated with yield, particularly at the lowest density of 40,710 plants per hectare. At this density, silk delay for the secondary ear was negatively associated with kernel recovery from the primary ear (Figs. 2.25 and 2.26). With silk delay, in part, determining kernel sink strength, this association may suggest that sink strength of the secondary ear influenced kernel development in the primary ear. If the secondary ear competes with the primary ear then the path coefficient between silk delay for the secondary ear and kernel recovery for the primary ear should be positive. In other words, as silk delay of the secondary ears increases, the competitive ability of the primary ear increases due to sink strength of the secondary ear declining. However, the path coefficient is negative, possibly suggesting that the reduced sink strength of the secondary ear with longer silk delays impacts negatively on the primary ear. The negative association may indicate a loss in overall sink strength. Prolific hybrids have a superior propensity to translocate N from other plant parts to the grain after silking (Pan et al., 1984; Reed and Hageman, 1980). This was confirmed by Anderson et al. (1984a, 1984b, 1985), and later by Moll et al. (1987) who found a greater N utilisation efficiency (i.e., grain weight/total plant N) in prolific hybrids. With prolificacy declining with density, the propensity to translocate N may also decline. Therefore, in support of Camberato's (1987) and Durieux et al.'s (1993) studies, the presence of a secondary ear is associated with increased weight of the primary ear for both SS42 and Jubilee.

Positive correlations between tiller number and kernel recoveries (Figs. 2.25-2.28) may suggest that tillers were a photosynthetic source. While this observation supports other workers who suggest that tillers contribute to yield (Downey, 1972; Dungan, 1931; Lyon, 1905; Montgomery,

1909; Rosenquist, 1968), it contradicts others who believe that tillers are a net sink (Dungan et al., 1958; Tetio-Kagho and Gardner, 1988a; Wianko, 1911). Certainly the photosynthetic rate of tillers declines as they become shaded with a closing canopy (Hesketh and Musgrave, 1962; Kasperbauer and Karlen, 1986; Tetio-Kagho and Gardner, 1988a), but the time at which tillers fail to contribute photoassimilate to the main plant will depend on density. Lower correlation and path coefficients for both cultivars at the higher density (cf. Figs. 2.25 and 2.27, 2.26 and 2.28) suggest that any contributions were more limited at the higher density.

At low densities, tillers apparently contributed photoassimilate primarily to the secondary ear (Figs. 2.25 and 2.26), probably a consequence of their proximity. Lower leaves partition photoassimilate to the lower stem, whereas higher leaves partition photoassimilate predominantly to the stem and primary ear (Eastin, 1970; Edmeades et al., 1979; Fairey and Daynard, 1978a, 1978b; Palmer et al., 1973; Tripathy et al., 1972). At high densities, tillers appeared to contribute more to primary ears than secondary ears as evidenced by the higher path coefficients (cf. Figs. 2.25 and 2.27, 2.26 and 2.28). This trend is attributed to the low number of secondary ears at 100,660 plants per hectare (Tables 2.3 and 2.5). Thus, despite a declining photosynthetic rate with density (Kasperbauer and Karlen, 1986), tillers may still make a significant contribution to yield even at 100,660 plants per hectare.

Although tillers appear to contribute to yield, their influence for SS42 at 100,660 plants per hectare was largely indirect via the stalk (Table 2.7a). When the indirect effect of stalk diameter was removed, the direct effect of tillers on kernel recovery from primary ears was negligible. Tillers of Jubilee, on the other hand, had a large direct influence on kernel recovery from primary ears. These differences may suggest that the photosynthetic capacity of tillers at 100,660 plants per hectare for SS42 was significantly lower than for Jubilee. Alternatively, tillers for Jubilee may have remobilised more nutrients (e.g., DM or N) than those of SS42. Work with maize (Alofe and Schrader, 1975; Tetio-Kagho and Gardner, 1988a), as well as barley and wheat (Gu and Marshall, 1988; Kirby and Jones, 1977; Mohamed and Marshall, 1979) suggest that tillers may compete with the main plant for photoassimilate, particularly if they become shaded or develop ears. Further research would be necessary to quantify the importance of tillers to yield.

Regardless, these results suggest that tillers are more important for yield of Jubilee than SS42, particularly at higher densities.

Canonical discriminant analysis provided further insight into the relationships between yield and yield components and how they adjust to density. For both cultivars, the first CDF discriminated among variables associated with the secondary ear (e.g., cob length and kernel recovery) and those associated with supplying nutrients to the ear (i.e., tillers and stalk diameter) (Table 2.8). Thus, this CDF may be interpreted as being a measure of source strength for maintaining the growth and development of a secondary ear. In this context, the two cultivars may differ in the overall importance of tillers for supplying photoassimilate to the secondary ear. Whereas CDF_1 for SS42 places little emphasis on tillers, CDF_1 for Jubilee indicates that tillers are important for supporting growth of the secondary ear. This is consistent with results from path analysis discussed earlier.

The second CDF for Jubilee and SS42 are more difficult to interpret. CDF_2 for SS42 contrasts between the number of tillers and kernel recovery from the secondary ear (Table 2.8). Figure 2.29a shows that there are two clusters for CDF_2. The first cluster contains the densities 55,710 to 80,270 plants per hectare, whereas the second contains both the 40,710 and 100,660 plants per hectare densities. The contrast may indicate that secondary ears compete with tillers for nutrients (e.g., photoassimilate) and hence the two groupings indicate that tillers are more competitive at both the high and low densities. This would be consistent with the large secondary ears produced at the low density placing great demand on photosynthetic apparatus (Barnett and Pearce, 1983; Tollenaar, 1977) and other nutrient sources (e.g., tillers). Nutrient reserves would also be under strong sink pressure at the highest density because the photoassimilate supply is lower. Thus, at both 40,710 and 100,660 plants per hectare the shortage of photoassimilate would entail a greater demand on tillers to supply photoassimilate. CDF_2 for Jubilee may be argued similarly. This CDF contrasts stalk diameter and kernel recovery from the primary ear against kernel recovery from the secondary ear. Examining the horizontal axis in Fig. 2.29b (i.e., CDF_2) indicates that there are the same two clusters as identified for SS42. This contrast may also be explained in terms of photoassimilate supply, although in this instance, the stem is the nutrient source. However, with both the primary and secondary ears drawing on the stem for

photoassimilate and other nutrients, the primary and secondary ear appear to compete for photoassimilate in the stem. Thus, for continued growth the secondary ear must use alternative sources of photoassimilate (i.e., from tillers) as indicated by CDF_1.

Having identified a density range of 69-77,000 plants per hectare for maximising yield of both SS42 and Jubilee the first broad objective discussed in Chapter 1 has largely been met. Only with further studies using different sowing times to alter the pattern of radiation interception relative to radiation incidence can this density range be applied to the entire growing season with confidence. This study has also partially met objective two relating to better managing N inputs for yield. Importantly, there is a possibility that SS42 requires less fertiliser than Jubilee for maximum yield. Certainly this is an area worthy of further research which would seek to not only quantify these differences in N requirements but also answer questions relating to the physiology of the different response to N rate by these cultivars.

Chapter 3

Effect of nitrogen rate on dry matter and nitrogen partitioning in sweet corn

3.1 Introduction

The efficient use of N by crops of sweet corn and maize has become increasingly important because of increased costs of manufacture and distribution of N fertiliser (Moll et al., 1982a). Not only does excess application represent unnecessary expense, but may potentially pollute the environment (Bigeriego et al., 1979; Fox et al., 1989; Stanford, 1973). An earlier study (Chapter 2) indicated that SS42 is more efficient at using N fertiliser as it requires less fertiliser N for maximum yield than Jubilee (cf. Figs. 2.4a and 2.11a). Tsai et al. (1984) attributed such genotype differences to differences in the rate and duration of grain filling, rate of zein synthesis, and differences in the ability to assimilate N during grain filling.

The ratio of kernel DM to applied N is a measure of how efficiently fertiliser N is transferred from the soil to kernels (i.e., N use efficiency or NUSE; Moll et al., 1982a). This efficiency depends on how efficiently N is taken up (NUPE) and on how efficiently endogenous N is transferred to the grain (NUTE) (Beauchamp et al., 1976; Pollmer et al., 1979). Hybrids efficient at both uptake and utilizing N have a high NUSE, and hence are most desired (Kamprath et al., 1982; Moll et al., 1982b, 1987; Rhoads and Stanley, 1984).

Examining the contribution of NUTE and NUPE to variation in NUSE provides a framework to evaluate genotypes as related to plant physiological processes (Huggins and Pan, 1993). Salardini et al. (1992[1]) grew Jubilee with 50 or 150 kg N/ha and reported that NUPE contributed 23 and 1%, respectively, to variability in NUSE. Comparing their data with Kamprath et al.'s (1982) study, they concluded that Jubilee was inefficient at N uptake because NUPE explained a smaller proportion of the variability in NUSE. This conclusion is, however, incorrect as the lower proportion of variability explained by NUPE suggests that root uptake mechanisms of Jubilee were saturated at a lower N rate than for the maize hybrids. Thus, NUSE for Jubilee in Salardini et al.'s (1992) study was more limited by the transfer of endogenous N into kernel DM than uptake efficiency.

[1] NUSE and components were calculated on cobs (i.e., kernels plus rachis) at 28% SMC.

Nitrogen requirements for kernel development are met by the plant either accumulating sufficient N during vegetative growth, or maintaining the ability to assimilate N throughout ontogeny (Mackay and Barber, 1986). Proteins are degraded, and amino acids and newly assimilated N are translocated to kernels (Arruda and DaSilva, 1979; Chandler, 1960; Feller et al., 1977; Friedrich and Schrader, 1979; Hanway, 1962b; Reed et al., 1980; Venekamp et al., 1985). If N assimilation is unable to meet the metabolic and storage requirements of developing kernels, degradation and remobilisation of enzymic and structural N components from vegetative tissues to meet reproductive requirements can become extensive (Hageman, 1986; Tsai et al., 1991). Degrading leaf proteins leads to a reduced photoassimilate supply (Dwyer et al., 1995; Millard, 1988; Prioul, 1996; Tsai et al., 1986; Wolfe et al., 1988b) which may negatively impact on yield (Friedrich et al., 1979; Ta and Weiland, 1992).

Stems and, to a lesser extent, leaves act as transitory reserves for reduced N (i.e., protein) and photoassimilate for grain filling (Chanh Ta et al., 1993; Cliquet et al., 1990a, 1990b; Hume and Campbell, 1972; Novoa and Loomis, 1981; Ta and Weiland, 1992). In 23 of 28 maize hybrids examined by Rizzi et al. (1991), stem N at R1 was predominantly (> 80%) as protein. Similar findings were reported by Dijkshoorn and Van Wyk (1967). Vegetative organs are an important source of N for kernel development (Anderson et al., 1984a; Below et al., 1981; Chandler, 1960; Hanway, 1962b) as shown by the loss of labelled N from vegetative tissue being accounted for with gain in the ear (Friedrich and Schrader, 1979). Roots may also be an important source of N during kernel growth (Fairey and Daynard, 1978a; Friedrich et al., 1979; McClung et al., 1990; Pethö, 1967; Weiland and Ta, 1992) as large quantities of N accumulate in roots up to R1 (Viets et al., 1946; Weiland, 1989a) which may be translocated to the kernel during grain filling (Pethö, 1967). However, roots are ignored in most field studies because of problems related to their recovery from soil (Fairey and Daynard, 1978a). Hence, little published information exists on patterns of partitioning and remobilisation of N and DM in whole plants (with roots) during ear development (Olson and Kurtz, 1982; Ta and Weiland, 1992).

Non-kernel components of the ear (i.e., shank, rachis, and husk) are also considered conduits for temporary storage of precursors used in the synthesis of starch, proteins, and lipids in developing kernels (Crawford et al., 1982; Daynard et al., 1969; Fairey and Daynard, 1978b; Palmer et al.,

1973; Swank et al., 1982). Using ^{14}C labelling, Moutot et al. (1986) concluded that these tissues serve as short-term storage reservoirs of photoassimilate for kernel growth. Crawford et al. (1982) similarly demonstrated with ^{15}N labelling that these organs were successively N sinks then N sources.

Improved partitioning of photoassimilate to the economic yield component has generally been responsible for the increased yields obtained from many field crops over the last century (Gifford et al., 1984; Sarquís et al., 1998; Sinclair, 1998; Tollenaar, 1989). An index used by researchers to achieve the goal of increased yield is the harvest index (HI). The HI, a measure of partitioning expressed at a single point in time, quantifies the proportion of total DM in the harvestable organ (Donald, 1962; Donald and Hamblin, 1976). Maize researchers (e.g., Anderson et al., 1984a, 1984b; Below and Gentry, 1987) have used a modified HI in which organ DM or N content is substituted for kernel DM or N content to give a partitioning ratio for each organ throughout ontogeny. Although this approach describes the distribution of N or DM in the plant at defined ontogenetic stages, it does not directly reflect changes in N or DM content between ontogenetic stages. Partitioning ratios, therefore, provide a simple but coarse measure of N and DM partitioning.

Partitioning coefficients provide a more sensitive measure of short term changes in assimilate partitioning than HI (Boerboom, 1978; Keating et al., 1982). As partitioning coefficients are standardized by the total DM or N accumulated within each ontogenetic period, quantities of N or DM remobilised or accumulated for organs of different cultivars can be compared. They can therefore be used to examine source-sink relationships since the magnitude of the coefficient reflects relative source or sink strength. Thus, they can be used to indicate mechanisms involved in photoassimilate partitioning (Funnell, 1993). McCullough et al. (1994a) are one of the few groups of researchers who have used partitioning coefficients to describe partitioning in maize.

Although partitioning coefficients indicate the source or sink strength of an organ within a defined ontogenetic period, they do not explicitly determine the origin of the N or DM being partitioned. Movement of endogenous N between organs can only be tracked with radioisotope labelling because kernels may contain N derived from recent assimilation, remobilisation, or

both. An exception occurs when all organs are partitioned N; in this instance the source can only be newly assimilated N. Although the source of N in each organ cannot be determined, overall proportions remobilised or from newly assimilated N can be estimated (Below et al., 1981). Hay et al. (1953) estimated that about 60% of the N in kernels at R6 was from remobilisation with the remaining 40% from newly assimilated N. While DM for reproductive growth may similarly be derived from remobilisation, most is derived from current photoassimilation (Allison and Watson, 1966; Below et al., 1981; Duncan et al., 1965; Sawada et al., 1995; Simmons and Jones, 1985; Tanaka and Yamaguchi, 1972). Simmons and Jones (1985) estimated that less than 10% of ear DM was from remobilisation. Thus, maintaining a high photoassimilation rate after anthesis is essential for maximising yield (Allison and Watson, 1966; Evans et al., 1975; Gifford and Jenkins, 1982; Reed et al., 1988). This requirement was highlighted in studies where defoliating plants at R1 significantly decreased grain yield (Eddowes, 1969; Fujita et al., 1994; Tollenaar and Daynard, 1978c).

In studying source-sink relationships, two scenarios can be envisaged in the control of DM and N accumulation within the plant: either the system is source or sink limited (Wareing and Patrick, 1975). Tollenaar (1977) and others (e.g., Below et al., 1981, 1984; Cliquet et al., 1990b; Hanway, 1962a, 1962b; Reed et al., 1988; Swank et al., 1982) suggest that the reproductive sink capacity limits grain yield of maize. More specifically, Below et al. (1981) suggested that photosynthetic capacity generally exceeded ear requirements, while the supply of newly assimilated N was generally inadequate. It is not known whether this situation also exists for sweet corn, which is harvested earlier than maize (R4 compared with R6). Determining whether this situation also exists for sweet corn may have important implications for both the breeding of future sweet corn cultivars and the management of sweet corn crops. The objective of this experiment was therefore to provide a better understanding of the processes involved in partitioning N and DM to kernels of sweet corn with the goal of identifying traits for improving NUSE and yield of SS42 and Jubilee.

3.2 Materials and methods

3.2.1 Cultural

Data presented in this chapter were derived from the experiment described previously (Section 2.2).

3.2.2 Plant sampling

Five plants from each plot were removed at sequential ontogenetic stages (Table 3.1). Soil was shaken from roots and the remainder removed with water. Root loss during harvesting and washing was assumed to be less than 10%. Nutrient loss from roots during washing was assumed to be minimal (Böhm, 1979) and was ignored. Plants were fractioned into laminae, stem (including leaf sheaths and tassel), shank, husk, kernels, cobs (i.e., rachis plus kernels), and roots. Roots were severed at the root crown. Plants were stored at 5 C between harvest and fractioning. Storage duration ranged between one and 24 hours. Fractioned material was frozen (-18 C).

Table 3.1. Relationship between accumulated GDD and ontogenetic stage.

Jubilee		SS42		Difference in GDD between cultivars[z]
Ontogenetic stage	Accumulated GDD	Ontogenetic stage	Accumulated GDD	
V3	301	V3	309	-8
V7	485	V6	472	13
V13	676	V12	661	15
R1	864	R1	803	61
R3	1106	R2/R3	1002	104
R4	1252	R4	1204	48

[z] Calculated as accumulated GDD for Jubilee minus that accumulated for SS42.

3.2.3 Tissue analysis

As a density of approximately 70,000 plants per hectare was determined as being optimum for marketable kernel yield of both SS42 and Jubilee (Section 2.4), only plant material from the 68,980 plants per hectare treatment was used in this experiment. Further, only plants from the 0, 115, and 230 kg N/ha treatments were used as differences among N rates were generally nonsignificant (Section 2.3).

Fractioned material was dried to constant weight in a forced air oven at 80 C. Cobs were fractioned into kernels and rachis after drying. After weighing, a 15 g sub-sample was taken and ground to pass a 0.5 mm screen. The N concentration of each fraction was determined from a 0.1 g sample using the semi-micro Kjeldahl method (Bremner, 1960).

3.2.4 Data analysis

Discarding plant material (Section 3.2.3) "reduced" each experiment from a split-plot design (Section 2.2.2) to a randomised complete block design. Thus the experimental design for each cultivar consisted of three N rates (0, 115, or 230 kg/ha) randomly allocated into each of four blocks.

Data sets for Jubilee and SS42 were combined to test genotypic differences. As ontogenetic stages and accumulated GDD were similar (Table 3.1), pooling the data was valid. However, in doing this, genotypic differences become confounded with differences in incident radiation levels (2065 $MJ \cdot m^{-2}$ for Jubilee and 1850 $MJ \cdot m^{-2}$ for SS42). Data for each cultivar were standardized to rate of DM or N accumulation per GDD to eliminate possible influences of differences in the accumulated GDD for each cultivar. Both raw and standardised data were analysed by ANOVA to check whether differences in GDD between the cultivars influenced significance tests. As both analyses yielded similar results, only the results of analyses on raw data are presented. For ease of discussion, ontogenetic stages from Table 3.1 are discussed as V3, V6, V12, R1, R3, and R4 for the combined data set.

The DM and N that accumulated up to R1 were defined as pre-anthesis DM and N accumulation, respectively. Post-anthesis accumulation was calculated as DM or N at R4 less that at R1. Correlation analysis was used to determine the association between variables. As curvilinear or nonlinear relationships between two variables will distort the correlation coefficient (Myers, 1990), the need for transformations was checked by plotting each variable pair as recommended by MacKay (1995). The assumption of normality was checked for each variable using SAS (PROC UNIVARIATE; SAS Institute, 1989).

Principal component analysis

High correlations between kernel DM and N content at R4 with post-anthesis DM and N accumulation suggested that the relationship may be explained by fewer variables. Principal component analysis was therefore used to reduce the dimensionality of the data set into a set of new variables. Following Jolliffe (1972), all principal components with an eigenvalue less than 0.7 were rejected.

Nitrogen use efficiency and components

Nitrogen uptake efficiency and NUTE were calculated using Equations 3.1 and 3.2, respectively. Together these equations multiplicatively determine NUSE (Equation 3.3).

$$NUPE = \frac{Nt}{Ns} \tag{3.1}$$

$$NUTE = \frac{Gw}{Nt} \tag{3.2}$$

$$NUSE = \frac{Gw}{Ns} \tag{3.3}$$

where Nt is the total N content at maturity; Gw is grain weight at maturity; and Ns is N applied all expressed in units of g·plant^{-1}.

The contribution of the efficiency components (i.e., NUTE and NUPE) to variability in NUSE was determined by linearising the NUSE function by taking logarithms of NUSE, NUPE, and NUTE, denoted as Y, X_1, and X_2, respectively (Moll et al., 1982a). Sums of squares for Y, and sums of products of Y with X_1 and X_2 were computed and the contributions of X_1 and X_2 to $\sum Y^2$ expressed as $\sum X_i Y / \sum Y^2$ calculated (Kamprath et al., 1982).

Unlike maize, the marketable commodity of sweet corn may also be cobs (i.e., kernels plus rachis). Efficiency components for cobs were also investigated by substituting *Gw* in Equations 3.2 and 3.3 with cob DM. As efficiency components calculated using cobs were similar to those calculated using kernel DM data were not presented. Similarly, the proportion of variability in NUSE explained by NUTE and NUPE were similar to those calculated using kernel DM, and hence, also not presented.

Partitioning coefficients

Nitrogen partitioning coefficients (NPCs) were calculated as the ratio of the N accumulation rate of the plant fraction to the whole plant N uptake rate over the ontogenetic interval in question (McCullough et al., 1994a; Equation 3.4). For example, if a plant accumulated 20 mg of N per day between V12 and R1, of which leaves were partitioned N at a rate of 2 mg per day during this interval, the NPC is 0.1 or 10%. In other words, 10% of the total N accumulated between V12 and R1 was partitioned to leaves. A positive coefficient therefore reflects net accumulation, while a negative coefficient reflects remobilisation. The magnitude of the coefficient relative to other organs therefore reflects sink or source strength. Dry matter partitioning coefficients (DMPCs) were calculated by substituting DM for N in Equation 3.4.

$$NPC = \frac{\delta\ Organ\ N}{\delta\ Total\ N} \tag{3.4}$$

where δ represents the rate of change between two ontogenetic stages.

As a consequence of the calculation, partitioning coefficients between V12 and R1 do not sum to 100% because ears were not harvested until R1. For this reason, the difference between 100% and the sum of the partitioning coefficients during this period was attributed to growth of the ears.

Source of N and DM within ontogenetic stages

Quantities of N and DM derived from newly assimilated N and current photoassimilate during ear development were calculated following the method of Below et al. (1981), adjusted to include all organs in the calculations. The adjustment was necessary as it was not possible to track remobilisation from one organ with partitioning to another without radioisotope labelling. Overall quantities of N or DM derived from newly assimilated N or current photoassimilate were therefore calculated as total accumulation within an ontogenetic period less remobilisation.

3.3 Results

3.3.1 Ontogenetic changes in total DM and N content

Plants of Jubilee and SS42 accumulated N and DM in a curvilinear fashion between V3 and R4 (Fig. 3.1). The similarity of the N and DM accumulation patterns was reflected in a highly significant correlation ($r=0.97$; $P<0.001$). Although both cultivars accumulated DM with a similar pattern, plants of Jubilee accumulated a significantly greater quantity from V6 onwards. At R4, plants of Jubilee contained 18% more DM than those of SS42. R4 was the only ontogenetic stage where DM contents were significantly influenced by N rate. Dry matter contents at this ontogenetic stage were 21% higher with 230 kg N/ha than the control. In addition, R4 was the only ontogenetic stage where N contents were significantly increased with the addition of N fertiliser, increasing 20% as N rate increased from 0 to 230 kg/ha. Aside from V6 and R4, both cultivars accumulated similar quantities of N throughout ontogeny. At V6, plants of SS42 contained significantly more (35%) N than those of Jubilee, but significantly less (20%) at R4.

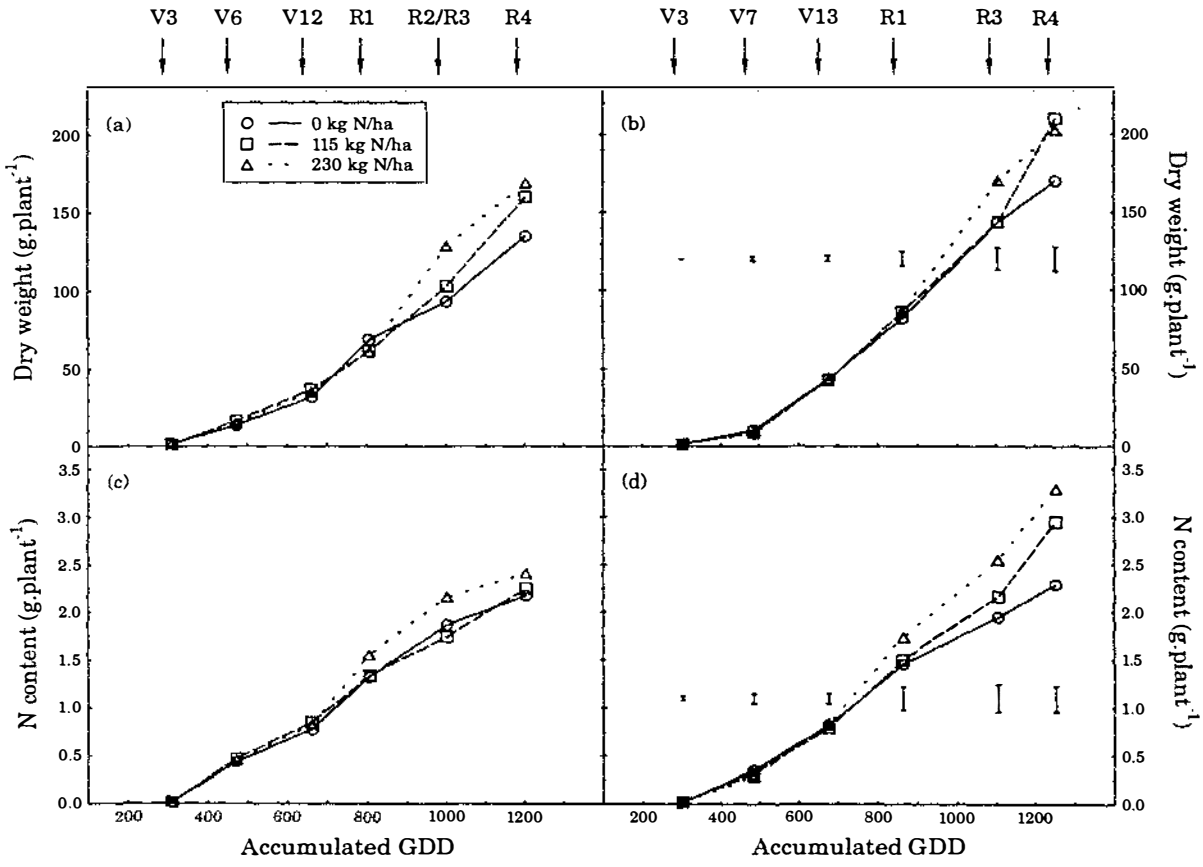

Fig. 3.1. Effect of N rate on total DM accumulation for (a) SS42 and (b) Jubilee, and total N accumulation for (c) SS42 and (d) Jubilee. Vertical bars represent the pooled standard error for each harvest (n=24).

3.3.2 Pre- and post-anthesis DM and N accumulation

Although both cultivars accumulated similar proportions of their total DM during both the pre- and post-anthesis stages, Jubilee accumulated 25% more DM than SS42 (Table 3.2). Of this, about 42% was accumulated during the pre-anthesis stage. Although N rate did not influence pre-anthesis DM accumulation, a significant influence was detected for post-anthesis accumulation for both cultivars. Plants of both cultivars accumulated 32% more DM during the post-anthesis period when grown with 230 kg N/ha than those of the control.

Similar quantities of N were accumulated by both cultivars during the pre-anthesis period (Table 3.2). In contrast, Jubilee accumulated significantly more (47%) N than SS42 during the post-anthesis period. Post-anthesis N accumulation in both cultivars was also significantly influenced by N rate. Averaged across cultivars, post-anthesis N accumulation increased 34% as N rate increased from 0 to 230 kg/ha. Of the total N accumulated, SS42 and Jubilee accumulated about 34% and 47% during the post-anthesis period, respectively.

Table 3.2. Effect of N rate on pre- and post-anthesis N and DM accumulation for Jubilee and SS42.

		DM accumulated ($g \cdot plant^{-1}$)		N accumulated ($mg \cdot plant^{-1}$)	
Cultivar	N rate (kg/ha)	pre-anthesis	post-anthesis	pre-anthesis	post-anthesis
Jubilee	0	82	92	1455	968
	115	86	125	1500	1466
	230	86	119	1735	1671
SS42	0	69	63	1328	576
	115	62	98	1340	909
	230	61	108	1554	672
5% LSD		11	16	299	322
		---------- Significance levels ----------			
Cultivar		**	*	NS	**
N rate		NS	**	NS	*
Cultivar × N rate		NS	NS	NS	NS

NS, *, **, ***; Nonsignificant or significant F test at $P \leq 0.05, 0.01, 0.001$, respectively.

Pre-anthesis DM accumulation was highly correlated with pre-anthesis N uptake (r=0.79; $P<0.001$), as was post-anthesis N uptake with the quantity of DM accumulated post-anthesis (r=0.77; $P<0.001$). However, neither post-anthesis N nor DM accumulation were linearly associated with pre-anthesis N or DM accumulation.

3.3.3 Ontogenetic changes in DM, N concentration, and N content of stems

The ontogeny of DM accumulation in stems was generally sigmoidal (Figs. 3.2a and 3.2b). The 230 kg N/ha treatment was an exception, however, as DM continued to accumulate to R3 before declining between R3 and R4. These varying trends resulted in significant differences between the N rates at R3. At this ontogenetic stage, stems in the 230 kg N/ha treatment contained 22% more DM than those of the control. Differences between N rates at earlier ontogenetic stages were not significant. Stems of Jubilee contained significantly more DM than those of SS42 from V12 onwards. Depending on ontogenetic stage, stems of Jubilee contained 13-33% more DM than those of SS42.

Nitrogen concentrations increased to V6, then generally declined with ontogeny (Figs. 3.2c and 3.2d). Although stems of Jubilee contained a significantly higher concentration of N than those of SS42 at V6, concentrations for SS42 were significantly higher at both R1 and R3, being 18% higher at these latter two ontogenetic stages. Nitrogen concentrations were similar between Jubilee and SS42 at the other ontogenetic stages. Only at R3 were the N concentrations in stems significantly enhanced with N fertiliser, being 23% higher with 230 kg N/ha than the control.

Nitrogen contents increased to R1 then declined (Figs. 3.2e and 3.2f). At R4, 26 and 48%, respectively, of the N present in stems of SS42 and Jubilee at R1 had been remobilised. Aside from V12 and R1, N contents were similar between the cultivars. At V12 and R1, stems of Jubilee contained 22 and 26% more N than those of SS42, respectively. Nitrogen contents were similar between the N rates at all ontogenetic stages.

Dry matter content of stems was highly correlated with N content ($r=0.81$; $P<0.001$). However, increased DM content was inversely associated with N concentration ($r=-0.52$; $P<0.001$). Nitrogen content was not correlated with N concentration.

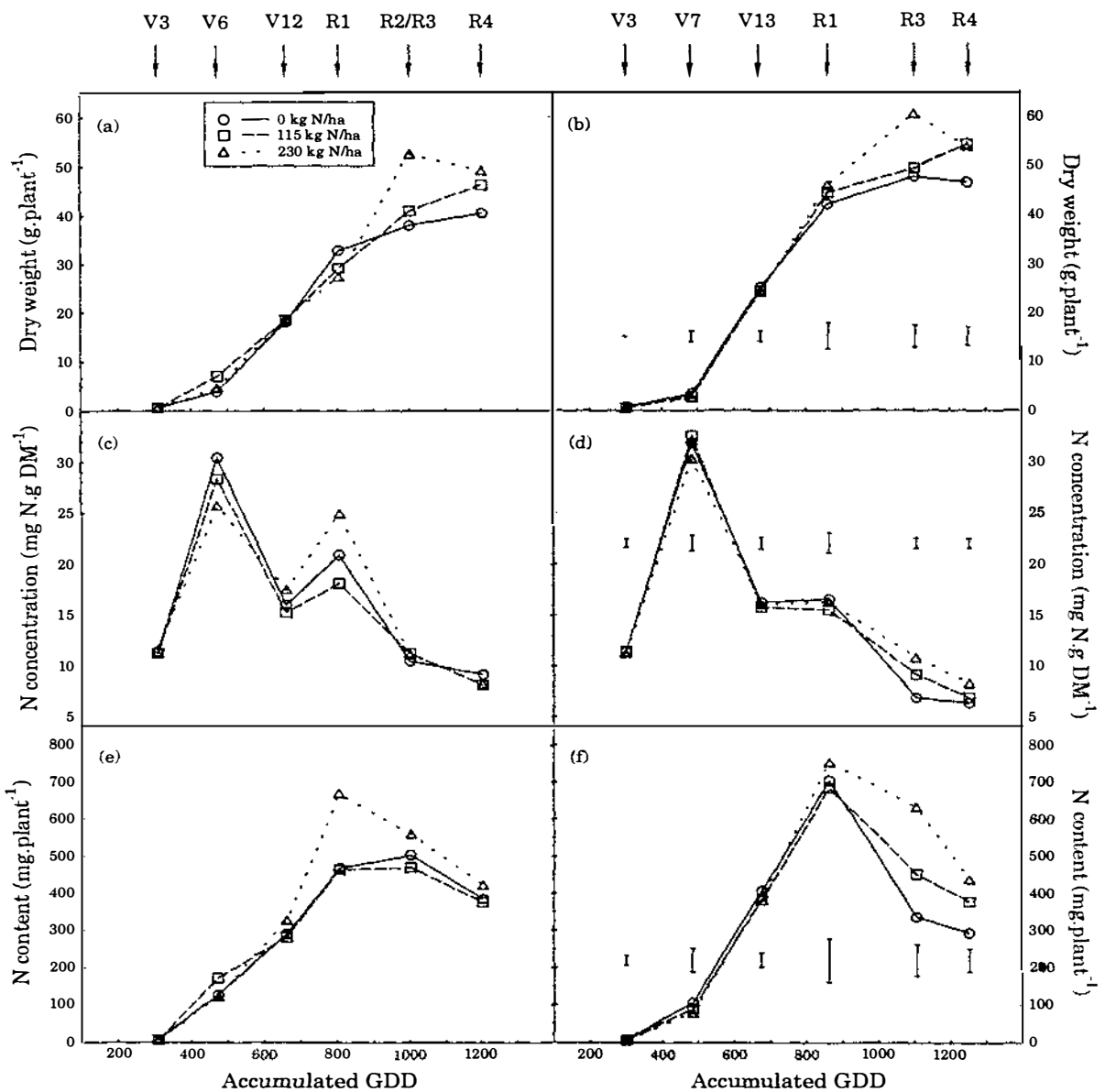

Fig. 3.2. Effect of N rate on DM accumulation in stems of (a) SS42 and (b) Jubilee, N concentration in stems of (c) SS42 and (d) Jubilee, and N accumulation in stems of (e) SS42 and (f) Jubilee. Vertical bars represent the pooled standard error for each harvest (n=24).

3.3.4 Ontogenetic changes in DM, N concentration, and N content of leaves

Dry matter accumulated in leaves to R1 before plateauing (Figs. 3.3a and 3.3b). As with stems, however, the 230 kg N/ha treatments were an exception to this trend with DM continuing to accumulate between R1 and R3 before declining between R3 and R4. Nevertheless, DM contents at all ontogenetic stages were similar between the N rates. Significant cultivar differences were detected only at V6 and R4. At V6, leaves of SS42 contained 41% more DM than those of Jubilee, but 18% less at R4.

Nitrogen accumulated in leaves with a similar fashion to DM (cf. Figs. 3.3a, 3.3b, 3.3e, and 3.3f). This similarity was reflected in a highly significant correlation (r=0.94; $P<0.001$) between the two variables. Unlike the other N treatments, leaves in the 230 kg N/ha treatments continued to accumulate N to R3 before most of this gain was remobilised between R3 and R4. Such varying trends resulted in significant differences among the N rates at R3. At this ontogenetic stage, leaves in the 230 kg N/ha treatment contained 34% more N than those of the control. Nitrogen contents were similar among the N rates at other ontogenetic stages. The N content of leaves was significantly different between the cultivars at V6 where leaves of SS42 contained 29% more N than those of Jubilee.

The N concentration in leaves declined 29 and 43% for SS42 and Jubilee, respectively, between V6 and R4 (Figs. 3.3c and 3.3d). Leaves of SS42 and Jubilee contained a similar concentration of N at V3, but the concentration in leaves of Jubilee was higher at V6. The N concentration in leaves of Jubilee declined rapidly between V6 and V12 in contrast to SS42. As a consequence, significant cultivar differences were detected from V12 onwards. Cultivar differences detected at R1 were due to a significant cultivar × N rate interaction. Jubilee contained N at higher concentrations than SS42, and unlike SS42, responded to N rate. At R3 and R4, the N concentration of SS42 leaves was at least 16% higher than in Jubilee. Significant increases in the N concentration of leaves with N fertiliser were also recorded at R3. At this ontogenetic stage, leaves in the 230 kg N/ha treatment contained an 18% higher N concentration than the control. Differences among the N rates at other ontogenetic stages were not significant.

Despite highly significant correlations, the N concentration in leaves was only weakly associated with DM content (r=0.28; $P<0.001$) and only moderately associated with N content (r=0.47; $P<0.001$).

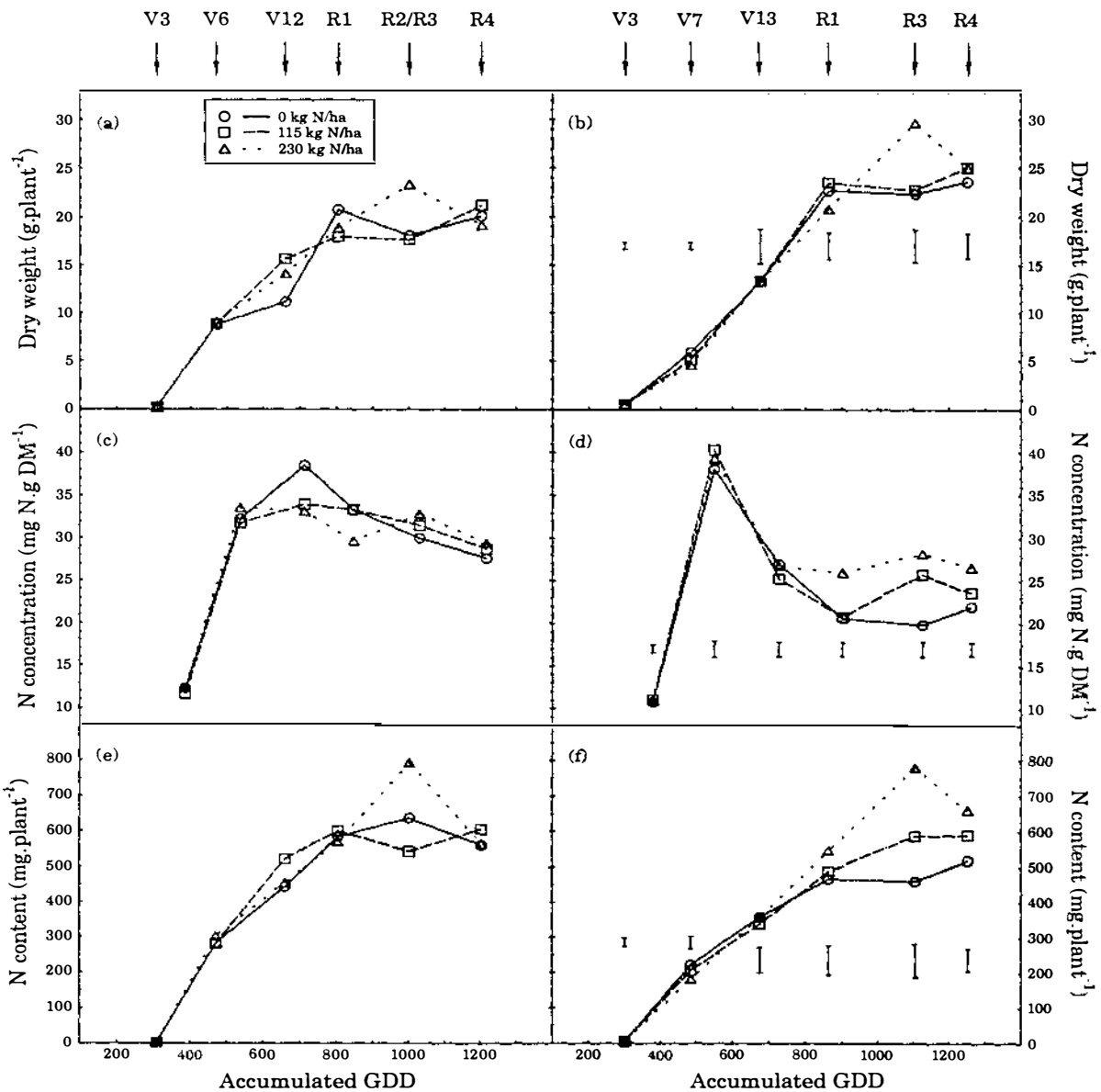

Fig. 3.3. Effect of N rate on DM accumulation in leaves of (a) SS42 and (b) Jubilee, N concentration in leaves of (c) SS42 and (d) Jubilee, and N accumulation in leaves of (e) SS42 and (f) Jubilee. Vertical bars represent the pooled standard error for each harvest (n=24).

3.3.5 Ontogenetic changes in DM, N concentration, and N content of roots

About 81% of the DM accumulated by roots accumulated between V3 and R1 (Fig. 3.4a and 3.4b). Although roots in the 230 kg N/ha treatment of SS42 continued to accumulate DM to R3, root weights at R3 were similar among the N rates. Moreover, root weights were similar among the N treatments at all ontogenetic stages except R4. At this ontogenetic stage root weights of plants in the 115 kg N/ha treatment were 19% higher than the control. Significant cultivar differences were observed at V12, R1, and R4. At each of these ontogenetic stages roots of Jubilee contained significantly more (at least 19%) DM than those of SS42.

The N concentration of roots increased between V3 and V6 before declining about 64% between V6 and R4 (Figs. 3.4c and 3.4d). Roots of both cultivars contained similar concentrations of N at all ontogenetic stages except V12, at which, roots of SS42 contained N at a concentration 14% higher than for Jubilee. Concentrations at V12 were also significantly different among the N rates, being 25% higher with 230 kg N/ha than the control. The N concentration was also significantly influenced by N rate at V12, with the N concentration of roots in the 230 kg N/ha treatment 29% higher than the control.

Roots of both cultivars accumulated N to R1, after which their N contents declined (Figs. 3.4e and 3.4f). Depending on N rate, up to 52% of previously accumulated N was remobilised from roots between R1 and R4. Roots of both cultivars contained similar quantities of N up to V12, with the quantities accumulated also similar among the N rates. However, at V12 roots of Jubilee contained significantly more N than those of SS42 and unlike SS42, accumulation was positively influenced by N rate. Significant cultivar and N rate effects were also detected at R1. At this ontogenetic stage roots of Jubilee contained 35% more N than those of SS42, with their N contents increasing 44% as N rate increased from 0 to 230 kg/ha. Nitrogen contents were similar between both the cultivars and N rates at R3 and R4.

Root DM was positively correlated with N content ($r=0.78$; $P<0.001$), but negatively correlated with N concentration ($r=-0.66$; $P<0.001$). The N concentration of roots was not associated with their N content.

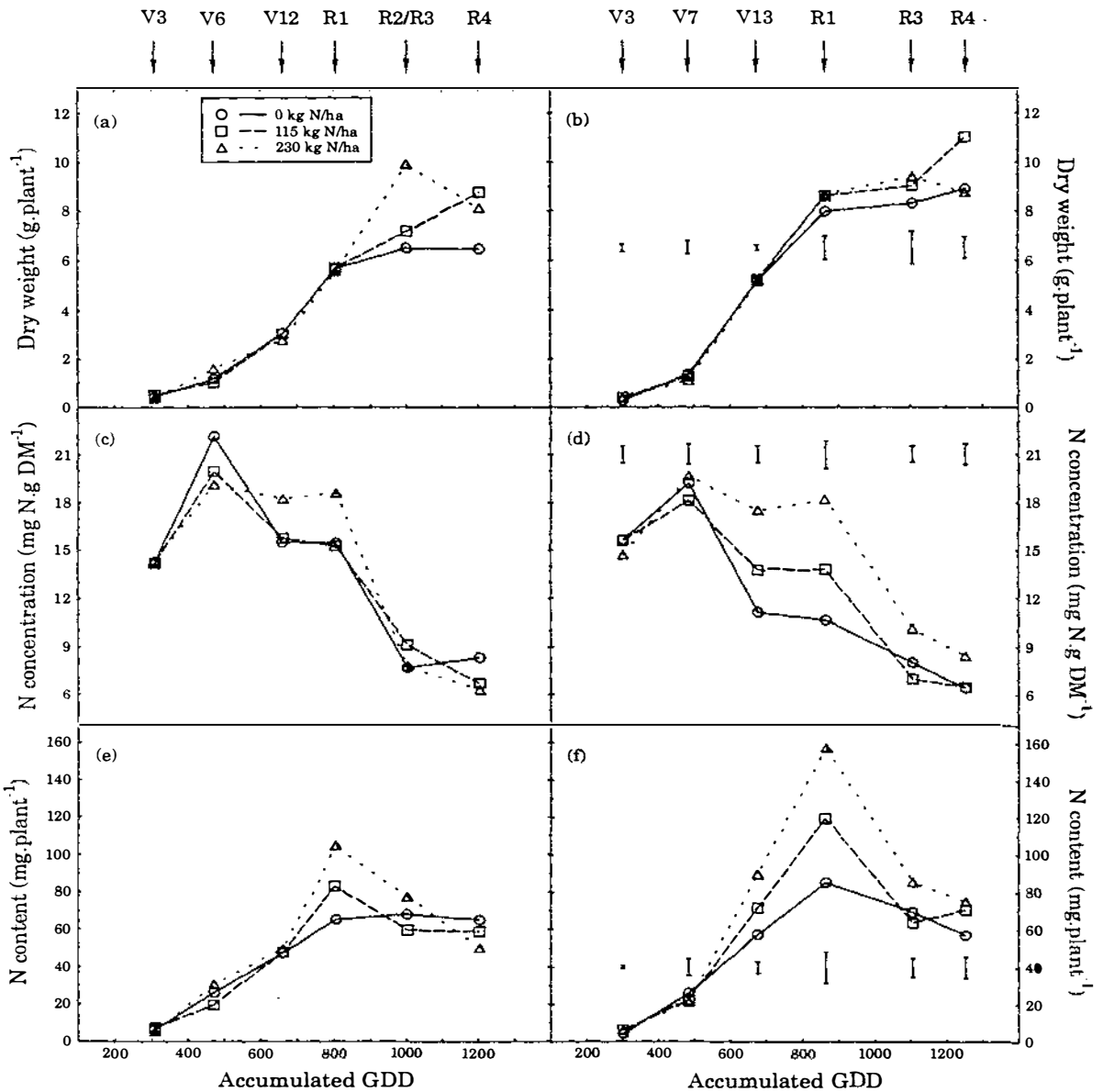

Fig. 3.4. Effect of N rate on DM accumulation in roots of (a) SS42 and (b) Jubilee, N concentration in roots of (c) SS42 and (d) Jubilee, and N accumulation in roots of (e) SS42 and (f) Jubilee. Vertical bars represent the pooled standard error for each harvest (n=24).

3.3.6 Ontogenetic changes in DM, N concentration, and N content of the shank

Shank DM of SS42 and Jubilee increased 68 and 80% between R1 and R3, respectively (Figs. 3.5a and 3.5b). However, between 5 and 11% of the DM present in shanks at R3 was remobilised between R3 and R4. Although shank DM was similar between the cultivars at R1, shanks of Jubilee contained significantly more (at least 41%) DM at both R3 and R4. Nitrogen rate did not influence shank DM content at any ontogenetic stage.

Nitrogen concentration in shanks decreased about 69% between R1 and R4 (Fig. 3.5c and 3.5d). Although concentrations declined with ontogeny, concentrations at R1 were significantly enhanced with N fertiliser, being 20% higher with 230 kg N/ha than the control. While N concentrations were similar between the cultivars at R1, significant cultivar differences were detected at R3. At this ontogenetic stage, the N concentration in shanks of SS42 was 31% higher than for Jubilee. At R4, N concentrations for SS42 were higher than Jubilee, but unlike SS42, concentrations for Jubilee increased with N rate.

While the N content of shanks increased between R1 and R3, almost all of this gain was remobilised between R3 and R4 (Figs. 3.5e and 3.5f). Only at R4 were N contents significantly different between the cultivars. At this ontogenetic stage, shanks of Jubilee contained 37% more N than those of SS42. Nitrogen rate did not influence the N content of shanks at any ontogenetic stage.

Nitrogen concentration in shanks was negatively correlated with both DM ($r=-0.78$; $P<0.001$) and N content ($r=-0.26$; $P<0.05$). Nitrogen content, on the other hand, was positively correlated with DM content ($r=0.71$; $P<0.001$).

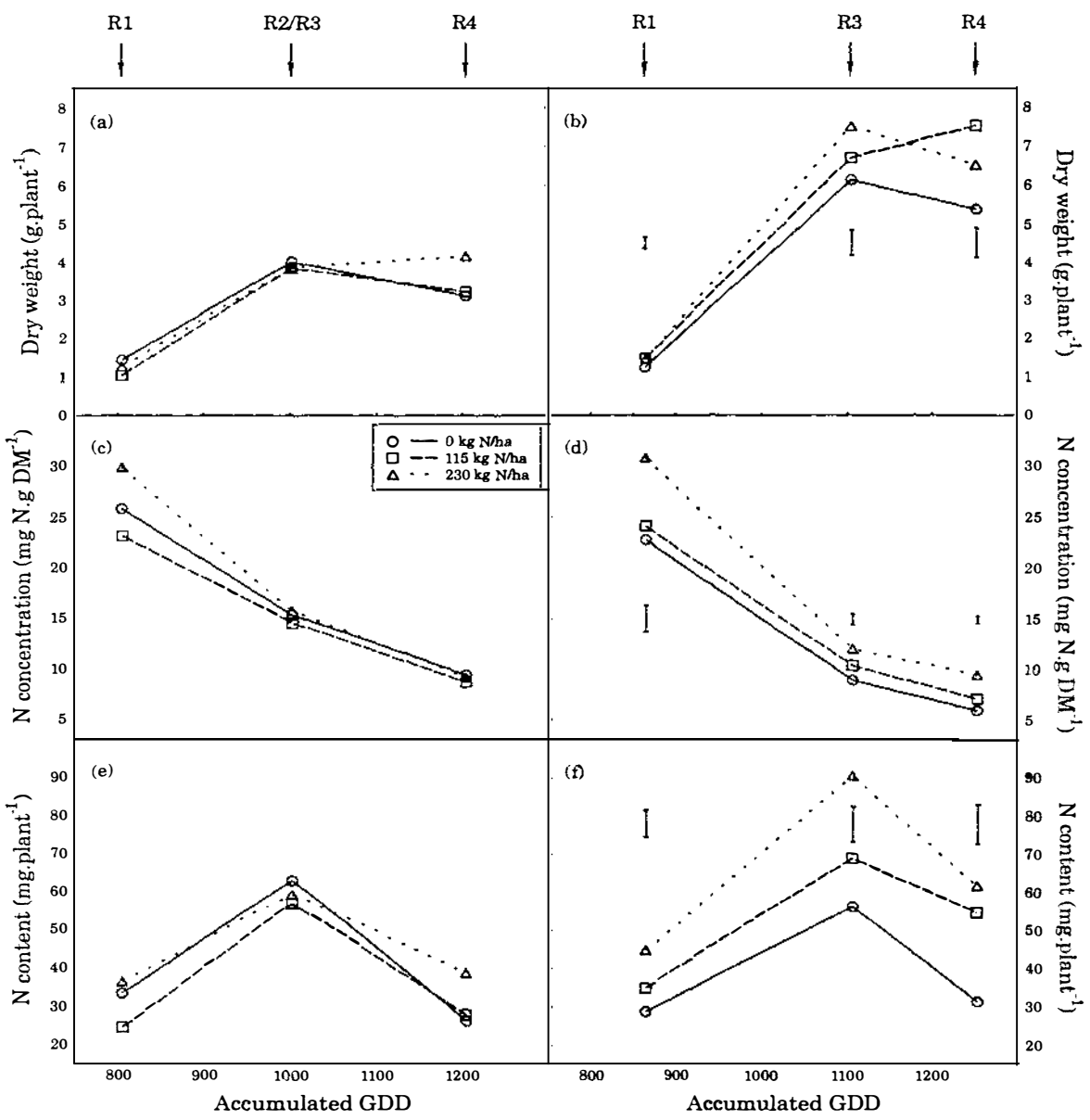

Fig. 3.5. Effect of N rate on DM accumulation in shanks of (a) SS42 and (b) Jubilee, N concentration in shanks of (c) SS42 and (d) Jubilee, and N accumulation in shanks of (e) SS42 and (f) Jubilee. Vertical bars represent the pooled standard error for each harvest (n=24).

3.3.7 Ontogenetic changes in DM, N concentration, and N content of rachis

The pattern of DM accumulation in rachis differed markedly between the cultivars. Jubilee accumulated 84% of total rachis DM between R1 and R3 compared to 11% by SS42 (Figs. 3.6a and 3.6b). Accumulation trends were reversed between R3 and R4 with SS42 accumulating 85% of total rachis DM with Jubilee only 14%. While DM contents were similar between the cultivars at R1 and R4, significant cultivar differences were observed at R3 with rachis of Jubilee containing 83% more DM than those of SS42. Nitrogen rate did not influence DM contents at any ontogenetic stage.

The pattern of N accumulation was similar to that of DM accumulation (cf. Figs. 3.6a, 3.6b, 3.6e, and 3.6f; r=0.91; $P<0.001$) and as with DM accumulation, both cultivars contained similar quantities of N at both R1 and R4. While N rate generally did not influence N contents, a significant cultivar × N rate interaction was observed at R3. Not only did rachis of Jubilee contain significantly more N than those of SS42 at this ontogenetic stage, but responded positively to N fertiliser, unlike SS42, which did not respond to N.

With the exception of the control N treatment of SS42, N concentrations in rachis declined with ontogeny (Figs. 3.6c and 3.6d). Depending on cultivar, concentrations declined 39-50% between R1 and R4. The increase in N concentration for the control N treatment of SS42 between R3 and R4 contributed to a significant cultivar × N rate interaction at R4. The N concentration for Jubilee was not influenced by N rate at this ontogenetic stage. At both R1 and R3, rachis of Jubilee contained a significantly higher concentration of N than those of SS42. Concentrations at these ontogenetic stages were 17 and 35% higher, respectively. Nitrogen concentration was negatively correlated with both DM (r=-0.52; $P<0.001$) and N content (r=-0.30; $P<0.001$).

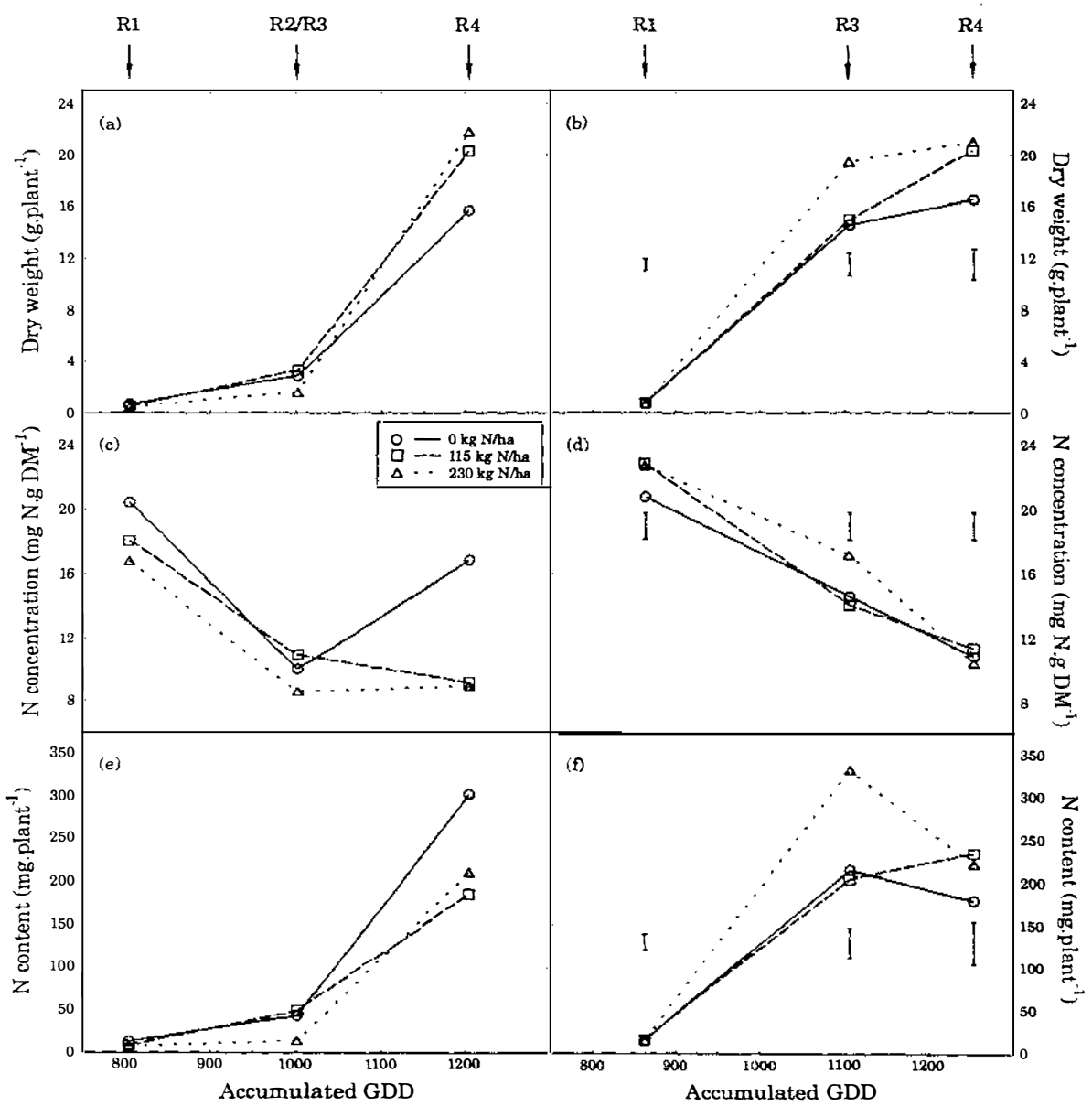

Fig. 3.6. Effect of N rate on DM accumulation in rachis of (a) SS42 and (b) Jubilee, N concentration in rachis of (c) SS42 and (d) Jubilee, and N accumulation in rachis of (e) SS42 and (f) Jubilee. Vertical bars represent the pooled standard error for each harvest (n=24).

3.3.8 Ontogenetic changes in DM, N concentration, and N content of kernels

Nitrogen and DM accumulated in kernels with a curvilinear pattern (Figs. 3.7a, 3.7b, 3.7e, 3.7f; r=0.99; $P<0.001$). While both cultivars contained similar quantities of N and DM at R1, kernels of Jubilee contained significantly more N and DM at both R3 and R4. At R3, kernels of Jubilee contained about 73% more N and DM than those of SS42. The magnitude of this difference declined between R3 and R4, with kernels of Jubilee containing 35 and 40% more DM and N, respectively. Neither the N content, nor the DM content of kernels at any ontogenetic stage were significantly influenced by N rate.

Nitrogen concentration of kernels increased to R3, then declined to levels similar to those originally at R1 (Figs. 3.7c and 3.7d). The 230 kg N/ha treatment for Jubilee was an exception to this trend as concentrations declined between R1 and R3 before increasing between R3 and R4. Despite this varying trend, N concentrations were similar among the N rates at all ontogenetic stages. Significant cultivar differences were recorded only at R1. At this ontogenetic stage, kernels of Jubilee contained N at a concentration 17% higher than those of SS42. The N concentration of kernels was neither correlated with their DM nor N content.

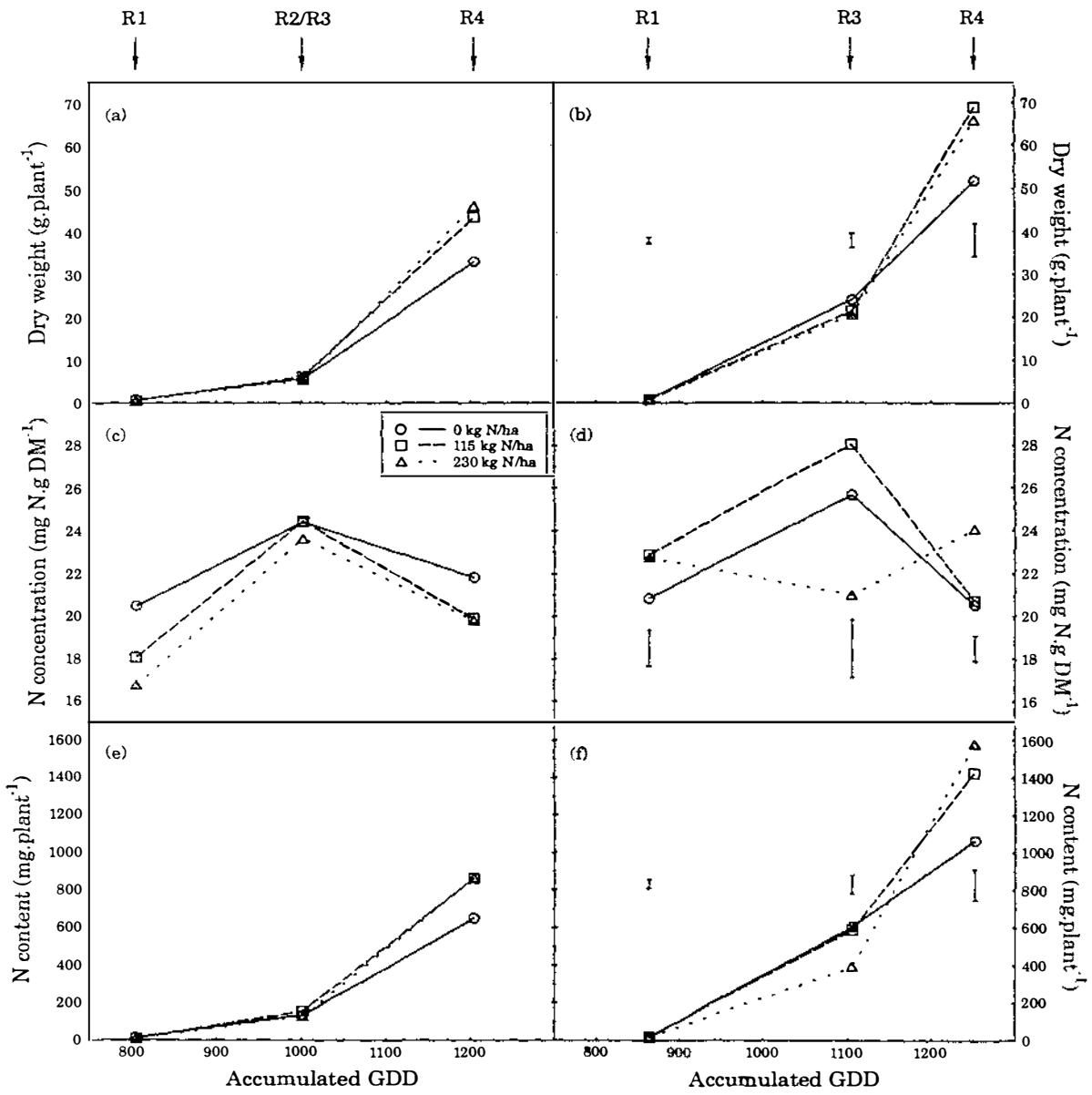

Fig. 3.7. Effect of N rate on DM accumulation in kernels of (a) SS42 and (b) Jubilee, N concentration in kernels of (c) SS42 and (d) Jubilee, and N accumulation in kernels of (e) SS42 and (f) Jubilee. Vertical bars represent the pooled standard error for each harvest (n=24).

3.3.9 Influence of post-anthesis N uptake and DM accumulation on kernel N and DM content

Post-anthesis N uptake was linearly associated with kernel DM content at R4 (Fig. 3.8). Kernel DM trebled as N uptake increased from 0 to 2 g·plant^{-1}. Principal component analysis indicated that the relationship between post-anthesis N uptake, post-anthesis DM accumulation, kernel DM at R4, and kernel N content at R4 could be described by one dimension (Fig. 3.8). This first principal component accounted for 98% of the total variability among the four variables. This result was consistent with the high correlations between kernel N and DM contents (Section 3.3.8) and also for post-anthesis DM and N accumulation (Section 3.3.2).

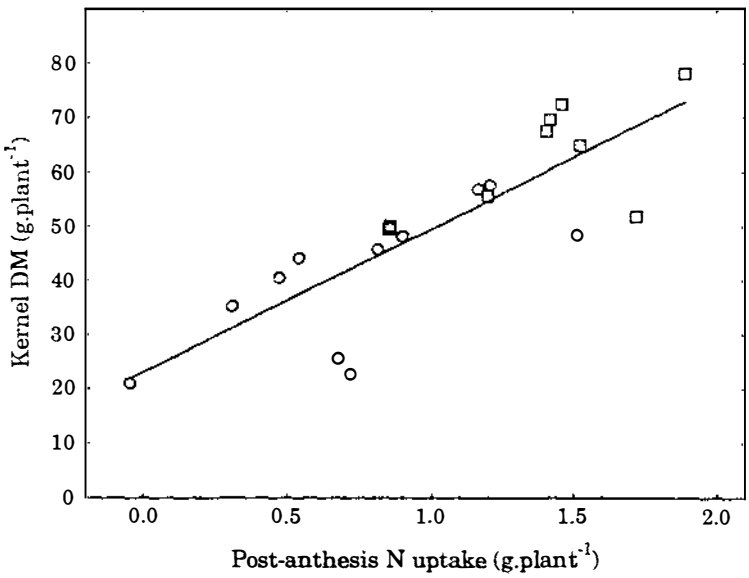

Fig. 3.8. Relationship between post-anthesis N uptake and kernel DM at R4; ○ = SS42, □ = Jubilee (r=0.83).

Kernel N concentration at R4 was neither associated with post-anthesis DM nor N accumulation.

3.3.10 Ontogenetic changes in DM, N concentration, and N content of husks

Husks accumulated DM to R3 before their contents either declined (SS42; Fig. 3.9a) or plateaued (Jubilee; Fig. 3.9b). Although husks of SS42 lost 28% of previously accumulated DM between R3 and R4, both cultivars had similar DM contents throughout ontogeny. Moreover, DM contents were not influenced by N rate. While N contents followed a similar trend, significant cultivar differences were observed at R3. At R1, both cultivars contained similar quantities of N (Figs. 3.9e and 3.9f). However, whereas N contents increased 300% between R1 and R3 for SS42, they increased only 28% for Jubilee. Such different rates of accumulation resulted in significant cultivar differences at R3. At R4, N contents had returned to levels similar to those previously at R1, such that, husks of SS42 and Jubilee contained similar quantities of N at this ontogenetic stage. Nitrogen contents were similar among the N rates at each ontogenetic stage.

The concentration of N in husks declined between R1 and R4 (Figs. 3.9c and 3.9d). While concentrations were similar between the cultivars at both R1 and R4, concentrations at R3 were not. At this ontogenetic stage, the N concentration in husks of SS42 was significantly higher (33%) than for Jubilee. Only at R4 were N concentrations significantly improved with the addition of N, increasing 23% as N rate increased from 0 to 230 kg/ha.

The N content of husks was highly correlated with their DM content ($r=0.79$; $P<0.001$) but not with their N concentration. Dry matter content, on the other hand, was negatively associated with N concentration ($r=-0.65$; $P<0.001$).

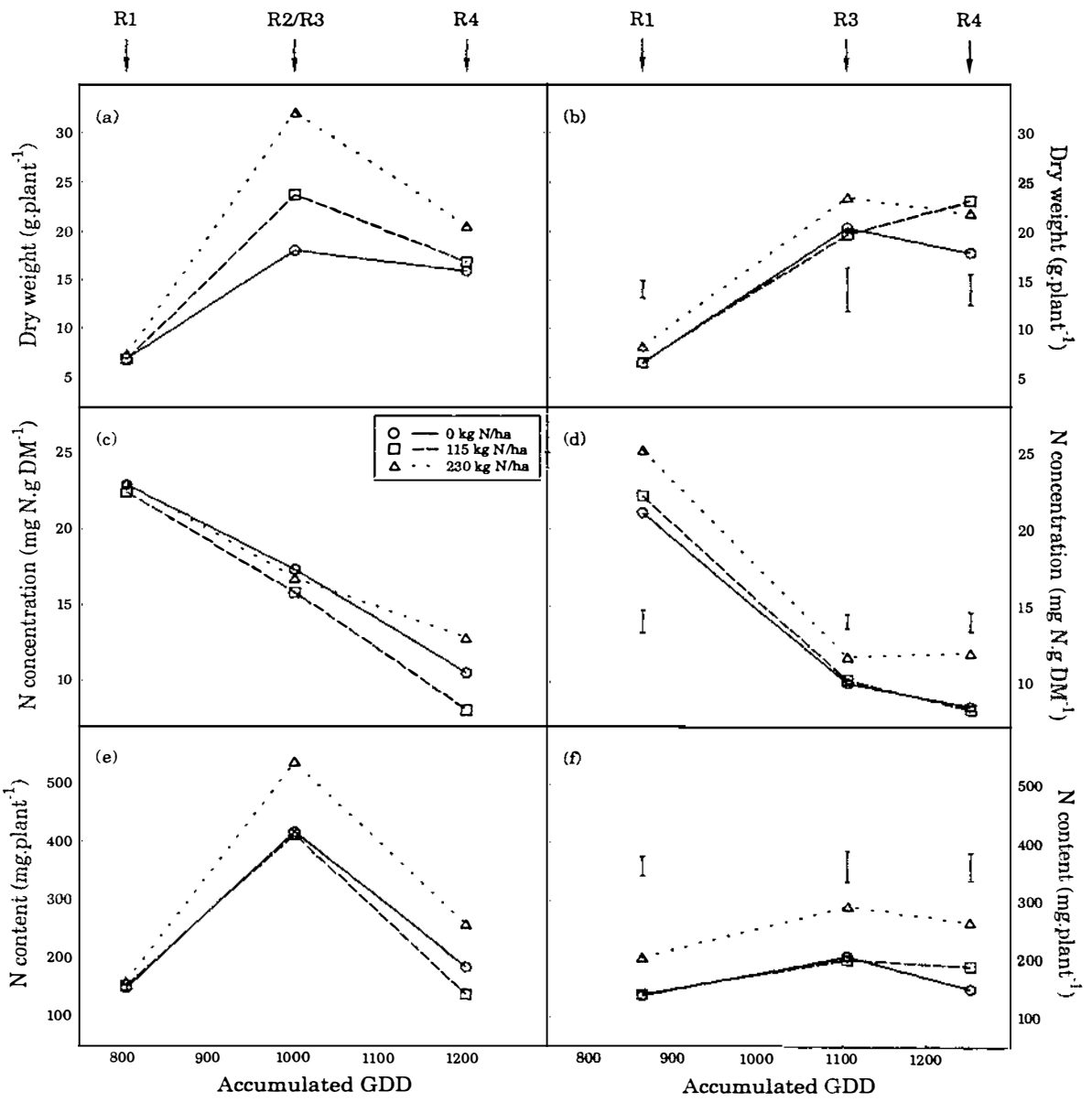

Fig. 3.9. Effect of N rate on DM accumulation in husks of (a) SS42 and (b) Jubilee, N concentration in husks of (c) SS42 and (d) Jubilee, and N accumulation in husks of (e) SS42 and (f) Jubilee. Vertical bars represent the pooled standard error for each harvest (n=24).

3.3.11 Nitrogen use efficiency and components

Jubilee was 34% more efficient than SS42 at converting applied N into kernel DM (Table 3.3) because it was significantly more efficient at taking up N (i.e., NUPE) and translating endogenous N into kernel DM (i.e., NUTE). Increasing N rate significantly decreased the NUSE for both cultivars. With 115 kg N/ha (1.66 g·plant^{-1}), plants were twice as efficient at translating fertiliser N into kernel DM than those grown with 230 kg N/ha (3.32 g·plant^{-1}). Such lower efficiency resulted from a significant reduction in the efficiency with which plants took up N. Compared to the 115 kg N/ha treatment, plants were only half as efficient at taking up N when grown with 230 kg N/ha. Nitrogen utilization efficiency was not influenced by N rate.

Table 3.3. Effect of N rate on N use efficiency and efficiency components for Jubilee and SS42.

Source of variation		NUSE[z]	NUPE[y]	NUTE[x]
			P > *F*	
Cultivar		**	*	*
N rate		***	***	NS
Cultivar × N rate		NS	NS	NS
ANOVA means	N rate (g·plant^{-1})	NUSE	NUPE	NUTE
SS42	1.66	26.3	1.36	19.0
	3.32	13.9	0.73	18.9
Jubilee	1.66	41.5	1.77	23.7
	3.32	19.8	0.99	19.9
5% LSD		6.7	0.27	2.7

NS, *, **, ***; Nonsignificant or significant *F* test at $P \leq 0.05, 0.01, 0.001$, respectively.
[z] Nitrogen use efficiency
[y] Nitrogen uptake efficiency
[x] Nitrogen utilization efficiency

Nitrogen utilization efficiency contributed more to the variation in NUSE than NUPE for both SS42 and Jubilee (Table 3.4). With 115 kg N/ha, NUTE explained at least 85% of the variability

in NUSE. This proportion increased as N rate increased, with NUTE explaining all of the variation in NUSE for plants grown with 230 kg N/ha.

Table 3.4. Contribution of efficiency components to variation in N use efficiency for Jubilee and SS42.

Cultivar	N rate ($g \cdot plant^{-1}$)	Efficiency trait		
		NUSE[z] (Y)	NUPE[y] (X_1)	NUTE[x] (X_2)
		----------	$\sum X_i Y / \sum Y^2$	----------
Jubilee	1.66	-	0.15	0.85
	3.32	-	0.00	1.00
SS42	1.66	-	0.09	0.91
	3.32	-	-0.02	1.02

[z] Nitrogen use efficiency
[y] Nitrogen uptake efficiency
[x] Nitrogen utilization efficiency

Partitioning coefficients (Section 3.2.4) were used to further investigate the partitioning of N and DM in plants of Jubilee and SS42. Only DM partitioning to stems between R1 and R3 and N partitioning to rachis between R3 and R4 were significantly influenced by N rate, therefore data for all other tissues was pooled across N rates.

3.3.12 Dry matter and N partitioning between V3 and V6

Leaves were the dominant sink for both N and DM between V3 and V6, being partitioned over 60% of the available N and DM (Fig. 3.10). In comparison, stems were partitioned about 25% of the available N and DM. Partitioning to stems and leaves was similar between the cultivars, but roots of Jubilee were partitioned a significantly greater proportion of available DM than those of SS42 (5% versus 11%). Roots of both cultivars were partitioned about 5% of the available N.

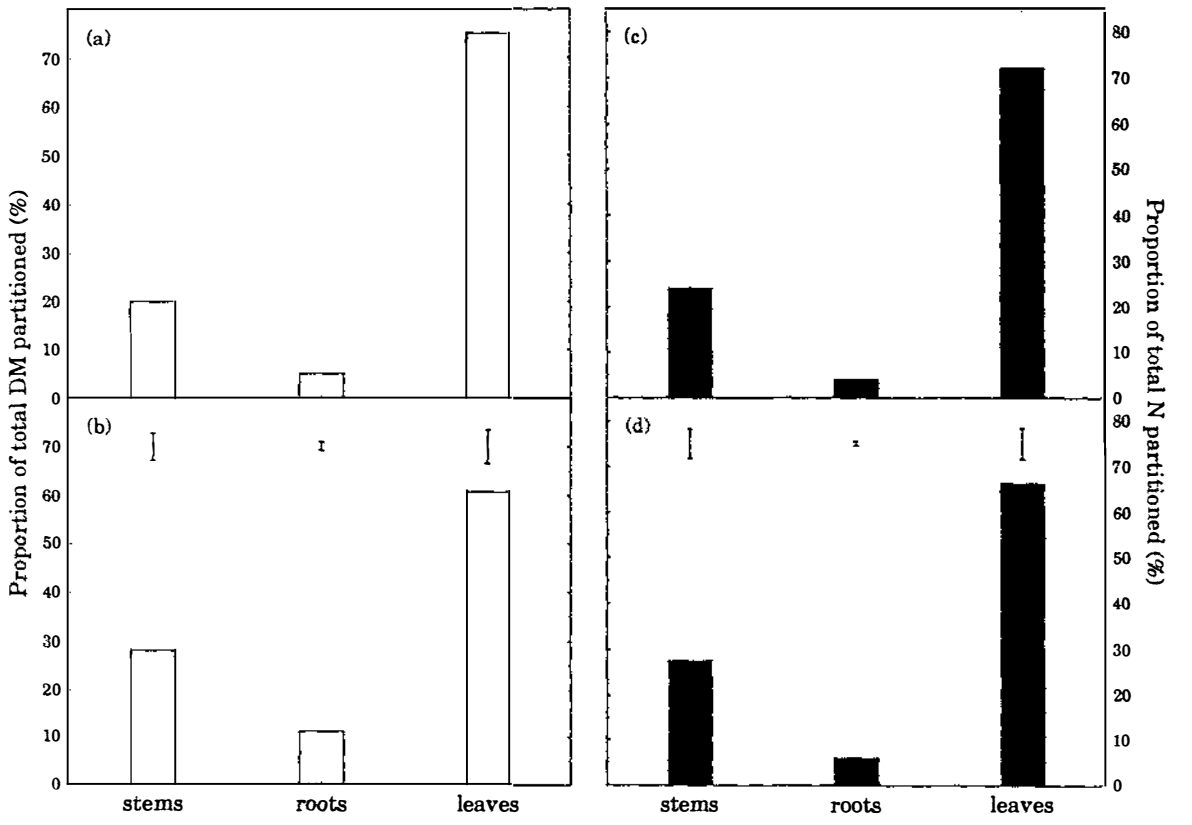

Fig. 3.10. Dry matter partitioning for (a) SS42 and (b) Jubilee and N partitioning for (c) SS42 and (d) Jubilee between V3 and V6. Vertical bars represent the pooled standard error for each organ (*n*=24).

3.3.13 Dry matter and N partitioning between V6 and V12

Stems were the dominant DM sink between V6 and V12, being partitioned about 71% of available DM (Figs. 3.11a and 3.11b). Leaves and roots were comparatively minor sinks being partitioned about 19% and 10% of available DM, respectively. Partitioning of DM to the various organs was similar between the cultivars.

SS42 partitioned 65% of available N to leaves between V6 and V12, twice the proportion partitioned by Jubilee (Figs. 3.11c and 3.11d). Conversely, Jubilee partitioned 61% of available N to stems, whereas SS42 partitioned 30%. Such different partitioning trends resulted in highly significant cultivar differences for the partitioning of N to both stems and leaves. Roots of Jubilee were partitioned a three-fold greater proportion of the available N than those of SS42.

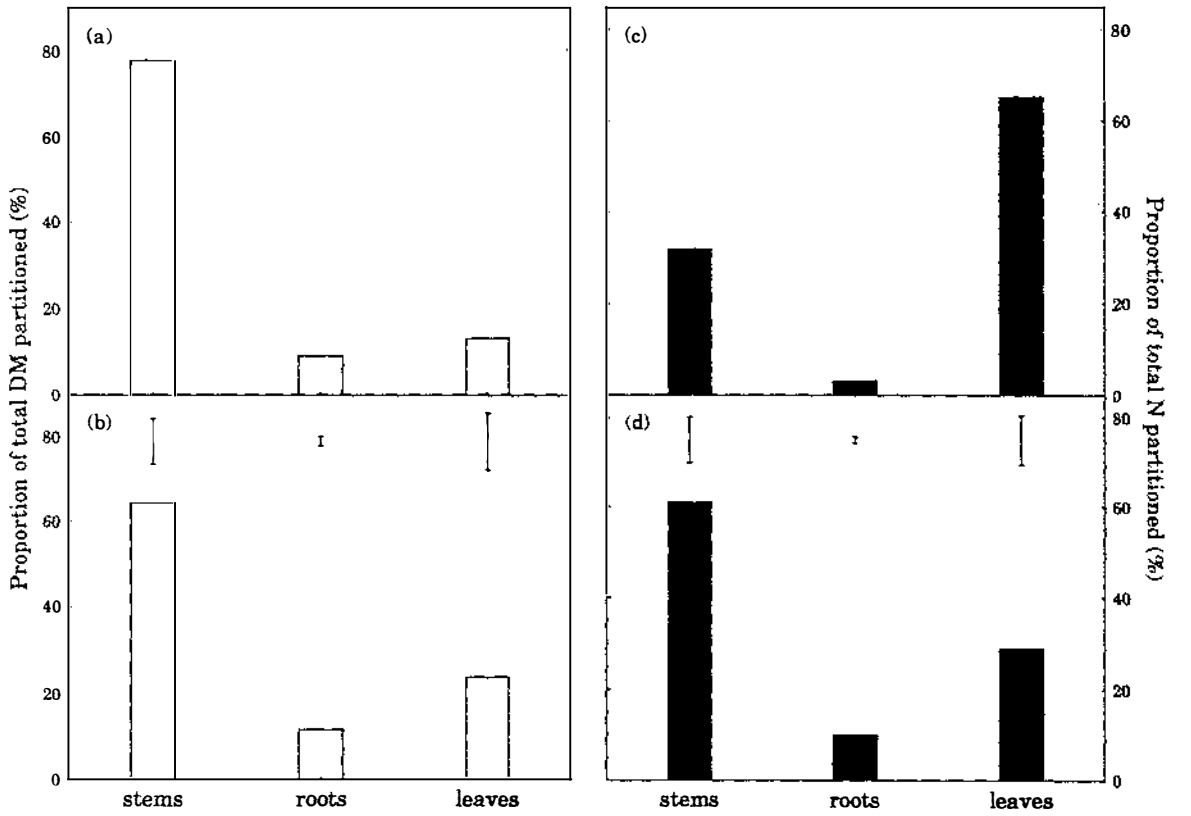

Fig. 3.11. Dry matter partitioning for (a) SS42 and (b) Jubilee and N partitioning for (c) SS42 and (d) Jubilee between V6 and V12. Vertical bars represent the pooled standard error for each organ (n=24).

3.3.14 Dry matter and N partitioning between V12 and R1

Partitioning of N and DM to ears was detected between V12 and R1. During this period about 35% of available DM was partitioned to ears with a further 39% partitioned to stems (Figs. 3.12a and 3.12b). Stems and ears were also dominant N sinks, being partitioned 40 and 35% of the available N, respectively (Figs. 3.12c and 3.12d). Roots and leaves were comparatively minor sinks, being partitioned about 7 and 20% of the available N and DM, respectively. Partitioning of both N and DM to the various organs was similar between SS42 and Jubilee.

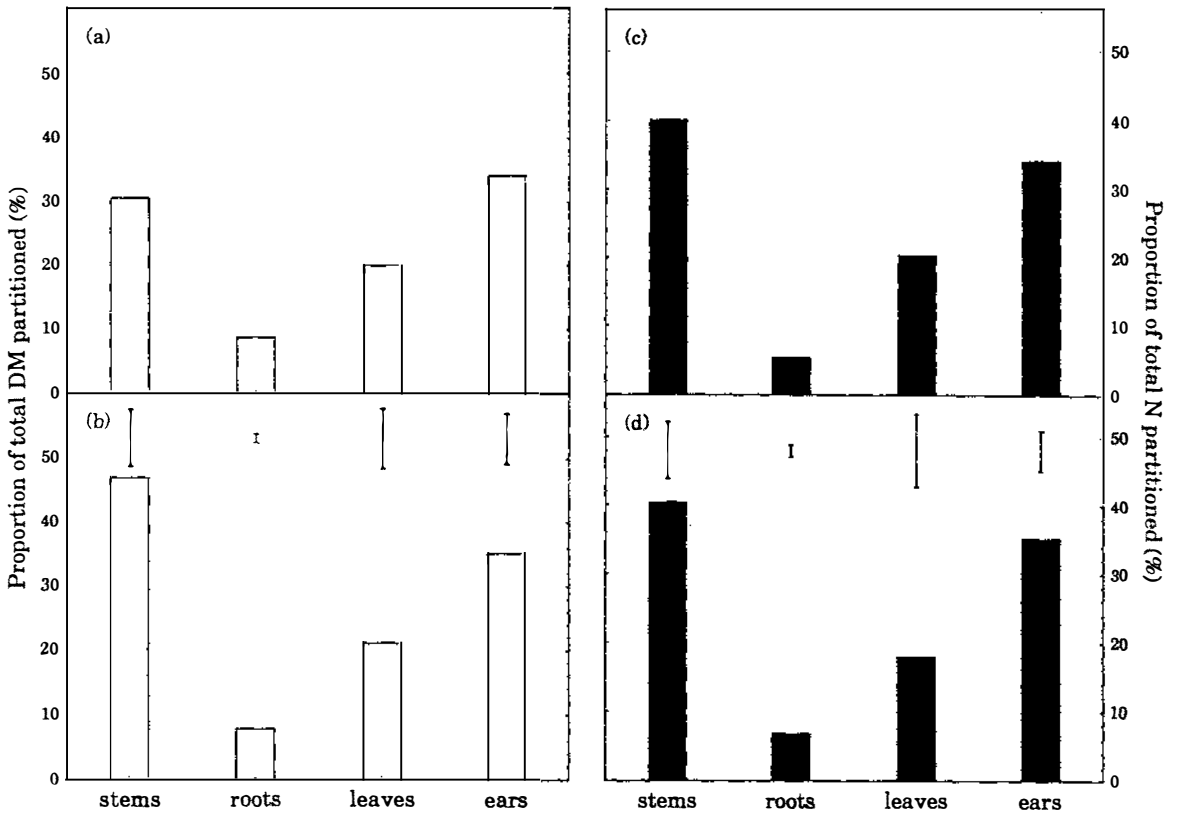

Fig. 3.12. Dry matter partitioning for (a) SS42 and (b) Jubilee and N partitioning for (c) SS42 and (d) Jubilee between V12 and R1. Vertical bars represent the pooled standard error for each organ (n=24).

3.3.15 Dry matter and N partitioning between R1 and R3

Jubilee partitioned DM to all organs between R1 and R3 (Fig. 3.13b). SS42 also partitioned DM to all organs except leaves (Fig. 3.13a). Although SS42 remobilised DM from leaves, cultivar differences for this organ were not significant. Partitioning to stems, on the other hand, was significantly different between the cultivars. SS42 partitioned 28% of available DM to stems, while Jubilee partitioned only 11%. Partitioning of DM to stems was also significantly influenced by N rate, increasing from 21 to 54% as N rate increased from 0 to 230 kg/ha. With the exception of the shank, significant cultivar differences were recorded for partitioning of DM to all ear fractions. SS42 partitioned 49% of available DM to husks, over twice the proportion partitioned by Jubilee. In contrast, Jubilee partitioned 34% of available DM to kernels, twice the proportion partitioned by SS42. Jubilee also partitioned a four-fold greater proportion of DM to rachis than SS42. Shanks of both cultivars were partitioned about 7% of the available DM and roots about 0.2%.

Jubilee partitioned most N to kernels between R1 and R3 (Fig. 3.13d) while SS42 partitioned most N to the husk (Fig. 3.13c). Jubilee also partitioned a significantly greater proportion of N to both rachis and leaves. For both cultivars, partitioning to these sinks was associated with remobilisation from the stem and roots. The proportion of N remobilised from the stem and roots was similar between the cultivars. Both cultivars partitioned about 6% of the available N to shanks within this period.

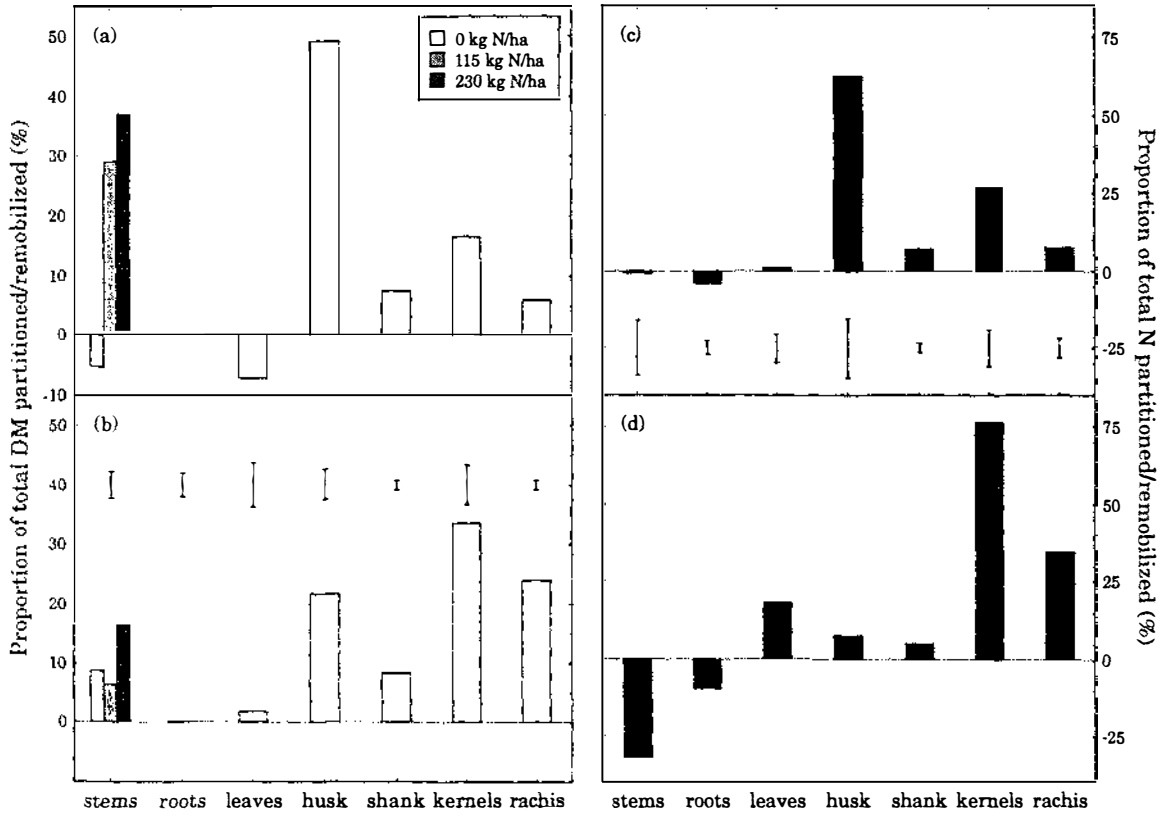

Fig. 3.13. Dry matter partitioning for (a) SS42 and (b) Jubilee and N partitioning for (c) SS42 and (d) Jubilee between R1 and R3. Vertical bars represent the pooled standard error for each organ (n=24).

3.3.16 Dry matter and N partitioning between R3 and R4

Kernels of both cultivars were partitioned about 78% of the available DM between R3 and R4 (Figs. 3.14a and 3.14b). In addition to partitioning DM to kernels, SS42 also partitioned large proportions of DM to rachis and husks, significantly more than Jubilee. Compared to Jubilee, SS42 partitioned a five-fold greater proportion of DM to rachis, and a 26-fold greater proportion

to husks. Jubilee, on the other hand, partitioned a significantly greater proportion of DM to roots than SS42. Whereas SS42 partitioned 0.1% of available DM to roots, Jubilee partitioned 3.7%. Dry matter partitioning coefficients for stems, leaves, kernels, and the shank were similar between the cultivars.

All organs except kernels and rachis of SS42 remobilised N between R3 and R4 (Figs. 3.14c and 3.14d). While largest proportions were remobilised from husks for SS42, largest proportions were remobilised from stems for Jubilee. Although the proportion of N remobilised from stems was similar between the cultivars, husks of SS42 remobilised a significantly greater proportion (over four-fold) of N than those of Jubilee. A significant cultivar × N rate interaction was recorded for the partitioning of N to rachis. This resulted from SS42 partitioning N to the rachis while N was remobilised from rachis of Jubilee. Further, partitioning was significantly influenced by N rate for SS42, but not for Jubilee. Aside from the rachis and husk, NPCs for all organs were similar between the cultivars and not influenced by N rate.

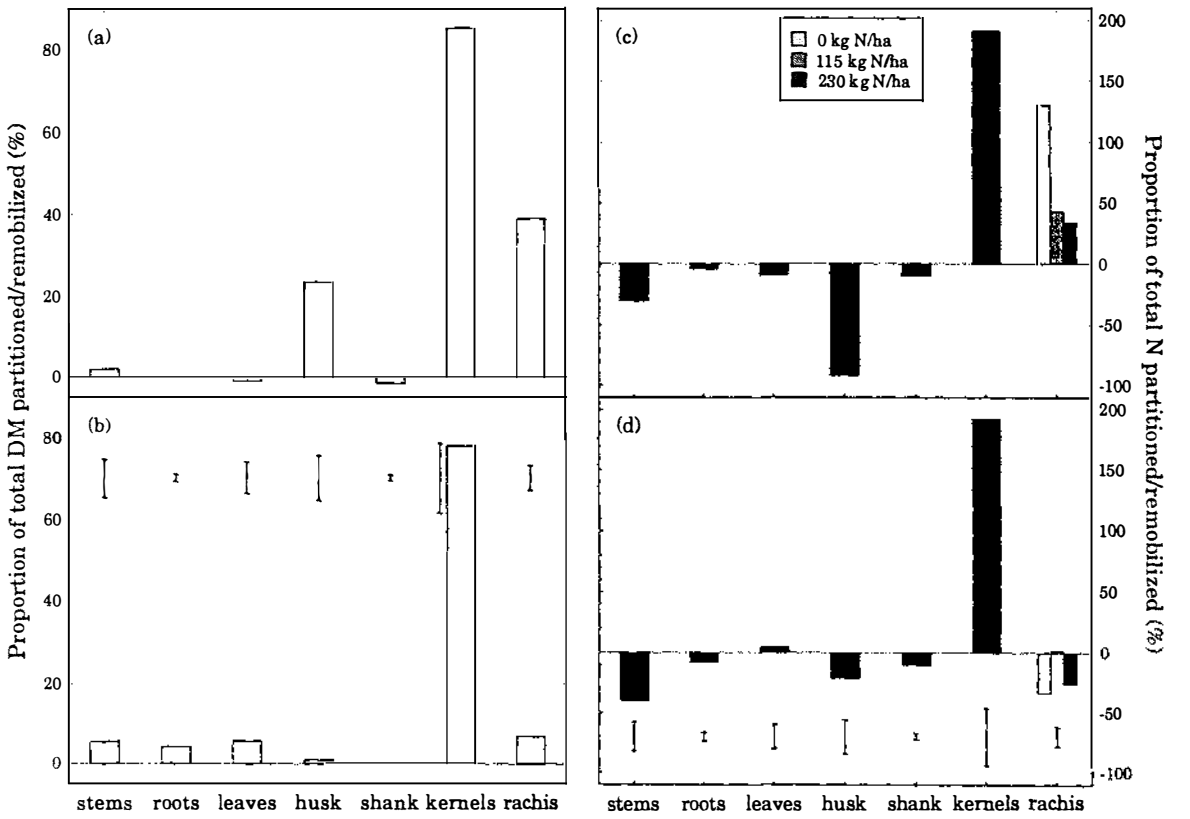

Fig. 3.14. Dry matter partitioning for (a) SS42 and (b) Jubilee and N partitioning for (c) SS42 and (d) Jubilee between R3 and R4. Vertical bars represent the pooled standard error for each organ (n=24).

3.3.17 Source of DM and N within ontogenetic periods

In the absence of remobilisation of DM up to R1, DM was apparently sourced entirely from current photoassimilate (cf. Figs. 3.10-3.12). However, remobilisation and current photoassimilate were both sources of DM after R1. Between R1 and R3, current photoassimilate accounted for 94% of the DM partitioned (Table 3.5), with remobilisation accounting for the

remainder. While the proportion derived from current photoassimilate was similar between both cultivars and N rates, significant N rate effects were detected for the quantity derived from current photoassimilate. Compared to the control, the quantity derived from current photoassimilate was 47% higher with 230 kg N/ha. Quantities remobilised were similar between both the cultivars and N rates.

Table 3.5. Influence of cultivar and N rate on the quantities of DM derived from current photoassimilate and remobilisation between R1 and R3.

N rate (kg/ha)	Quantity derived from remobilisation	Quantity derived from PS[z]	Proportion derived from PS
	g·plant^{-1}		(%)
0	5.3[y]	38.3	87.8
115	2.5	49.4	95.4
230	0.9	72.3	98.8
5% LSD	4.4	26.8	17.6
	Significance levels		
N rate	NS	*	NS
Cultivar	NS	NS	NS
Cultivar × N rate	NS	NS	NS

NS, *, **, ***; Nonsignificant or significant F test at $P \leq 0.05$, 0.01, 0.001, respectively.
[z] Quantity derived from current photoassimilate (PS).
[y] Data were pooled across cultivars.

Current photoassimilate was also the dominant source of DM between R3 and R4. Jubilee derived 95% of total DM from current photoassimilate during this period, while SS42 derived 78% (Table 3.6). Although increasing soil N fertility did not influence the proportion of DM derived from current photoassimilate, significant increases in the quantities remobilised were detected for SS42. Remobilisation for SS42 increased 52% as N rate increased from 0 to 230 kg N/ha. Averaged across N rates, Jubilee remobilised about 3 g·DM plant^{-1}. This was significantly less than the 14 g·plant^{-1} remobilised by SS42. Despite the greater remobilisation by SS42, both

cultivars derived similar quantities of DM from current photoassimilate. However, quantities for Jubilee were significantly influenced by N rate, being 41 % higher with 230 kg N/ha than the control.

Table 3.6. Influence of cultivar and N rate on the quantities of DM derived from current photoassimilate and remobilisation between R3 and R4.

Cultivar	N rate (kg/ha)	Quantity derived from remobilisation	Quantity derived from PS[z]	Proportion derived from PS
		g·plant^{-1}		(%)
Jubilee	0	1.2	39.9	97.1
	115	3.1	63.4	95.5
	230	5.5	67.5	92.4
SS42	0	10.2	48.0	82.5
	115	10.8	57.3	84.1
	230	21.4	46.2	68.3
5% LSD		5.8	13.3	10.7
		Significance levels		
N rate		*	*	NS
Cultivar		**	NS	**
Cultivar × N rate		NS	NS	NS

NS, *, **, ***; Nonsignificant or significant F test at $P \leq 0.05$, 0.01, 0.001, respectively.
[z] Quantity derived from current photoassimilate.

Up to R1, N was sourced entirely from newly assimilated N (cf. Figs. 3.10-3.12). Subsequent to R1, the proportion of N derived from newly assimilated N declined to about 76% of the N accumulated between R1 and R3 (Table 3.7). While cultivar differences were not detected for the proportion of N derived from newly assimilated N, significant differences were observed for quantities remobilised. In this regard, Jubilee remobilised 55% more N than SS42. Both cultivars, on the other hand, sourced similar quantities of N from newly assimilated N, although

significant increases were detected only for SS42, being 46% higher with 230 kg N/ha than the control.

Table 3.7. Influence of cultivar and N rate on the quantities of endogenous N derived from newly assimilated N and remobilisation between R1 and R3.

Cultivar	N rate (kg/ha)	Quantity derived from remobilisation	Quantity derived from uptake	Proportion derived from uptake
		mg·plant^{-1}		(%)
Jubilee	0	353	599	62.9
	115	338	662	66.2
	230	209	815	79.7
SS42	0	156	564	78.3
	115	21	555	77.1
	230	94	1048	91.7
5% LSD		177	231	19.5
		Significance levels		
N rate		NS	*	NS
Cultivar		*	NS	NS
Cultivar × N rate		NS	NS	NS

NS, *, **, ***; Nonsignificant or significant F test at $P \leq 0.05, 0.01, 0.001$, respectively.

After R3, 72% of the N in plants of Jubilee was sourced from newly assimilated N (Table 3.8). This proportion was significantly higher than the 42% recorded for SS42. While the proportion of N derived from newly assimilated N differed significantly between the cultivars, the actual quantities did not. Although the quantity of N derived from newly assimilated N was significantly influenced by N rate, the effect was only significant for Jubilee. In this instance, increasing N rate from 0 to 230 kg/ha increased the quantity derived from newly assimilated N by 58%. A significant cultivar × N rate interaction was recorded for the quantity of N derived

from remobilisation. Whereas the quantity remobilised for Jubilee increased significantly with increasing N rate, the quantity remobilised for SS42 decreased with increasing N rate.

Table 3.8. Influence of cultivar and N rate on the quantities of endogenous N derived from newly assimilated N and remobilisation between R3 and R4.

Cultivar	N rate (kg/ha)	Quantity derived from remobilisation	Quantity derived from uptake	Proportion derived from uptake
		mg·plant^{-1}		(%)
Jubilee	0	185	369	66.6
	115	183	750	80.4
	230	404	921	69.6
SS42	0	682	285	29.5
	115	469	305	39.4
	230	428	597	58.2
5% LSD		99	361	14.4
		Significance levels		
N rate		NS	*	NS
Cultivar		***	NS	***
Cultivar × N rate		**	NS	NS

NS, *, **, ***; Nonsignificant or significant F test at $P \leq 0.05$, 0.01, 0.001, respectively.

3.3.18 Results from additional data analysis using data from Stone et al. (1998)

There was a 10% difference in the amount of solar radiation potentially available for the two cultivars used in the current study (2065 MJ·m^{-2} for Jubilee and 1850 MJ·m^{-2} for SS42), an influence which was not quantified in this study. However, the magnitude of this difference can be estimated using data from Stone et al. (1998) in conjunction with data from the current study. Using regression analysis with dummy variables (Section 2.2.6) data were adjusted using the variable leaf area. That is, maximum leaf area (which occurred at R1) was determined from Stone et al. (1998) and then again with 10% less solar radiation. The proportionate difference

in leaf area was then used as a basis to adjust data in the current study in conjunction with regression analysis using dummy variables. In the case of Stone et al. (1998), 10% less incident radiation corresponded to leaf area decreasing from 3.9 m^{-2} per plant to 3.3 m^{-2} per plant (i.e., a 16% reduction). Analysis was confined to DMPCs and NPCs from R1 onwards as these were the most important variables.

Following data adjustment and re-analysis only the significance of one result was changed; N partitioning to leaves between R1 and R2/R3. In this instance, both cultivars partitioned about 10% of available N to leaves. In the original data set Jubilee partitioned 18% of available N to leaves with SS42 partitioning 3%. While partitioning of N and DM to other organs was also reduced (at most 4%) the significance of cultivar differences was not altered.

3.4 Discussion

This study shows that kernel sink strength of Jubilee during early grain filling is significantly greater than for SS42. Compared to SS42, kernel sink strength of Jubilee was two-fold greater for DM and three-fold greater for N (Fig. 3.13). As a consequence, kernels of Jubilee contained 34% more DM than those of SS42 at R4 (Figs. 3.7a and 3.7b). The greater sink strength is unlikely due to plants of Jubilee being significantly larger than those of SS42 (18% based on DM; Figs. 3.1a and 3.1b) as partitioning coefficients, being standardised by the amount of DM or N accumulated, eliminate such confounding influences. Anderson et al. (1984a) also discounted plant size as a variable influencing N and DM partitioning to kernels. Thus, factors other than plant size must be responsible for the greater kernel sink strength of Jubilee.

Differences in the amount of radiation available to each hybrid (about 10% more for Jubilee) may have contributed to the greater kernel sink strength of Jubilee. From this experiment there is no way to quantify the extent to which these differences influenced results. However, using a data set from Stone et al. (1988) (Section 3.3.18) and re-analysing data from the current study using this data set, the influence of the 10% difference in radiation interception can be speculated. Analysis revealed that both cultivars partitioned similar proportions of N to leaves between R1

and R2/R3. Aside from this result, the significance of cultivar differences remained unchanged. Limited change may be due to several factors. It is possible that analysis was not sensitive enough to adequately determine cultivar differences. The only variable measured with ontogeny in Stone et al.'s (1998) study data was leaf area. Therefore, only leaf DM in the current study could be adjusted. By only adjusting this variable the effect of source strength (i.e., lower leaf DM caused by less incident radiation being intercepted) on other plant fractions was not truly accounted for. It is recognised that the quantity of DM partitioned to plant fractions is influenced by incident radiation (e.g., leaves, stems, and ears; Cirilo and Andrade, 1994a). However, it is not well understood how partitioning is altered for ear fractions with ontogeny under varying degrees of incident radiation. Given that data adjustment generally did not alter the significance of cultivar differences in the current study, yet it is possible that the confounding influence of incident radiation levels between the cultivars may remain, only comparisons between the cultivars where the difference is highly significant are discussed.

It is possible that kernel sink strength of Jubilee was higher than for SS42 between R1 and R3 due to plants of Jubilee being harvested at a more advanced ontogenetic stage; plants of SS42 were harvested at R2/R3, while those of Jubilee were harvested at R3 (Table 3.1). Harvesting at an advanced ontogenetic stage would have allowed kernels of Jubilee to accumulate more DM (Hanft et al., 1986; Johnson and Tanner, 1972). However, in comparing the GDD accumulated from R1 to these ontogenetic stages, the difference between the cultivars is only 43 GDD (i.e., at most, four days; Fig. 2.1a). Hence, the influence of ontogenetic stage on partitioning coefficients in this instance is likely negligible.

Tsai et al. (1978a) suggested that kernel sink strength was influenced by the level of zein in the kernel. Observing that zein level was correlated (r=0.98) with endosperm DM, Tsai et al. (1980) concluded that zein was associated with kernel DM accumulation, and hence, kernel sink strength. Genetic mutations influence levels of zein and the accumulation of kernel DM (Boyer and Shannon, 1984). As discussed above, Jubilee, carrying the *su1* mutation, contained 34% more DM in kernels at R4 than SS42, a *sh2* mutant (cf. Figs. 3.7a and 3.7b). Similar differences between these endosperm mutants were reported by Dalby and Tsai (1975) and Tsai et al. (1978a) who found that *su1* mutants contained at least 47% more zein than *sh2* mutants.

Therefore, the greater accumulation of DM in kernels of Jubilee may result from increased sink strength through greater zein accumulation.

Although kernels of Jubilee are speculated to have accumulated more zein than those of SS42 at both R3 and R4, partitioning coefficients for the period R3 to R4 indicate that kernels of both cultivars had a similar sink strength (Fig. 3.14). However, kernel sink strength for Jubilee was significantly higher than for SS42 between R1 and R3 (Fig. 3.13). Such differences in kernel sink strength between the cultivars may be explained by differences in the rate of zein synthesis, as suggested by Tsai et al. (1984). One possible explanation is that zein synthesis in kernels of Jubilee was initially more rapid than for SS42. Zein would have accumulated until physiological mechanisms slowed transcription (Singletary and Below, 1989; Tollenaar and Daynard, 1978b) which would therefore have allowed SS42 to accumulate similar proportions. This may explain the similar sink strength of both cultivars between R3 and R4 (assuming sink strength is dependent on the level of zein in the kernel and not just an association). Misra et al. (1975b) attributed reduced sink strength in an *o2* mutant to delays in the onset of zein synthesis, along with reduced total zein production.

If greater kernel sink strength of Jubilee gives rise to a greater quantity of kernel DM, it is interesting to consider why yields of Jubilee and SS42 in Chapter 2 were generally similar (e.g., cf. Figs. 2.9a and 2.16a). This similarity suggests that the results obtained in the current study were not apparent in the first experiment. The most probable reason why these differences were not manifested may result from the different procedures used. Whereas kernels were completely removed from rachis in the current study, only kernels from harvestable ears were removed in the previous study. Moreover, kernels in the previous study were not completely removed as they were cut from the rachis (Fig. 2.3). Yields of SS42 and Jubilee in Chapter 2 were not directly comparable due to the ears being harvested at different SMCs (Section 2.2.5).

The general lack of hybrid response to N fertiliser in the current study was consistent with results presented earlier (Section 2.3). As discussed (Section 2.4), the presence of 259 kg N/ha of soil available N (Table 2.1) largely negated any influence of N fertiliser. Nevertheless, a few significant effects of N rate were detected. Among these was a significant influence on total N

and DM accumulation at R4 whereby DM and N contents were 21% higher with 230 kg N/ha than the control (Figs. 3.1a and 3.1b). With either nil, or a limited response to N rate at earlier ontogenetic stages, this result is consistent with soil N reserves becoming more depleted with ontogeny. Thus, even though 259 kg N/ha was available to plants from the soil, the significant response to N rate suggests that additional N was required during late ontogeny (Allison, 1984; Tsai et al., 1991).

The requirement for additional N during late season growth is consistent with increased zein accumulation in kernels. Zein is the only protein fraction in the endosperm which dramatically responds to N supply (Tsai et al., 1980, 1983). Under N restriction, the endosperm of normal maize genotypes produce only small amounts of zein, with non-zein protein unaffected (Tsai et al., 1980, 1983). However, when plants are grown with high levels of N, zein is synthesised preferentially (Frey, 1951; Keeney, 1970; Rendig and Broadbent, 1979; Sauberlich et al., 1953; Schneider et al., 1952; Tsai et al., 1978a, 1980). Significant increases in total N and DM contents at R4 are therefore consistent with kernels requiring N for zein production, and hence, depleting soil N reserves. Significant increases in kernel N and DM content with N fertiliser at R4 support this hypothesis (Fig. 3.7) as does the linear association between kernel DM content at R4 and post-anthesis N uptake (Fig. 3.8).

With an apparently greater kernel sink strength, Jubilee was significantly more efficient than SS42 at translating endogenous N into kernel DM (i.e., NUTE; Table 3.3). Jubilee was also significantly more efficient at taking up fertiliser N (i.e., NUPE; Table 3.3). The greater efficiency of Jubilee may be explained by its significantly larger root biomass. Compared to SS42, roots of Jubilee contained 20% more DM than those of SS42 (cf. Figs. 3.4a and 3.4b). With Eghball and Maranville's (1993) study demonstrating that N uptake is partially determined by the size of the root system, the larger root system of Jubilee (as determined by DM) would have contributed to a greater NUPE. This is also consistent with Jackson et al.'s (1986) suggestion that NUSE depends on the extent and size of the root system. The greater efficiency of Jubilee at transferring endogenous N to kernels was consistent with kernels having a greater sink strength during early grain filling, as discussed earlier. Together, the larger root system and

the greater kernel sink strength resulted in Jubilee being 34% more efficient than SS42 at using N fertiliser.

A distinction must be made here to clarify the ambiguous use of the word 'efficiency'. The observation that Jubilee is more efficient than SS42 at using N fertiliser contrasts my earlier suggestion (Section 3.1) that SS42 is more efficient at using N fertiliser than Jubilee. In Chapter 2 it was observed that yield and yield components of Jubilee responded positively to N fertiliser, whereas those of SS42 did not (cf. Sections 2.3.1 and 2.3.2). Therefore, in one sense SS42 is more efficient than Jubilee at using N fertiliser because maximum yield may be attained at a lower rate of N. However, SS42 is less efficient than Jubilee at both taking up N and translating fertiliser N into kernel DM (Table 3.3). Although both cultivars were similarly efficient at these tasks with 230 kg N/ha, Jubilee was significantly more efficient at both tasks with 115 kg N/ha (Table 3.3). Thus, under low N fertility conditions, kernel DM and hence, yield of Jubilee will increase more rapidly in response to N fertiliser than SS42, in accord with the hypothesis of Kamprath et al. (1982).

As N rate increased, NUSE for both cultivars declined significantly (Table 3.3). This trend, consistent with studies on sweet corn and maize (Eichelberger et al., 1989; Kamprath et al., 1982; Moll et al., 1982a; Rhoads and Stanley, 1984; Sabata and Mason, 1992; Salardini et al., 1992; Tsai et al., 1992) results from the quantity of kernel DM produced per unit of fertiliser N decreasing as N rate increases. Consequently, the NUSE × N rate function would be expected to be a declining exponential. Although the decreasing trend was consistent with these studies, values of NUSE in the current study were notably lower (cf. Table 3.3 with Eichelberger et al., 1989; Kamprath et al., 1982; Moll et al., 1982a; Sabata and Mason, 1992; Salardini et al., 1992; Tsai et al., 1992). The lower values may result from sweet corn being harvested substantially earlier than maize (R4 compared with R6). At R4, kernels have not reached their maximum DM content (Hanft et al., 1986; Johnson and Tanner, 1972; Maddonni et al., 1998). Reduced DM accumulation in kernels of endosperm mutants compared to wild types (Dalby and Tsai, 1975; Doehlert and Kuo, 1994; Misra et al., 1972, 1975a; Tsai et al., 1983) may also have resulted in lower NUSE values. Further, differences in the densities used (44,000 plants per hectare being the highest density in these reported studies) may also have contributed to the lower NUSE

values observed as grain yield per plant decreases with increased density (Anderson et al., 1984a, 1984b, 1985; Edmeades et al., 1979; Poneleit and Egli, 1979; Reed and Hageman, 1980; Schrader, 1978; Tetio-Kagho and Gardner, 1988b). Despite NUSE values being lower, proportionate decreases over similar ranges of N were comparable. For example, decreases calculated from Salardini et al.'s (1992) study with Jubilee (48%) were consistent with decreases recorded for Jubilee (51%) and SS42 (47%), as were decreases calculated from Eichelberger et al.'s (1989) study with maize.

The relative contribution of the two components, NUPE and NUTE, to variation in NUSE differed notably among the N rates. With 115 kg N/ha, NUTE contributed to 85% of the variability in NUSE and practically all the variability with 230 kg N/ha (Table 3.4). This trend contrasts Moll et al.'s (1982a) study on maize where NUTE contributed 95% to variation in NUSE with 56 kg N/ha, but only 17% with 224 kg N/ha. It similarly contradicts Moll et al.'s (1987) study. On the other hand, this trend is consistent with studies on both sweet corn (Salardini et al., 1992) and maize (Kamprath et al., 1982; Lafitte and Edmeades, 1994a). It is unclear why such discrepancy occurs between these studies.

Nitrogen uptake efficiency contributed 15% to variation in NUSE (Table 3.4), even with a potential 373 kg N/ha[2] available to plants from the soil. This finding suggests that both Jubilee and SS42 are inefficient at N uptake. If these cultivars were efficient at N uptake then NUPE would have contributed nil to variation in NUSE at such a high level of N fertility as root uptake mechanisms would be saturated with N (Edwards and Barber, 1976).

To suggest that Jubilee is inefficient at N uptake contrasts my earlier statement in Section 3.1 regarding Salardini et al.'s (1992) study. Although they appear to have correctly concluded that Jubilee is inefficient at N uptake, the process by which they reached this conclusion is dubious. The assumption that Salardini et al. (1992) had to make when comparing their data with that of Kamprath et al. (1982) was that levels of soil available N (i.e., residual and mineralizable N) were similar. As neither study quantified mineralizable N levels, this assumption is questionable.

[2] Sum of mineralizable-, residual- (Table 2.1), and fertilizer-N

Moreover, with the proportions of variability in NUSE explained by NUTE for Jubilee being similar between both the current and Salardini et al.'s (1992) study suggests that mineralizable N levels in Salardini et al.'s (1992) study were high. Only if levels of soil available N in Kamprath et al.'s (1982) study were low would the conclusion that Jubilee was inefficient at N uptake be valid from comparing the two data sets.

Under the high N fertility conditions of the current study, NUSE was probably limited more by the translation of endogenous N into kernel DM than by the uptake of N. This conclusion is made because NUTE contributed most (> 85%) to variability in NUSE (Table 3.4). Realising that the transfer of N to kernels within the plant appears to limit kernel DM accumulation, discussion now focuses on source-sink relationships through ontogeny.

Leaves were the dominant sink between V3 and V6, being partitioned over 60% of the available N and DM (Figs. 3.10a and 3.10b). This result is consistent with Simmons and Jones's (1985) and Thom and Watkin's (1978) studies. The sink dominance of the leaves suggests that establishing a photosynthetic source is a physiological priority. With photosynthesis vital for seedling survival and growth (Kasperbauer and Karlen, 1994), over 50% of N in leaves is directly associated with chloroplasts (Hageman, 1986; Stocking and Ongun, 1962). Thus, expanding leaves are strong sinks for both N and DM (Fig. 3.11; Cliquet et al., 1990b; Weiland and Ta, 1992). Roots, on the other hand, were comparatively minor sinks during this period, being partitioned less than 15% of available N and DM, and continued to be a minor sink (Figs. 3.11-3.14). While this result supports many studies (e.g., Anderson, 1987; Baligar, 1986; Cliquet et al., 1990b; Mengel and Barber, 1974), it contrasts work by McCullough et al. (1994a). With roots being partitioned 28-44% of newly reduced N between V4 and V12, McCullough et al. (1994a) concluded roots were a large sink. However, as they grew plants in a solution culture, partitioning may have been influenced by the growing method, therefore making results difficult to compare.

Leaves continued to be a dominant sink for N between V6 and V12 (Figs. 3.11c and 3.11d), presumably reflecting their continued expansion and development (Crawford et al., 1982; Rendig and Crawford, 1985; Ta and Weiland, 1992). However, their sink strength for N between V12

and R1 was considerably lower (at least 38%) than between V6 and V12 (cf. Figs. 3.11 and 3.12). The decline in sink strength may be characteristic of the ontogenetic stage as maximum leaf area had probably been reached (Allison, 1969; Hanway, 1962a; Muchow, 1988; Uhart and Andrade, 1995b). Attaining maximum leaf area would therefore be consistent with DM partitioning to leaves essentially ceasing from R1 onwards (cf. Figs. 3.12-3.14).

Stems were the dominant DM sink between V6 and V12 (Figs. 3.11a and 3.11b). As stem elongation begins at V6 and continues until V18 (Hanway, 1963; Ritchie and Hanway, 1984) the large DMPCs for stems relative to leaves and roots during this period reflects the high sink demand for photoassimilate by the growing stem. In addition to stems using photoassimilate for growth, stems may also begin to store photoassimilate for remobilisation during grain filling (Daynard et al., 1969; Hume and Campbell., 1972). Stems continued to elongate between V12 and R1, although their sink strength was only about half that between V6 and V12 (cf. Figs. 3.11 and 3.12). While this may be a consequence of stem elongation beginning to slow (Ritchie and Hanway, 1984), it may also be due to increased competition from developing ears (Alofe and Schrader, 1975). The appearance of ears between V12 and R1 coincided with DM partitioning to stems declining from 71% to 38%. With ears being partitioned about 34% of available DM between V12 and R1, they were strong sinks for DM. Nevertheless, stems appeared to remain strong sinks for DM between V12 and R1 (Fig. 3.12), consistent with other studies Alofe and Schrader, 1975; Cliquet et al., 1990a; Daynard et al., 1969; Hume and Campbell, 1972; Simmons and Jones, 1985; Treat and Tracy, 1994). Allison et al. (1975b) considered that such competition for DM by the stem did not affect ear size. However, an excessively strong stem sink may restrict ear growth and be detrimental to grain filling (Setter and Meller, 1984; Tietz et al., 1981).

Stems were also a strong sink for N between V6 and R1 (Figs. 3.11 and 3.12). Such activity is consistent with the stem storing N for remobilisation during grain filling (Below et al., 1981; Setter and Meller, 1984; Ta and Weiland, 1992). Other studies have also reported stems to be a dominant sink for N during this period (e.g., Beauchamp et al., 1976; Cliquet et al., 1990a; Swank et al., 1982; Weiland, 1989b). However, NPCs in the current study, particularly during early ontogeny, may be inflated. The inflated NPCs may have occurred from stem fractions including leaf sheath of fully expanded leaves, and laminae of emerging leaves. Emerging leaves

are generally allocated more N to increase their net assimilation rate (McCullough et al., 1994b) and establish a photosynthetic source more quickly (Greef, 1994). Stem sink strength for both N and DM may further have been over-represented between V12 and R1 as stem fractions included the tassel. Reports of cessation of leaf initiation and axillary bud formation as tassel formation begins (Bonnett, 1966) and increased grain yield when the tassel was removed at, or prior to R1 (Chinwuba et al., 1961; Grogan, 1956; Hunter et al., 1969; Mostut and Marais, 1982) indicate that the tassel is a strong sink (Aluko and Fischer, 1987; Hume and Campbell, 1972).

Growth of ears and a consequent increase in sink strength was associated with marked decreases in the partitioning of DM to the vegetative organs (cf. Figs. 3.12 and 3.13). Partitioning of DM to vegetative organs further declined as ear sink strength increased between R3 and R4 (cf. Figs. 3.13 and 3.14). Nevertheless, stems were continuously partitioned DM between R1 and R4, a trend consistent with studies on maize (Crawford et al., 1982; Daynard et al., 1969; Friedrich and Schrader, 1979; Wolfe et al., 1988a). As changes in stem DM during reproductive growth are primarily due to changes in nonstructural carbohydrate content (Below et al., 1981; Christensen et al., 1981; Setter and Meller, 1984), increases in stem DM largely reflect photoassimilate not consumed in reproductive growth (Barnett and Pearce, 1983; Campbell, 1964; Hume and Campbell, 1972). This suggests that the photoassimilate supply between R1 and R4 was in excess of ear needs. Numerous studies with maize have suggested similarly (Allison et al., 1975a; Below et al., 1981, 1984; Cliquet et al., 1990b; Hanway, 1962a, 1962b; Hay et al., 1953; Prioul et al., 1990; Reed et al., 1988; Swank et al., 1982; Tollenaar, 1977).

In contrast to DM, N was remobilised from vegetative organs between R1 and R4 (Figs. 3.13 and 3.14). Even if all the newly assimilated N was translocated to ears, remobilisation would still have been required to satisfy their sink demand. Nitrogen was remobilised largely from stem and husks. Similar findings with maize (Below et al., 1981; Daynard et al., 1969; Fairey and Daynard, 1978b; Hay et al., 1953; Moutot et al., 1986; Palmer et al., 1973; Rendig and Crawford, 1985; Swank et al., 1982) suggest that aside from structural and protective roles, these organs have an important role in storing N for remobilisation during grain filling (Cliquet et al., 1990b; Friedrich and Schrader, 1979; Ta and Weiland, 1992). Further, remobilising N from shanks, roots, and rachis supports the notion that these organs serve as conduits for temporary storage

of reduced N (Below et al., 1981; Christensen et al., 1981; Cliquet et al., 1990b; Setter and Meller, 1984; Uhart and Andrade, 1995b; Weiland, 1989a; Weiland and Ta, 1992).

Large remobilisation of N from vegetative organs for both cultivars between R1 and R4 (Figs. 3.13 and 3.14) suggests that the supply of newly reduced N was inadequate for ear needs. As the rate of N uptake is dependent on the rate of photoassimilate supply to roots (Fujita et al., 1994; Jackson et al., 1980, 1986; Pan et al., 1995) the limited supply of N may have resulted from insufficient DM being partitioned to roots. As photoassimilate supply is dependent on the photosynthetic rate and use by shoot processes, grain filling and root functions compete for photoassimilate (Pan et al., 1986). Thus, the ability of Jubilee to partition DM to roots between R3 and R4 (Fig. 3.14a) may explain the significantly higher post-anthesis N uptake observed for this cultivar (Table 3.2). The sequential process of limited DM partitioning to roots followed by decreased N uptake supports the proposed hypothesis (cf. Fig 3.13 with Table 3.7 and Fig. 3.14 with Table 3.8).

Low N uptake after anthesis has been hypothesised (Hageman, 1986; Swank et al., 1982) to place greater demand on vegetative tissues to supply N. The observation that SS42 remobilised significantly more N than Jubilee between R3 and R4 (Table 3.8) supports this hypothesis. In meeting the sinks requirements, N was remobilised predominantly from the stem, husks and roots, as found in other studies (Cliquet et al., 1990a; McClung et al., 1990; Rendig and Crawford, 1985; Weiland, 1989a; Weiland and Ta, 1992). Leaves were also identified as a source of N for SS42 between R3 and R4 (Fig. 3.14c). In contrast, N was partitioned to leaves of Jubilee during this period (Fig. 3.14d). Remobilising N from leaves, usually from chlorophyll (Bouma, 1970; Morita, 1980), may decrease photosynthetic rates (Sinclair and deWit, 1976; Swank et al., 1982). Therefore, the remobilisation of DM from leaves and shanks of SS42 between R3 and R4 (Fig. 3.14a) may be a consequence of decreased photosynthetic rates from remobilising N from leaves. The photosynthetic ability of Jubilee, on the other hand, would likely have been preserved as N was not remobilised from leaves (Fig. 3.14d) and may explain why Jubilee did not remobilise DM from any organs between R3 and R4 (Fig. 3.14b).

Limited photoassimilate partitioning to roots followed by reduced N uptake and increased remobilisation of N from leaves may be the beginning of an inhibitory cycle. A cycle may develop because remobilising N from leaves resulting in decreased photosynthetic rates would further limit DM partitioning to roots. To what extent sink strength plays in this cycle can only be speculated in this study; particularly given the potentially confounding influences of radiation level and possibly moisture stress (Section 2.2.4). Between R1 and R3, SS42 partitioned large proportions of DM to both husks and stems, in contrast to Jubilee which partitioned most DM directly into kernels (Figs. 3.13a and 3.13b). As partitioning DM to vegetative tissue and husks reflects photoassimilate not consumed in reproductive growth (Below et al., 1981; Hume and Campbell, 1972; Palmer et al., 1973; Wilson and Allison, 1978b; Wolfe et al., 1988a) excess photoassimilate resulting from limited sink strength has the potential to decrease photosynthetic rates through 'feedback' inhibition (Neales and Incoll, 1968). Although Jubilee also partitioned DM to stems and husks, the proportion partitioned was significantly less than for SS42 (Figs. 3.13 and 3.14). The ability of Jubilee to partition DM to roots between R3 and R4 in contrast to SS42 may reflect inhibited photosynthesis for SS42.

With the lower sink strength of SS42 during early grain filling implicated as an indirect cause of reduced DM partitioning to roots, and resultant limited N uptake, the inhibitory cycle may help explain the physiology of DM and N partitioning to kernels. Therefore, with the potential that the inhibitory cycle offers to identifying ways to increase yield of SS42 and Jubilee, further research on this cycle is warranted.

Chapter 4

Effects of nitrogen rate on yield and yield components of sweet corn

4.1 Introduction

Nitrogen commonly limits vegetative growth and grain yield in maize (Lemcoff and Loomis, 1986; Tsai et al., 1991; Welch, 1979). As a consequence, applying N fertiliser onto soils of low N fertility can dramatically increase yield (Iragavarapu et al., 1997; Jacobs and Pearson, 1991; Muchow and Sinclair, 1995; Nunez and Kamprath, 1969; Roberts et al., 1980b; Sanchez et al., 1989; Wienhold et al., 1995). In many instances, yield increases in the order of 4-11 t/ha are achieved (Balko and Russell, 1980a; Fox; 1973; Lang et al., 1956; Sanmaneechai et al., 1984; Steele et al., 1982) through increased weight and number of both primary and secondary ears (Anderson et al., 1985; Krantz and Chandler, 1954; Salardini et al., 1992; Wong et al., 1995). In contrast to these reports, yield of SS42 and Jubilee (to a lesser extent) in the previous study (Chapter 2) generally did not increase in response to N fertiliser. Further investigation revealed that the lack of response was probably due to having 259 kg/ha of N already available in the soil at sowing (Table 2.1).

Sweet corn obtains N from three sources: N present in the soil at planting (residual N); N mineralized during the growing season; and from N fertilisers (Steele et al., 1982). The importance of these three sources of N for yield was recognised by Tsai et al. (1992) who suggested that when their combined levels are greater than 175 kg/ha grain yield would not increase significantly with fertiliser N. A similar result was indicated in Chapter 2, as discussed earlier. Such results highlight the importance of residual- and mineralizable-N for estimating fertiliser N requirements (Roberts et al., 1980b; Stanford and Hanway, 1955; Stanford and Smith, 1972). Moreover, with reports that soils with a history of high N fertilization or cropped straight from pasture may contain sufficient N for maximum yield, removing the need for supplementary applications (Cumberland and Douglas, 1970; Olson and Kurtz, 1982; Roberts et al., 1980b), soil analyses may prove highly cost effective.

Despite the apparent importance of mineralizable N for estimating fertiliser N requirements, levels are not commonly measured for sweet corn production in Gisborne. This is due primarily to a lack of knowledge among growers about mineralizable N and its importance to cropping. Instead, growers generally rely on residual N tests and their own experience as a basis for

estimating fertiliser N requirements (Steele, 1983; Steele et al., 1982). The consequence of failing to account for mineralizable N levels is that some growers in Gisborne may be applying excess fertiliser N (Steele, 1983). Excess fertiliser application not only reduces grower profit but increases the potential for nitrate pollution of water supplies (Balko and Russell, 1980b; Guillard et al., 1995; Jokela, 1992; Jokela and Randall, 1989; Roth and Fox, 1990).

Increases in yield for Jubilee with N fertiliser (Fig. 2.11), despite high levels of soil available N (259 kg/ha; Table 2.1) suggests that Jubilee requires more N for maximum yield than SS42. Confirming this would have important ramifications for both the management of these cultivars and grower profit. For example, the base N fertility of a site could potentially determine which cultivar was planted there and the fertiliser regime for that crop. Furthermore, a lower dependence on soil N fertility by SS42 would entail lower fertiliser and application costs.

Hybrid differences in the N requirement for maximum yield (e.g., Albus and Moraghan, 1995; Czyzewicz and Below, 1994; Sabata and Mason, 1992; Thiraporn et al., 1987; Tsai et al., 1984, 1992) have been attributed to differences in both the utilization of N by kernels and kernel sink strength (Chapter 3; Anderson et al., 1984b; Balko and Russell, 1980a; Smiciklas and Below, 1990). Chapter 3 not only showed that kernels of Jubilee had a significantly higher sink strength for both N and DM during early grain filling than those of SS42 (Fig. 3.13) but that the greater kernel sink strength contributed to Jubilee being significantly more efficient at transferring N to kernels (Table 3.3). Further investigation of the efficiency with which kernels of Jubilee and SS42 utilise N and their respective sink strengths is reserved for Chapters 5 and 6.

Although manipulating N rate may increase marketable yield of SS42 and Jubilee, their yield will unlikely increase further unless their yield potential is increased. Thus if yield is to be increased beyond manipulating fertiliser regimes, physiological barriers limiting yield must be identified so breeders can select for the right attributes. Clues to the nature of these barriers can be found by studying the association between yield and yield components (e.g., silk delay, stalk diameter, tillers per plant), and how they adjust to stress. Understanding how these variables influence yield under N stress conditions is further highlighted by the possibility that if growers are applying excessive quantities of fertiliser, and recommendations state that such applications

should be reduced, then the safety margin of high soil available levels will be reduced. As a consequence, growers who apply less fertiliser would be operating closer to the verge of N stress.

Silk delay, which increases with increasing N stress (Anderson et al., 1984b), may be an important yield determinant. Long delays may not only lead to barrenness (Hashemi-Dezfouli and Herbert, 1992), but also to significant yield reductions (Edmeades et al., 1993). However, little information exists on how silk delay for primary and secondary ears is influenced by N supply. With silk delay suggested to reduce sink strength of secondary ears (Section 2.4), and results of Chapter 3 indicating that excess photoassimilate inhibits N uptake, leading to reduced sink strength of kernels, long delays may have important physiological consequences to yield.

Tillers were implicated as being an important yield determinant in the previous study (Chapter 2) as positive correlations between tillers and kernel recoveries from both primary and secondary ears (Table 2.7a) suggested tillers were a source of photoassimilate. With tiller number and stalk diameter increasing with N (McClelland, 1928; Wu et al., 1993), N fertility may prolong their ability to contribute photoassimilate. However, under low N fertility, tillers may be a sink for photoassimilate as suggested by studies with barley and wheat (Gu and Marshall, 1988; Kirby and Jones, 1977; Mohamed and Marshall, 1979). Hence, while tillers may be physiologically important for yield at high N fertility levels, they may be a sink for N stressed plants. To my knowledge no studies have been published which have investigated the association between tillers and yield as influenced by N rate for sweet corn.

Yield by itself is not an important variable to growers of process sweet corn because it normally contains ears considered waste by processors (Pickett, 1944) and such ears are deducted from crop payments. Rather, marketable yield is more important. In particular, marketable cob and marketable kernel yield are the most important variables as these are the processor's saleable products. Although it was suggested in Chapter 2 that the density range of 69-77,000 plants per hectare maximised marketable cob yield, the absence of measures of tip fill meant that it was not possible to conclude whether all cobs produced within this "optimum" range were suitable for 'whole-cob corn', and hence, marketable cob yield. For whole-cob corn produced at Heinz Wattie's Gisborne factory, cobs must carry consistently mature kernels over at least 180 mm of

length. Thus, 69-77,000 plants per hectare may not be the density range which maximises marketable cob yield of Jubilee and SS42.

Confirming the finding that Jubilee requires more fertiliser N than SS42 would have important consequences for increasing grower profitability, particularly for SS42. Thus the first objective of this experiment was to investigate the relationship between yield and N rate for SS42 and Jubilee. The second objective was to examine the influence of yield components (e.g., tillers, stalk diameter, silk delay) on ear weights at varying levels of N stress. The final objective was to assess the suitability of primary and secondary ears for processing as whole-cob corn and hence, their contribution to marketable cob yield.

4.2 Materials and methods

This experiment, located near Gisborne, New Zealand (longitude 178°, latitude 38.7°) began during spring 1996. Twelve sites were initially chosen, with emphasis on selecting a site with both low residual- and mineralizable-N. Three samples to 150 mm were taken from each site, from which, levels of residual N were determined following the method of Keeney and Nelson (1982). On identifying three sites with low residual N, levels of mineralizable N (determined using aerobic incubation for two weeks following the method of Craighead and Clark, 1989), macro- and micro-nutrient levels, pH, CEC, and organic matter content were determined. A site was selected based on this information.

4.2.1 Soil characteristics

The site chosen was a Waihirere heavy silt loam (Pullar, 1962) with a cropping history of tomatoes and pasture. Sweet corn had been used as a rotational crop every 2-3 years. During October 1996 the field was ploughed and disced to 150 mm. Immediately after sowing, soil in each plot was sampled to a depth of 150 mm. Ammonium- and nitrate-N were extracted from each sample using 2M KCl, as described by Keeney and Nelson (1982). Mineralizable N levels were determined using aerobic incubation for two weeks following the method of Craighead and

Clark (1989). The mineralizable N level and residual N level (i.e., ammonium- plus nitrate-N) for each plot were used to explain some of the between-plot variation (i.e., analysis of covariance; Section 4.2.6). A further nine samples were analysed for mineralizable N using anaerobic incubation for two weeks (Craighead and Clark, 1989), after first being frozen (-18 C) for two months. Quantifying mineralizable N both aerobically and anaerobically permitted the two methods to be compared. This was important as mineralizable N in Chapter 2 was quantified using the anaerobic incubation method, whereas it was quantified using aerobic incubation in the current study. Analysis (PROC TTEST; SAS Institute, 1989) confirmed that both incubation methods gave similar estimates of mineralizable N levels, and therefore validated comparison of N fertility levels between the two studies. Results of soil analyses (Table 4.1) were expressed on an air-dried basis and converted to kg/ha following the method of Lemcoff and Loomis (1986) (i.e., nutrient concentration (μg/g) × depth sampled (m) × bulk density[1] (g soil/cm^3) × 10). Chi-square analysis of nutrient levels for the field indicated that no nutrient gradients were present.

[1] Soil correction factor (g/ml) was substituted for bulk density.

Table 4.1. Summary of soil test results.

Nutrient	kg/ha[z]
Ammonium N	11.9 (1.04)
Nitrate N	26.7 (3.45)
Mineralizable N	53.5 (1.75)
Phosphorous	62.8 (4.39)
Sulphate	43.9 (3.21)
	meq/100g
Potassium (exchangeable)	0.35 (0.08)
Calcium (exchangeable)	22.5 (1.11)
Magnesium (exchangeable)	1.09 (0.20)
Sodium (exchangeable)	0.15 (0.01)
Cation exchange capacity	32.1 (4.18)
pH	6.8 (0.21)
Organic matter (%)	3.31 (0.74)

[z] Brackets represent SE (n=45)

4.2.2 Experimental design

The experiment comprised a randomized complete block design with three blocks. Nitrogen rates were 0, 74, 115, 172, or 230 kg/ha. Each plot was 12 rows wide and 30 m long with the outer three rows serving as guard plants (Douglas et al., 1982). Blocks were separated by 6 m of plants with the experiment bounded on all four sides by a 24-row headland. Cultivars were not included in the treatment structure due to the risk of cross-pollination between the genotypes.

4.2.3 Crop management

On November 9 the field was sprayed with 2.7 kg atrazine/ha and harrowed. SS42, Jubilee, and Furio[2] (*Zea mays* 'Furio') were planted November 12, December 19, and January 10, respectively, to a depth of 25 mm using a John Deere four-row finger planter. Seed was sown at intervals of 188 mm in rows 760 mm wide to give a density of 70,000 plants per hectare. Counter 20G® (terbufos) granules were soil-incorporated above the seed at 1.0 kg a.i./ha for Argentine stem weevil (*Listronotus bonariensis*) control. No fertilizers were included at planting.

Urea (46% N) was side-dressed at 0, 74, 115, 172, or 230 kg N/ha at V4, being applied 50-100 mm either side of the plant and incorporated to a depth of 50 mm. Control N treatments were also cultivated. Weeds remaining after side-dressing were removed manually.

4.2.4 Growing degree days, rainfall distribution, and incident solar radiation during ontogeny

Meteorological data were recorded 21 km from the experimental site at a NIWA station. From planting to harvest SS42, Jubilee, and Furio accumulated 1323, 1242, and 1253 GDD (base 6 C), respectively (Fig. 4.1a). During this period, 258, 392, and 329 mm of rain fell for SS42, Jubilee, and Furio, respectively (Fig. 4.1b). Further, SS42, Jubilee, and Furio were exposed to a total of 2362, 1925, and 1788 $MJ \cdot m^{-2}$ of solar radiation, respectively.

[2] Although not discussed in this chapter, cultural practices and environmental conditions for Furio are presented to avoid repetition in Chapters 5 and 6.

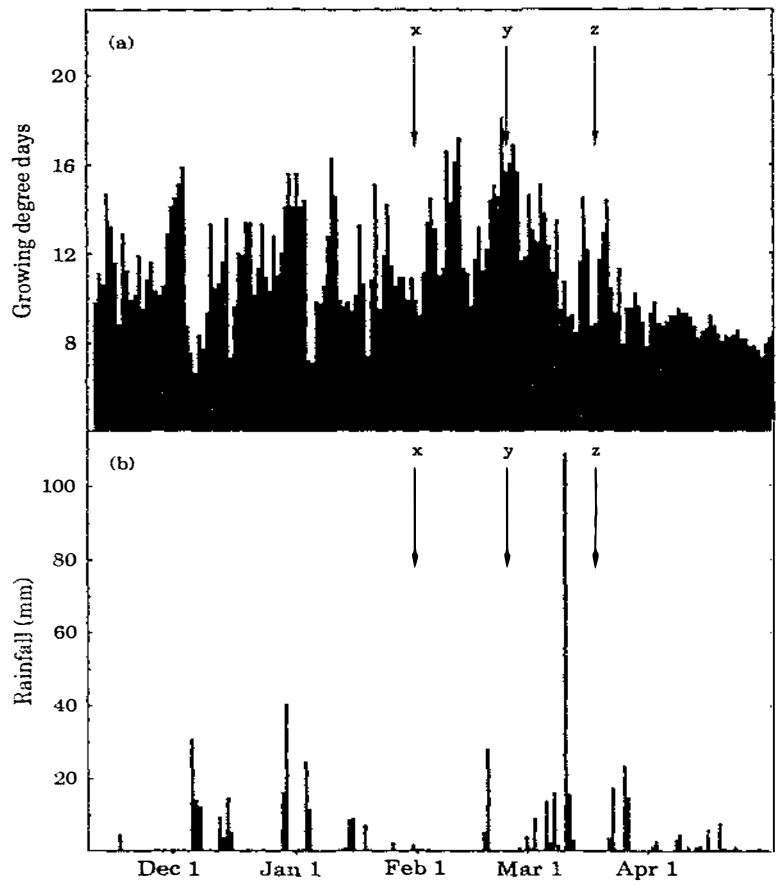

Fig. 4.1. Distribution of (a) growing degree days and (b) rainfall during the cropping period. Arrows *x*, *y*, and *z* indicate the date at which 50% of plants of SS42, Jubilee, and Furio, respectively had 'silked'; February 1, February 25, and March 20, respectively.

4.2.5 Pre- and post-harvest measurements

Twenty plants from each plot were labelled at the early stage of V6 to avoid possible bias in plant selection at later ontogenetic stages. The date of anthesis and silking, the number of ears which 'silked', stalk diameter, the number of tillers, and lodging were recorded for each of the 20 plants as previously described in Section 2.2.5.

Plots selected at random daily were used to assess seed moisture content (SMC). SS42 and Jubilee were harvested when SMCs of primary ears were 74 (March 2) and 72% (April 1), respectively, as set by processors. Ears were labelled according to position on the plant and were hand harvested. Harvested ears were graded as either harvestable or non-harvestable; a harvestable ear being either wider than 40 mm or longer than 150 mm (i.e., mechanically harvestable; Davis, pers. comm.). Non-harvestable ears were discarded. Plants for which the primary ear was discarded were classified as barren, while those for which the secondary ear was discarded were classified as secondary ear barren. Procedures and data collection for harvestable ears were as described in Section 2.2.5, with the exception of cob length. Rather than measuring cob length from the butt of the cob to the tip, cob length was measured from the butt to the where kernels were no longer marketable. Figure 2.30 is reproduced again (Fig. 4.2) to illustrate the point of transition between marketable and non-marketable kernels.

Fig. 4.2. A secondary cob illustrating the point at which kernels are no longer marketable.

4.2.6 Data analysis

Means for each plot were calculated and treatment effects analysed using ANOVA, with regression analysis used to model trends. Regression models were selected based on biological relevance, significance of coefficients at the 5% level, and reduction in RSS. Neither covariate (i.e., mineralizable- or residual-N) explained a significant proportion of the between-plot variation in any of the models. Chi-square analysis, logistic regression, and *z*-scores were also used to analyse data. Assumptions and data preparation for these data analysis techniques were described in Section 2.2.6.

Recoveries ≤ 70 g were of unacceptable quality, consistent with the previous study (Section 2.2.6). To determine whether the marketability criteria for rejecting ears and cobs in this previous study were also appropriate for the current study, logistic regression analysis was conducted with the explanatory variables cob length and cob weight. This analysis revealed that cob weight was a good predictor of whether a cob was marketable or not but cob length was not. This finding was consistent with the previous study (Section 2.4). Using simple linear regression, cob and ear weights giving recoveries of 70 g were estimated. As both the estimates and the variability of the predicted value were similar to the previous study, the marketability criteria of Sections 2.3.1 and 2.3.2 were also used in the current study.

Non-linear regression

Many of the N rate × yield relationships were modelled using an exponential term to represent an asymptotic tendency (Mitscherlich, 1909; Equation 4.1). Where an asymptotic tendency was not evident the square root quadratic model (Colwell, 1994; Equation 4.2) was used.

$$y = a + be^{-cx} \tag{4.1}$$

$$y = a + b\sqrt{x} + cx \tag{4.2}$$

Where non-constant variance was detected, models were weighted by the inverse of the SE of the mean for each N rate (Chatterjee and Price, 1991). Coefficients of determination for models with more than two parameters were calculated using Equation 4.3.

$$R^2_{adj} = 1 - \left(\frac{n-1}{n-p} \times \frac{RSS}{TSS} \right) \quad (4.3)$$

where R^2_{adj} is the adjusted coefficient of determination; n is the total degrees of freedom; p is the number of parameters in the model; RSS and TSS are the residual and total sums of squares for the model, respectively.

4.2.7 Commercial validation of the optimum density

In the same growing season an experiment was established to investigate the effect of density on yield of SS42. The experiment comprised three unreplicated densities; 51,000, 68,350, or 96,610 plants per hectare. Seed was sown on November 14 over approximately 1 ha for each density and the experiment was surrounded by a 24-row headland. The soil type was as described in Section 2.2.1 with crop management and environmental conditions as described in Sections 4.2.3 and 4.2.4. Urea was incorporated at planting to supply 30 kg N/ha with a further 115 kg N/ha side-dressed at V5.

Each area was mechanically harvested using a Byron 8400 corn harvester with a Byron 1630c six row header at 74% SMC (i.e., March 4). From the harvested bulk for each density, 40 ears were randomly selected. Each ear was weighed, husked, and then re-weighed. Cobs $\leq$ 164 g were discarded (Section 2.3.1.4). Kernels were cut from the remaining cobs to give an estimated recovery. Actual ear yields and kernel recoveries were determined from commercial harvesting and processing.

4.3 Results

4.3.1 Analysis of SS42 harvest data

Seed moisture content of kernels from primary and secondary ears at harvest were 74.3% (SE 0.91) and 76.6% (SE 1.07), respectively, and were independent of treatment. Kernel loss during processing was negligible.

4.3.1.1 Barrenness

Increasing N rate significantly decreased barrenness; 27% of plants were barren with the control N treatment, increasing to 13% with 230 kg N/ha (Table 4.2). Those plants primary ear barren were also secondary ear barren. However, the number of plants barren for the secondary ear were not influenced by N rate. Pooled across N rates, 82% (SE 1.7) of plants were barren for the secondary ear.

Table 4.2. Proportions of harvestable and non-harvestable primary ears of SS42 as affected by N rate.

	Nitrogen rate (kg/ha)					
	0	74	115	172	230	Total
Non-harvestable ears (%)	26.7	13.3	5.0	8.9	13.3	67.2
Harvestable ears (%)	73.3	86.7	95.0	91.1	86.7	432.8
Total	100.0	100.0	100.0	100.0	100.0	500.0

$\chi^2 = 13.6^{***}$

^{NS}, *, **, *** Nonsignificant or significant χ^2 test at $P \leq 0.05$, 0.01, and 0.001, respectively.

4.3.1.2 Harvestable ear yield

Maximum harvestable ear yield of 22.20 (SE 2.14) tonnes with 162 kg N/ha was significantly higher than the 15.22 (SE 1.84) tonnes recorded for the control (Fig. 4.3a). However, almost all of this yield increase was achieved between 0 and 74 kg N/ha. Thus, although yield was maximised with 162 kg N/ha, yield of 21.46 (SE 2.03) tonnes with 74 kg N/ha was not significantly different.

Yield of primary ears followed a similar trend to that of total yield (cf. Figs. 4.3a and 4.3b). Maximum yield of 20.10 (SE 1.67) tonnes with 136 kg N/ha was significantly higher than the 13.04 (SE 1.51) tonnes recorded for the control, but was similar to the 21.51 (SE 1.61) tonnes with 74 kg N/ha. A difference of 2.11 tonnes between total yield and that of primary ears with 136 kg N/ha was consistent with the 2.14 tonne (SE 0.41) contribution by secondary ears. However, unlike total yield or that of primary ears, yield of secondary ears was not influenced by N rate.

As yield data were based on harvestable weights for the 20 plants in each plot, means calculated may have included plants whose harvestable weight was nil (i.e., barren plants). Hence, inference regarding the distribution of weight of primary ears from Fig. 4.3b may be biased. To avoid this bias, non-harvestable ears were treated as missing values. This enabled variability between ears, and ear components to be examined.

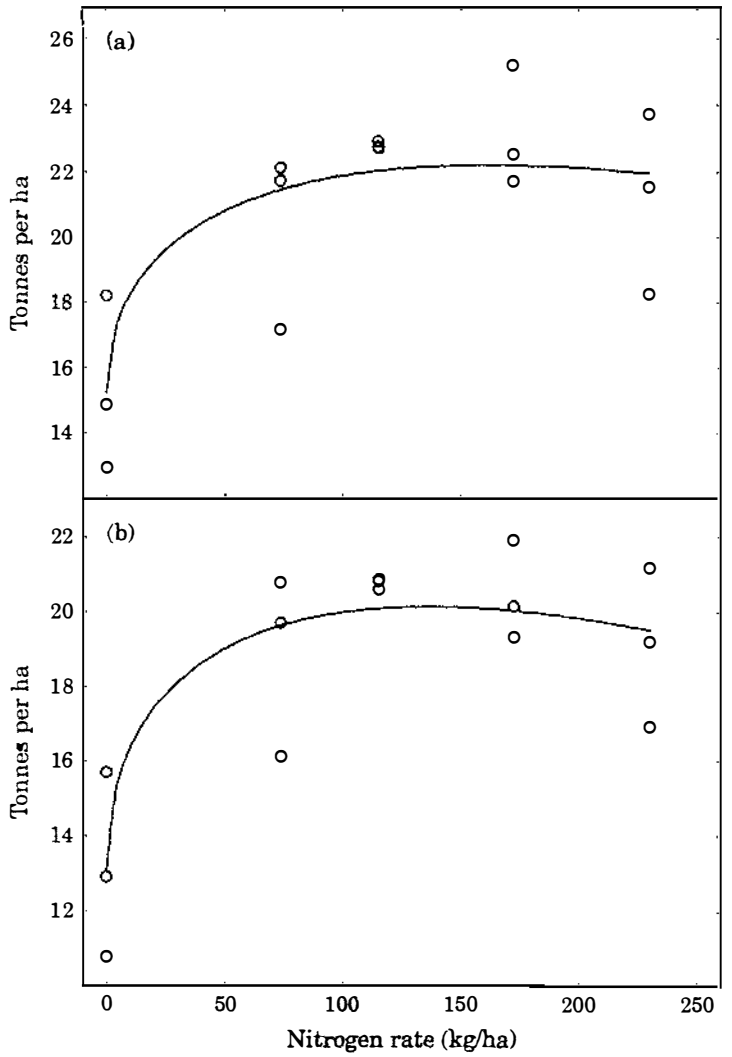

Fig. 4.3. Harvestable ear yield of SS42 as affected by N rate for (a) total and (b) primary ears. Data are the means for each N rate and block. Fitted function for (a) is $Y=15.22+1.10X^{0.5}-4.30\times10^{-2}X$ ($R^2_{adj}=0.68$). Fitted function for (b) is $Y=13.04+1.21X^{0.5}-5.19\times10^{-2}X$ ($R^2_{adj}=0.68$).

4.3.1.3 Kernel recoveries

Kernel recoveries from primary ears increased 33% as N rate increased from 0 to 230 kg/ha (Fig. 4.4). However, only the first increase in N rate significantly increased recoveries, increasing from 100 g (SE 12.3) to 138 g (SE 13.0) as N rate increased from 0 to 74 kg N/ha. Thus, recoveries of 148 g (SE 13.5) with 230 kg N/ha were of similar weight to those with 74 kg N/ha. Recoveries from secondary cobs, on the other hand, were not influenced by N rate. Pooled across N rates, recoveries from secondary cobs were 43 g (SE 4.6).

Using the criteria that cobs giving recoveries ≤ 70 g would be rejected by processors (Section 4.2.6), an estimated 28% of primary cobs (SD 56.3)[3] for the control N treatment would have been discarded. With recoveries increasing with N rate (Fig. 4.4), only 7% of cobs (SD 48.9) for the 230 kg N/ha treatment would have been discarded. In contrast, the lower recoveries from secondary cobs entailed that 89% would have been unacceptable for processing. Examples of secondary cobs expected to give a recovery of 70 g, and hence 'borderline' for being marketable are presented in Fig. 4.5.

[3] Standard deviations refer to the distribution of kernel recoveries at the N rate under discussion.

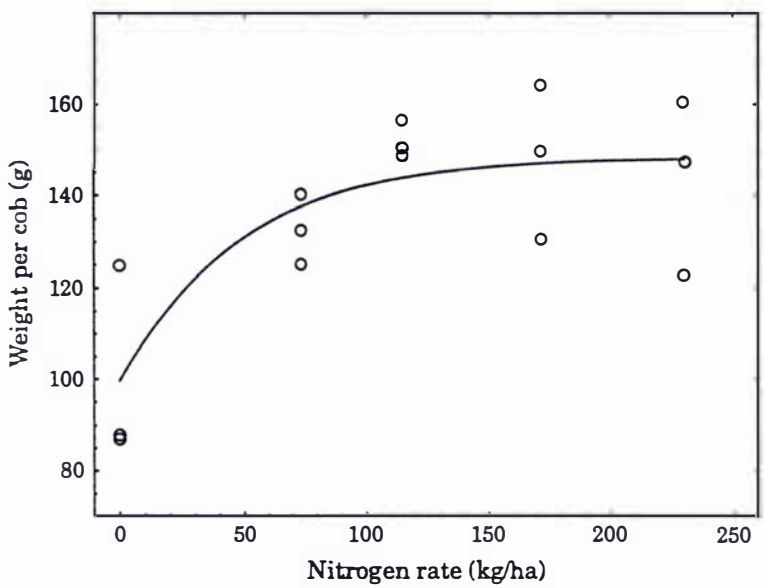

Fig. 4.4. Kernel recovery from primary ears of SS42 as affected by N rate. Data are the means for each N rate and block. Fitted function is $Y=148.4-48.84e^{-0.02X}$ ($R^2_{adj}=0.42$).

Fig. 4.5. Secondary cobs of SS42 borderline for being marketable. Each weighs 151 ± 3 g with an estimated kernel recovery of 70 g.

4.3.1.4 Harvestable ear and cob weights

Weight of primary ears increased 55 g as N rate increased to 74 kg N/ha, but only a further 8 g between 74 and 230 kg N/ha (Fig. 4.6). Thus, while the first increase in N rate significantly increased weight of primary ears, weights did not increase significantly with further increases. Nevertheless, with 230 kg N/ha, primary ears weighed 318 g (SE 11.2), 64 g heavier than those of the control N treatment (255 g (SE 10.1)). Weight of secondary ears were not influenced by N rate, averaging 165 g (SE 8.6).

Similar results were observed for the weight of primary cobs (cf. Figs. 4.6 and 4.7). Between 0 and 115 kg N/ha the weight of primary cobs increased 21%, but only a further 2% between 115 and 230 kg N/ha (Fig. 4.7). Thus, although primary cobs weighing 270 g (SE 11.2) for the 74 kg N/ha treatment were significantly heavier than the 220 g (SE 10.7) cobs of the control N treatment, they were of similar weight to those of higher N treatments. Weight of secondary cobs, on the other hand, were not influenced by N rate. Pooled across N rates, secondary cobs weighed 113 g (SE 7.9).

Applying the marketability criteria of Section 2.3.1.4 (i.e., that primary ears, $\leq$ 187 g, or secondary ears, $\leq$ 182 g would be discarded by processors) gave rejection rates similar to those for kernel recoveries (Section 4.3.1.3), and hence are not reported. Rejections rates for cobs using the marketability criteria of Section 2.3.1.4 were also similar, and hence also not reported.

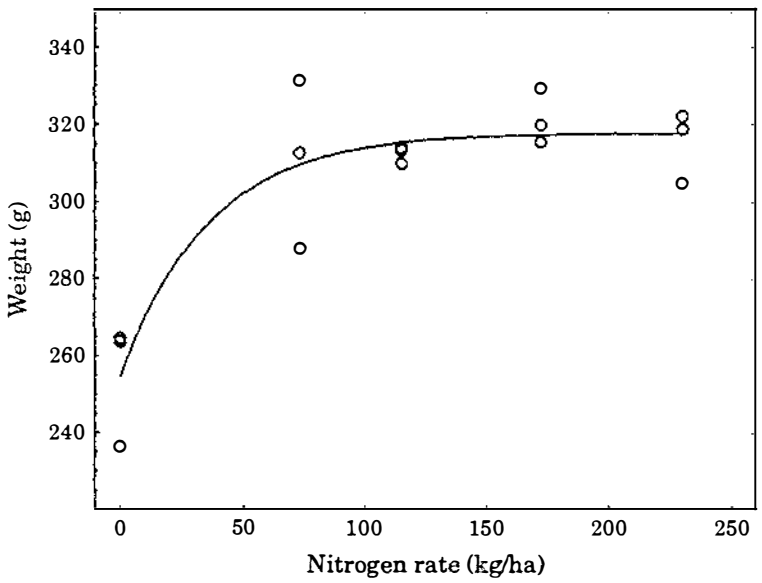

Fig. 4.6. Weight of primary ears of SS42 as affected by N rate. Data are the means for each N rate and block. Fitted function is $Y=317.7-63.13e^{-0.03X}$ ($R^2_{adj}=0.81$).

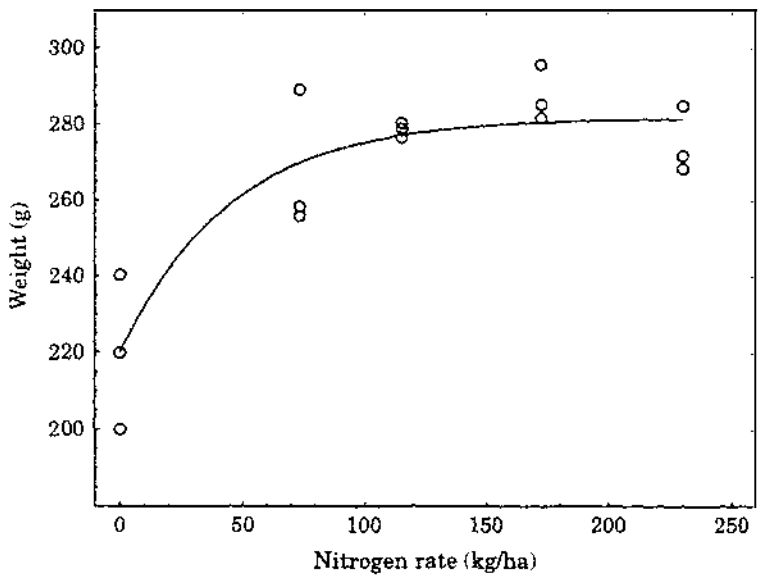

Fig. 4.7. Weight of primary cobs of SS42 as affected by N rate. Data are the means for each N rate and block. Fitted function is $Y=281.9-62.08e^{-0.02X}$ ($R^2_{adj}=0.78$).

4.3.1.5 Marketable kernel yield

Highest marketable kernel yield was achieved with 230 kg N/ha (Fig. 4.8a). Yield of 9.75 (SE 1.11) tonnes with this N rate was 48% greater than the 5.10 (SE 1.05) tonnes recorded for the control. Although yield was highest with 230 kg N/ha, yield of 8.80 (SE 1.16) tonnes with 74 kg N/ha was not significantly different.

Marketable kernel yield from primary ears followed a trend similar to that for total kernel yield (cf. Figs. 4.8a and 4.8b). Although a significant yield increase of 3.61 tonnes was achieved between 0 and 74 kg N/ha, yield did not increase significantly with further increases in N rate. Similar trends for kernel recovery from primary ears and total kernel yield resulted from secondary ears contributing only 0.21 (SE 0.08) tonnes to total yield. Kernel recovery from secondary ears was not influenced by N rate.

4.3.1.6 Marketable cob yield

As N rate increased from 0 to 230 kg/ha, marketable cob yield increased 45% (Fig. 4.9a). Despite yield with 230 kg N/ha being significantly higher than the 10.07 (SE 1.85) tonnes recorded for the control, yield of 16.24 (SE 2.04) tonnes with 74 kg N/ha was not significantly different. Secondary cobs contributed only 0.61 tonnes (SE 0.15) to total yield and were unaffected by N rate. Thus, primary cobs were the main constituent of total yield. Moreover, yield of 17.46 (SE 1.84) tonnes of primary cobs with 230 kg N/ha was similar to the 15.68 (SE 1.92) tonnes recorded with 74 kg N/ha. Yield of 9.71 (SE 1.74) tonnes recorded for the control N treatment, on the other hand, was significantly lower than the yields recorded with higher N rates.

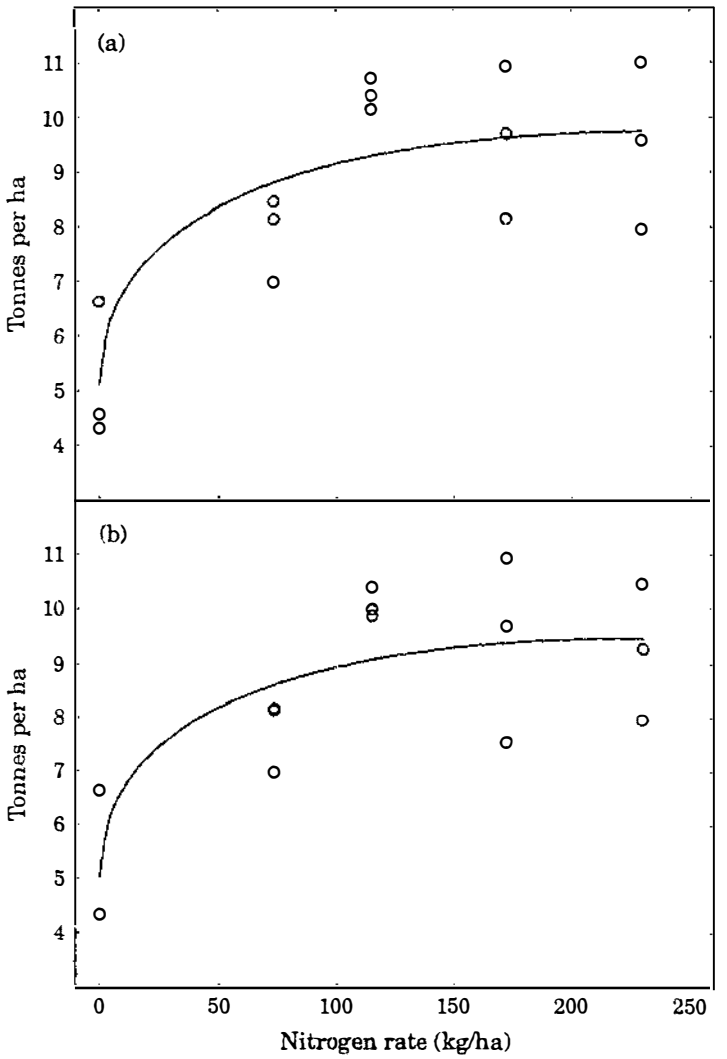

Fig. 4.8. Marketable kernel yield of SS42 for (a) total and (b) primary ears as affected by N rate. Data are the means for each N rate and block. Fitted function for (a) is $Y=5.10+0.59X^{0.5}-1.90\times10^{-2}X$ ($R^2_{adj}=0.65$). Fitted function for (b) is $Y=5.02+0.59X^{0.5}-1.93\times10^{-2}X$ ($R^2_{adj}=0.64$).

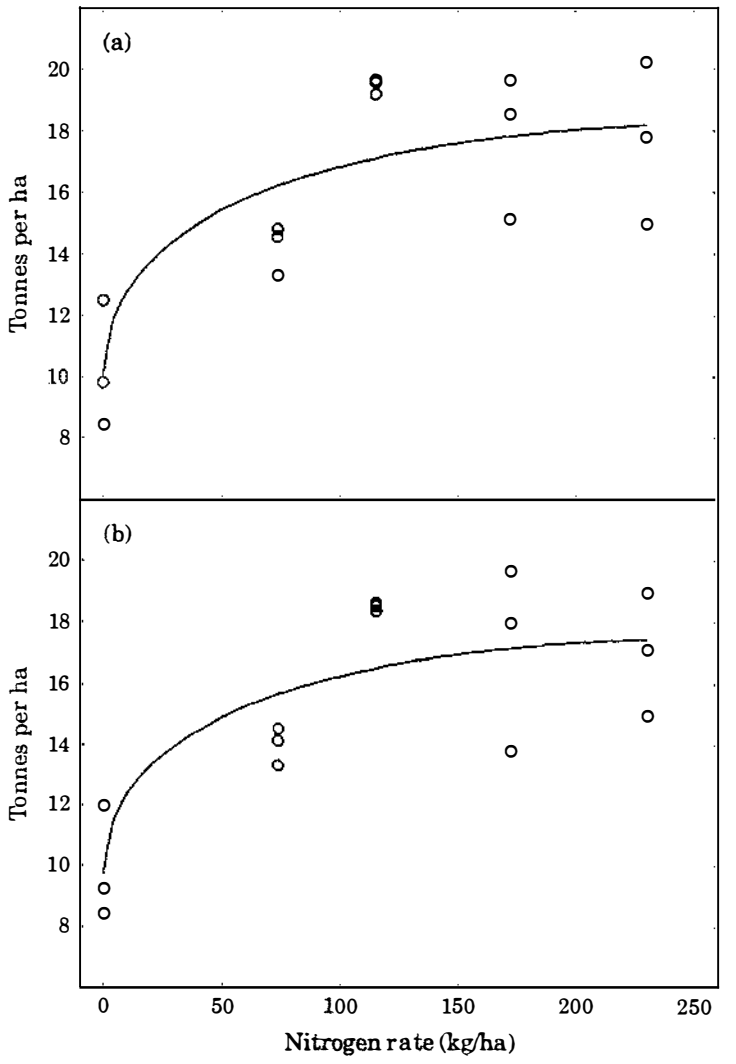

Fig. 4.9. Marketable cob yield of SS42 for (a) total and (b) primary cobs as affected by N rate. Data are the means for each N rate and block. Fitted function for (a) is $Y=10.08+0.95X^{0.5}-2.74\times10^{-2}X$ ($R^2_{adj}=0.62$). Fitted function for (b) is $Y=9.71+0.94X^{0.5}-2.81\times10^{-2}X$ ($R^2_{adj}=0.64$).

4.3.2 Analysis of Jubilee harvest data

As only three secondary ears from a total of 300 plants met the criteria for being harvestable (Section 4.2.5) only results for primary ears are presented. Notwithstanding the lack of data to perform significance tests on secondary ears, all three ears were rejected when marketability criteria were applied.

The SMC of kernels from primary ears was 72.1% (SE 0.80) and was not influenced by the N treatments. As with SS42, kernel loss during processing was negligible.

4.3.2.1 Barrenness

Although barrenness was significantly influenced by N rate, similar numbers of plants were barren with 230 kg N/ha as for the control (Table 4.3). While over 33% of plants were barren for these treatments, less than 7% were barren with 74 kg N/ha.

Table 4.3. Proportions of harvestable and non-harvestable primary ears of Jubilee as affected by N rate.

	Nitrogen rate (kg/ha)					
	0	74	115	172	230	Total
Non-harvestable ears (%)	33.3	6.7	8.3	25.0	39.7	113.0
Harvestable ears (%)	66.7	93.3	91.7	75.0	60.3	387.0
Total	100.0	100.0	100.0	100.0	100.0	500.0

$\chi^2 = 30^{***}$

^{NS}, *, **, *** Nonsignificant or significant χ^2 test at $P \leq 0.05$, 0.01, and 0.001, respectively.

4.3.2.2 Harvestable ear yield

With barrenness of over 30% recorded for both the control and 230 kg N/ha treatments compared to 8% with 115 kg N/ha (Table 4.3), the yield response to N rate was parabolic (Fig. 4.10). Maximum yield of 20.40 (SE 2.54) tonnes with 116 kg N/ha was 34% higher than with either 0 or 230 kg N/ha. While yield with N rates between 74 and 172 kg N/ha was similar to that with 116 kg N/ha, yield of 13.21 (SE 2.61) and 13.43 (SE 2.95) tonnes for the control and 230 kg N/ha treatments, respectively, was significantly lower.

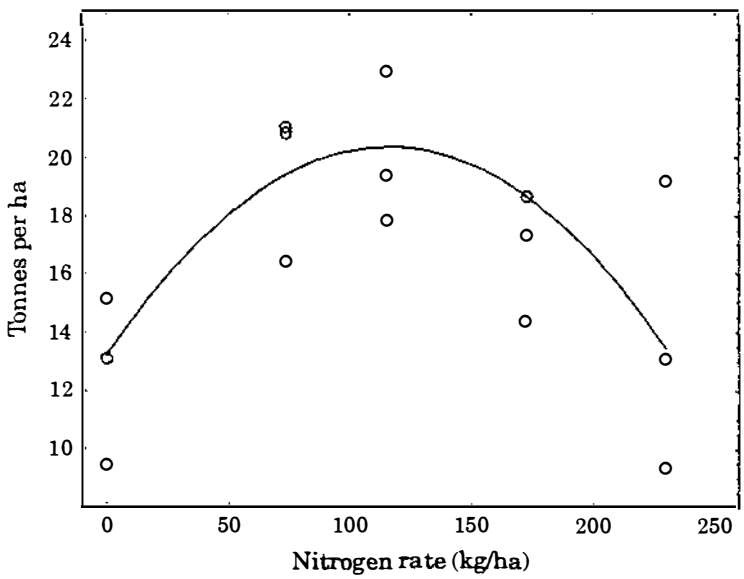

Fig. 4.10. Yield of primary ears of Jubilee as affected by N rate. Data are the means for each N rate and block. Fitted function is $Y=13.21+1.24\times10^{-1}X-5.35\times10^{-4}X^2$ ($R^2_{adj}=0.46$).

4.3.2.3 Kernel recoveries

Kernel recoveries from primary cobs increased from 111 g (SE 8.2) to 141 g (SE 8.9) per cob as N rate increased from 0 to 230 kg N/ha (Fig. 4.11). While recoveries for the control were significantly lower than with 230 kg N/ha, they were not significantly different from those with 74 kg N/ha (i.e., 137 g (SE 9.7)). Recoveries with 74 kg N/ha were of similar weight to those with 230 kg N/ha.

When marketability criteria (i.e., that cobs giving recoveries ≤ 70 g would be rejected; Section 4.2.6) were applied to kernel recoveries, an estimated 12% of primary cobs (SD 46.5)[4] would have been rejected with 230 kg N/ha. In comparison, about 22% would have been discarded (SD 37.3) for the control.

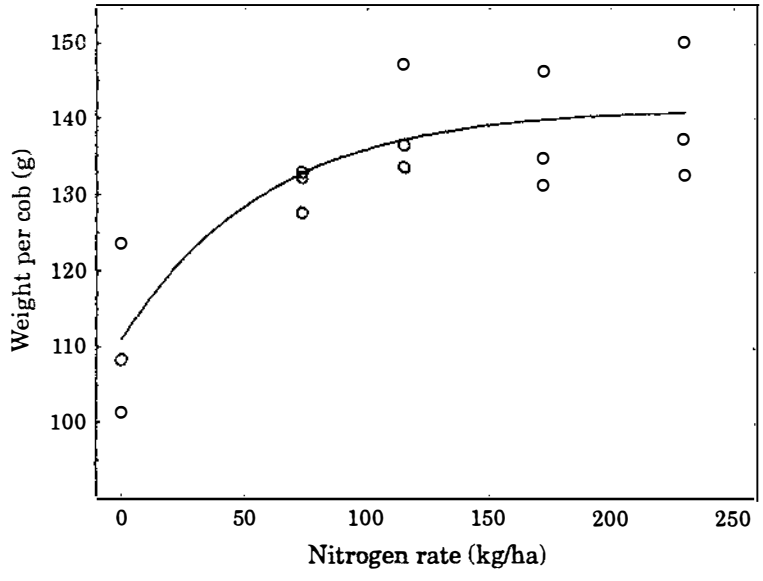

Fig. 4.11. Kernel recovery from primary ears of Jubilee as affected by N rate. Data are the means for each N rate and block. Fitted function is $Y=141.4-30.41e^{-0.017X}$ ($R^2_{adj}=0.52$).

[4] Standard deviations in this and the next Section refer to the distribution of the variable at the N rate under discussion.

4.3.2.4 Harvestable ear and cob weights

Although weight of primary ears increased almost linearly between 0 and 230 kg N/ha, their maximum weight was not identified in this study (Fig. 4.12). Nevertheless, primary ears from the 230 kg N/ha treatment weighed 334 g (SE 7.9), significantly heavier than those of the control (i.e., 269 g (SE 7.7)) and 74 kg N/ha (i.e., 297 g (SE 8.6)) treatments.

Weight of primary cobs followed a trend similar to that for ears in response to N rate (cf. Figs. 4.12 and 4.13). Thus, although primary cobs were heaviest with 230 kg N/ha (287 g (SE 9.8)) their maximum weight was not identified in this study. Nevertheless, with 230 kg N/ha, cobs were significantly heavier (23%) than those of the control N treatment (i.e., 221 g (SE 9.5)). While they were also significantly heavier than those with 74 kg N/ha, they were of similar weight to those from higher N rates.

With primary ears ≤ 187 g expected to give a recovery less than 70 g (Section 2.3.2.4), 18% of ears (SD 65.7) for the control N treatment would have been discarded. With ear weights increasing with N rate (Fig. 4.12), only 2% of ears (SD 58.1) would have been discarded for the 230 kg N/ha treatment. Similar results were observed for primary cobs. An estimated 22% of primary cobs (SD 58.9) for the control N treatment would have been ≤ 157 g, and hence, not marketable. In comparison, fewer than 3% would not have met marketability criteria for the 230 kg N/ha treatment (SD 56.5).

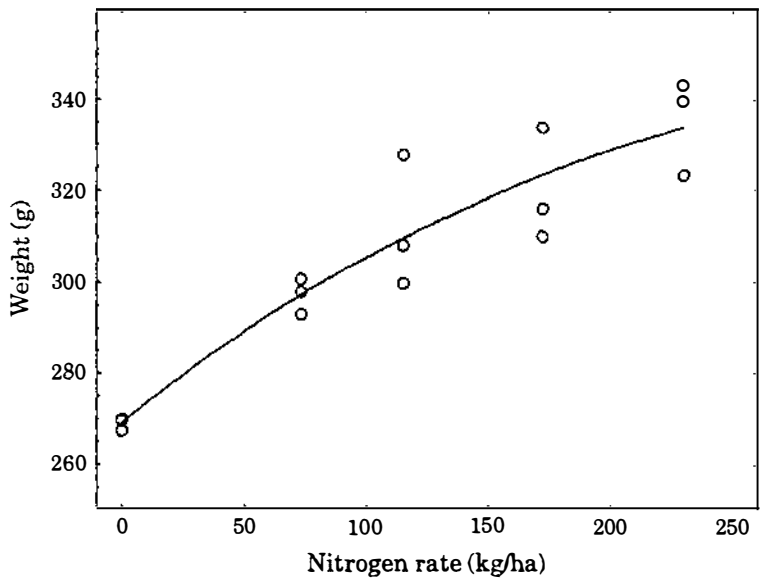

Fig. 4.12. Weight of primary ears of Jubilee as affected by N rate. Data are the means for each N rate and block. Fitted function is $Y=371.4-102.26e^{-0.004X}$ ($R^2_{adj}=0.86$).

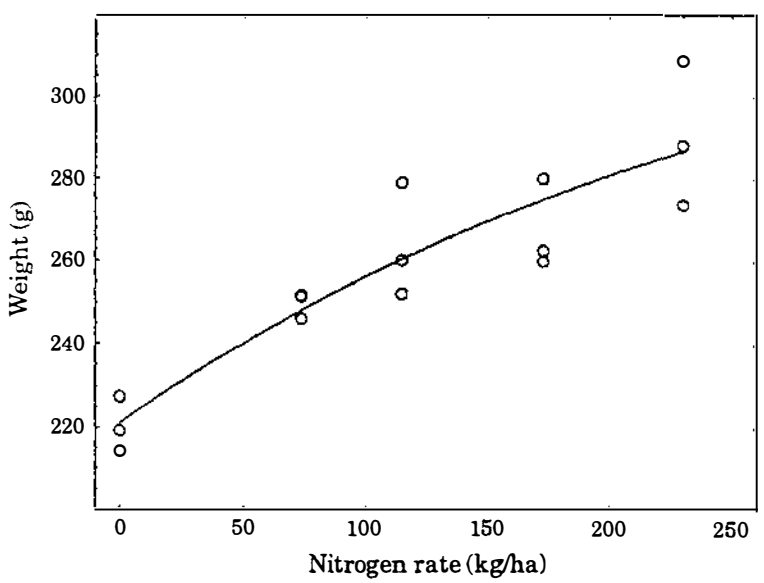

Fig. 4.13. Weight of primary cobs of Jubilee as affected by N rate. Data are the means for each N rate and block. Fitted function is $Y=340.0-118.82e^{-0.004X}$ ($R^2_{adj}=0.78$).

4.3.2.5 Marketable kernel yield

Marketable kernel yield increased as N rate increased to 114 kg/ha before declining (Fig. 4.14). This parabolic response was similar to the response exhibited by ear yield (Fig. 4.10). With maximum kernel yield of 8.48 (SE 1.07) tonnes recorded with 114 kg N/ha, yield was 50% higher than the control, and 52% higher than with 230 kg N/ha. While these yield differences were significant, the higher yields of 7.96 (SE 1.11) and 7.37 (SE 1.16) tonnes recorded with 74 and 172 kg N/ha, respectively, were not.

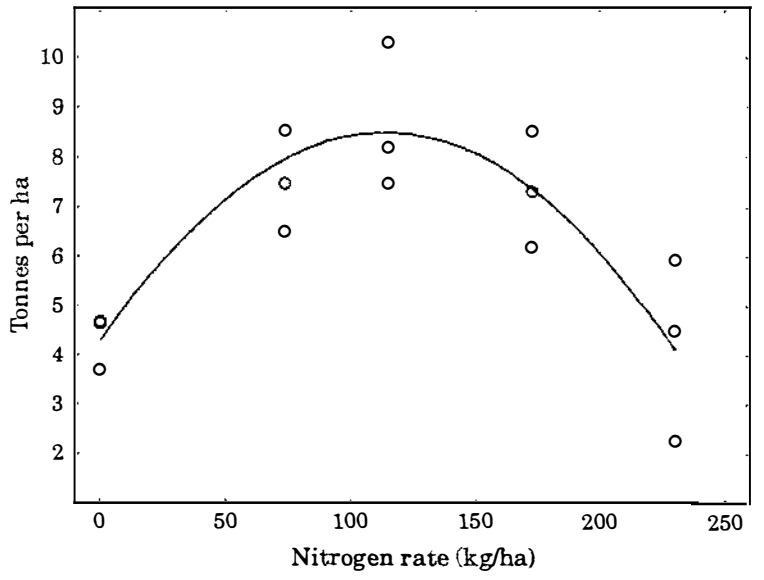

Fig. 4.14. Marketable kernel yield from primary ears of Jubilee as affected by N rate. Data are the means for each N rate and block. Fitted function is $Y=4.28+7.38\times10^{-2}X-3.24\times10^{-4}X^2$ ($R^2_{adj}=0.71$).

4.3.2.6 Marketable cob yield

As with marketable kernel yield (Fig. 4.14), marketable cob yield also exhibited a parabolic response to N rate (Fig. 4.15). Maximum yield of 16.35 (SE 1.94) tonnes with 118 kg N/ha, was 43% higher than the 9.31 (SE 1.92) tonnes recorded for the control, and 38% higher than the 10.18 (SE 2.13) tonnes recorded with 230 kg N/ha. Yield for the 115 and 172 kg N/ha treatments, on the other hand, was similar to that with 118 kg N/ha.

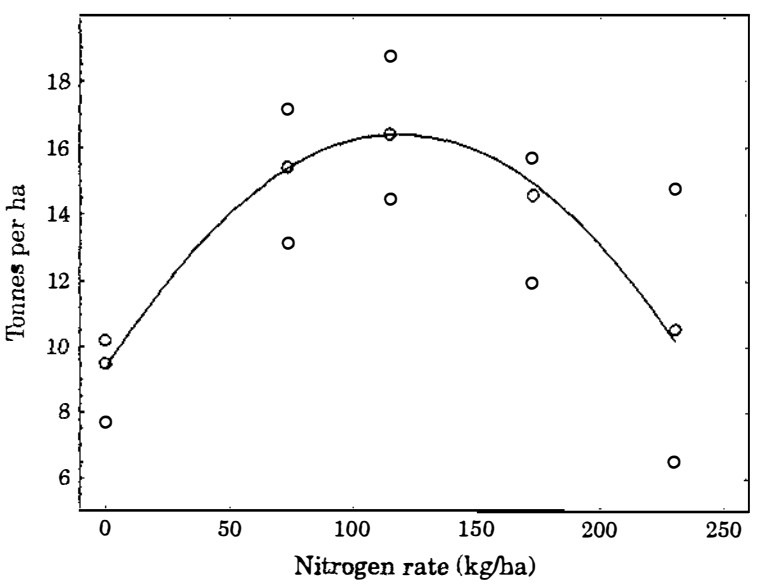

Fig. 4.15. Yield of marketable primary cobs of Jubilee as affected by N rate. Data are the means for each N rate and block. Fitted function is $Y=9.31+1.19\times10^{-1}X-5.03\times10^{-4}X^2$ ($R^2_{adj}=0.62$).

4.3.3 Cob lengths of SS42 and Jubilee

Primary cobs of SS42 carried marketable kernels consistently over 195 mm (SE 7.2) of length even with no added N fertiliser (Fig. 4.16). Adding N fertiliser significantly increased this length, with primary cobs grown with 230 kg N/ha carrying marketable kernels consistent over 215 mm (SE 6.7). However, most of this 20 mm increase was achieved at lowest N rates. Thus, while cob lengths with 74 kg N/ha were significantly greater than those of the control, they were similar to those with higher rates of N.

Unlike SS42, length of primary cobs of Jubilee was not influenced by N rate, the pooled average being 194 mm (SE 4.6). Similarly, length of secondary cobs of SS42 was not influenced by N rate, averaging 133 mm (SE 12.5).

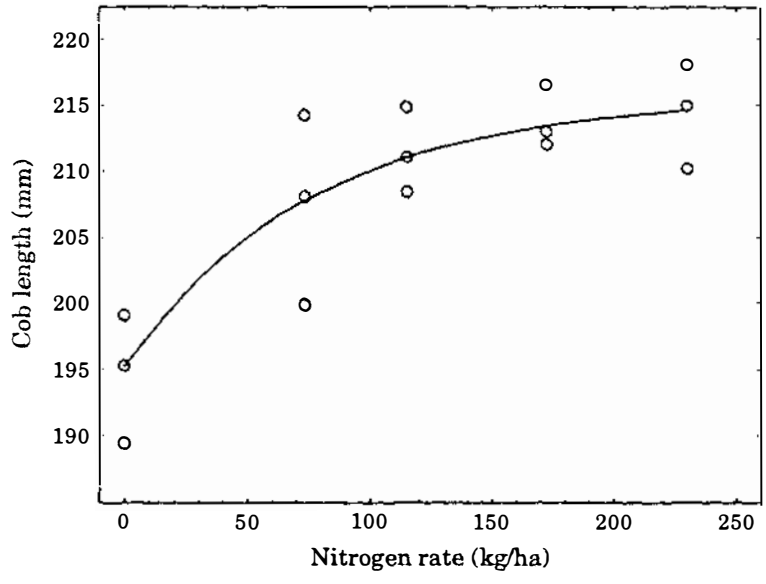

Fig. 4.16. Effect of N rate on length of primary cobs of SS42. Data are the means for each N rate and block. Fitted function is $Y=215.6-20.40e^{-0.013X}$ ($R^2_{adj}=0.76$).

4.3.4 Analysis of pre-harvest variables

Heavy rainfall and high winds at R2/R3 resulted in over 95% of Jubilee plants lodging. SS42, on the other hand, having been harvested before the bad weather, had no incidences of lodging. Lodging incidences were not significantly different among the N rates.

As with lodging, none of the pre-harvest variables were influenced by N rate. A summary of the data for these variables is presented in Table 4.4.

Table 4.4. Means and standard errors for the pre-harvest variables of SS42 and Jubilee. (n=15).

Variable	SS42		Jubilee	
	$\bar{x}$	SE	$\bar{x}$	SE
Tillers per plant	1.7	0.05	2.1	0.06
Stalk diameter (mm)	21.7	0.35	22.1	0.58
Number of ears which 'silked'	1.9	0.17	1.7	0.19
Silk delay; primary ear (days)	1.1	0.16	1.0	0.09
Silk delay; secondary ear (days)	3.0	0.27	4.3	0.20

4.3.5 Commercial validation of the optimum density

While ear and cob weights were influenced by density, yield and SMC were not (Table 4.5). As cob and ear weights declined with density, fewer cobs met marketability criteria. Those cobs discarded for the 51,000 plants per hectare treatment appeared to be secondary cobs, whereas at 96,610 plants per hectare the discards appeared to under-sized primary cobs. As fewest cobs were discarded for the 68,350 plants per hectare treatment, highest estimated recovery was observed for this density. This was supported by results of normal factory processing in which highest recoveries were also with 68,350 plants per hectare.

Table 4.5. Commercially important yield and yield components for SS42 as influenced by density.

Variable	Plants per hectare		
	51,000	68,350	96,610
Yield (t/ha)	21.66	21.81	21.57
Seed moisture content (%)	76.3	77	76.9
Ear weight (g)	321 (11.8)[z]	317 (8.0)	274 (10.0)
Cob weight (g)	261 (9.9)	269 (6.6)	231 (10.9)
Number of cobs ≤ 164 g	3	0	8
Estimated recovery (%)	37.0 (3.5)	42.2 (3.1)	41.0 (3.4)
Actual recovery (%)	30.1	32.2	29.6

[z] Brackets represent SE (n=40)

4.4 Discussion

Nitrogen fertiliser almost doubled marketable cob and kernel yields in many instances (e.g., Figs. 4.8, 4.9, 4.14, and 4.15). Such large increases were consistent with the numerous studies investigating the yield × N rate relationship for sweet corn (Dolan and Christopher, 1952; Fox, 1973; Roberts et al., 1980b; Rudert and Locascio, 1979; Salardini et al., 1992; Sanmaneechai et al., 1984; Smith, 1984; Taber and Cox, 1983; Yodpetch and Bautista, 1984).

Although marketable cob yield increases in the order of 7-8 tonnes (Figs. 4.9a and 4.15) were achieved with N fertiliser, the greatest response in this and many other instances, was with lowest rates of N (Figs. 4.3-4.15). This trend, consistent with other studies on sweet corn and maize (Sanmaneechai et al., 1984; Smith, 1984; Taber and Cox, 1983) was suggested by Donald (1963) to result from N most limiting growth at low N fertility. At higher fertility levels other factors (e.g., moisture (Fulton, 1970)) limit yield. Thus, significant yield increases were achieved as N rate increased to 74 kg/ha, but not with higher N rates. After taking account of the 92 kg N/ha supplied by the soil (Table 4.1), maximum yield was attained with 166 kg N/ha. This result is

consistent with the previous study (Chapter 2) in which 259 kg/ha of soil available N appeared to mask the effect of N fertiliser. Combining the two year's results suggests that maximum yield may be achieved when soil available N is 213 kg N/ha (i.e., the average of the levels of N above which no further significant response to N rate was recorded in the two studies). This is consistent with Tsai et al.'s (1992) suggestion that when soil available N is ≥ 175 kg/ha, yield response to fertiliser N will be limited.

Soil tests prior to planting aimed to select a site with low levels of soil available N. Despite sampling to 150 mm, it is possible that roots extended below this depth. Penetrating deeper would have enabled roots to extract N unaccounted for in sampling (Durieux et al., 1994; Gass et al., 1971). Fox et al. (1953) reported roots to penetrate to 2.4 m in a sandy soil, while roots in Linscott et al.'s (1962) study were found at 1.2 m in a silty clay loam. Equally plausible is the hypothesis of Jenkinson et al. (1985) that fertilizer N may have stimulated mineralization of N through a priming effect. While there may be many explanations for the limited response to N, results of both the current and previous study (Chapter 2) strongly suggest that in the absence of mineralizable N tests, some growers in Gisborne are applying fertilizer N in excess of crop requirements. With the potential to increase grower profit and reduce ground water pollution through reducing fertiliser applications, further research to investigate the relationship between soil available N and yield is warranted.

An objective of the current study was to compare the yield response of Jubilee and SS42 to N rate. However, a high incidence of lodging for Jubilee (> 95%; Section 4.3.4) as well as different incident radiation levels confounded results making it difficult to compare the cultivars. If Jubilee was more sensitive to N rate than SS42, yield of SS42 would have plateaued (i.e., became maximum) at a lower N rate than for Jubilee. This only occurred for ear and cob weights (cf. Figs. 4.6 with 4.12 and 4.7 with 4.13). In these instances ear and cob weights of Jubilee continued to increase, even with 230 kg N/ha, while they plateaued for SS42 at N rates greater than 74 kg/ha. Although this evidence suggests that Jubilee requires more N for maximum yield than SS42, it is not strong. However, results from both the current and previous studies (Chapters 2 and 3) collectively suggest that yield of Jubilee is more responsive to soil N fertility than that of SS42.

In the numerous studies which have reported cultivar differences in the response to N rate (Dalby and Tsai, 1975; Eghball and Maranville, 1991; Friedrich and Schrader, 1979; Pollmer et al., 1979; Reed and Hageman, 1980; Smith, 1934; Tsai et al., 1978b, 1992) a common explanation for such differences was a difference in sink strength of the cultivars. Chapter 3 confirmed that kernels of Jubilee and SS42 differ in their sink strength not only for DM but also for N (Fig. 3.13). Such higher sink strength may be attributed to Jubilee (*su1* mutant) accumulating significantly more zein (a hypothesised measure of sink strength; Russelle et al., 1983; Tsai et al., 1978a, 1980) than SS42 (*sh2* mutant). As zein synthesis dramatically responds to N supply (Frey, 1951; Keeney, 1970; Rendig and Broadbent, 1979; Sauberlich et al., 1953; Schneider et al., 1952; Tsai et al., 1978a, 1980, 1983), the differential response of Jubilee and SS42 to N rate may reflect the higher demand for N. Further research would be required to verify this hypothesis.

While yield data for SS42 correlate well with those of the previous study at the same density (e.g., cf. Figs. 4.3 and 2.4) data for Jubilee do not. These inconsistent results for Jubilee are likely due to there being fewer secondary ears of a harvestable size. Only 1% of secondary ears were harvestable in the current study (Section 4.3.2) compared to 19% in the previous study (Table 2.5). Although plants still carried secondary ears, they were too small for mechanical harvesting (i.e., they were less than 150 mm and less than 40 mm wide).

Reduced size of secondary ears of Jubilee may be due to damage incurred from severe lodging at R2/R3. Heavy rainfall combined with high winds resulted in over 95% of Jubilee plants lodging. High incidences of lodging were reported in studies by Genter and Jones (1970) and Robertson et al. (1968), but only those of Hume and Campbell (1972) and Krantz and Chandler (1951) have reported lodging to restrict ear development. Hume and Campbell (1972) attributed such restricted ear growth to the physical damage to roots and leaves incurred during lodging. While plants in the current study also exhibited similar damage, in laying almost parallel to the ground, leaves on one side of the plant were almost completely shaded. With damage and shading reducing the photosynthetic capacity of the plant (Andrade et al., 1993a; Cirilo and Andrade, 1994; Early et al., 1967), as well as impairing other physiological processes (e.g.,

nutrient and water uptake; Jackson et al., 1980; Lizaso and Ritchie, 1997; Yoshida, 1972) the reduced size of secondary ears observed is likely the consequence.

While the size of secondary ears was reduced with lodging, the size of primary ears was not obviously affected. This observation is evidenced by the number of plants barren for the primary ear generally being similar to that of the previous study (cf. Tables 4.2, 4.3, 2.2 and 2.4). With levels of secondary ear barrenness notably higher (cf. Section 4.3.2.1 and Table 2.5), however, suggests that stress is more likely to impact on the secondary ear than the primary ear. Other workers concluding similarly (Jacobs and Pearson, 1991; Otegui, 1997; Tetio-Kagho and Gardner, 1988b) suggested that ear priority for photoassimilate is in the order of ear 1 > ear 2 > ear 3 (Tetio-Kagho and Gardner, 1988a; Tollenaar, 1977). Consequently, reduced size of secondary ears is attributed to the dominance of the primary ear (Bauman, 1960; Durieux et al., 1993; Harris et al., 1976; Pinthus and Belcher, 1994; Prine, 1971) for attracting photoassimilate under the stress conditions imposed by lodging.

The dominance of the primary ear for attracting photoassimilate may explain, in part, the longer cob lengths observed for primary ears than secondary ears (Section 4.3.3). Whereas primary cobs, even for the control N treatment carried marketable kernels over 180 mm of length (the defining length for whole-cob corn), secondary cobs carried marketable kernels over only 130 mm. With primary cobs suitable for whole cob corn, yet secondary cobs were not, casts doubt on whether the conclusion drawn in Chapter 2 that 69-77,000 plants per hectare is the optimum density range for marketable cob yield.

Both primary and secondary cobs were longer than presented in Section 4.3.3. as nonmarketable kernels were not included in the measurement. Nonmarketable kernels generally reflect kernels that have aborted, the result of an inadequate photoassimilate supply (Early et al., 1967; Frey, 1981; Jones and Simmons, 1983; Reed et al., 1984, 1988; Schoper et al., 1982; Tollenaar and Daynard, 1978a). Reed and Singletary (1989) suggest that while the photoassimilate supply influences kernel abortion, the influence is indirect as it does not initiate the abortion process (Tollenaar and Daynard, 1978b). Rather, studies with in vitro kernel culture (Hanft et al., 1988) and on ears of field grown maize (Dill et al., 1987) have shown that ethylene induces kernel

abortion. Since ethylene is generated in the ear when silks/ovules are pollinated (Dill et al., 1987), ethylene may initiate abortion of slower growing kernels at the ear tip (Reed and Singletary, 1989). Increased length of marketable kernels on primary cobs with N rate is therefore consistent with these N treatments preserving the photosynthetic capacity (Gifford, 1987; Greef, 1994) and thus maintaining a high photoassimilate supply. Greater kernel abortion for secondary ears than primary ears, on the other hand, is consistent with being less competitive for photoassimilate as discussed earlier.

Levels of barrenness were generally consistent with the previous study, although the 172 and 230 kg N/ha treatments for Jubilee were an exception. Compared to the previous study (Chapter 2) where 88% of plants carried a harvestable primary ear (Table 2.4), only 75% were of a harvestable size for the 172 kg/ha treatment, and only 60% for the 230 kg N/ha treatment (Table 4.3). In contrast, over 91% of plants in the 74 and 115 kg N/ha treatments carried a harvestable ear (Table 4.3). The greater incidence of barrenness for these treatments may be attributed to a greater susceptibility to, and increased damage from lodging. Enhanced N fertility is associated with heavier ears (Figs. 4.6 and 4.12; Durieux et al., 1993; Mack, 1972; Moss and Mack, 1979), which tends to make plants 'top heavy', and thus more susceptible to lodging (Below et al., 1984; Campbell, 1964; Krantz and Chandler, 1951). With the 172 and 230 kg N/ha treatments likely being associated with heavier ears at R2/R3, plants in these treatments (presumably those which were later deemed barren) may have made them more susceptible to lodging. Moreover, damage to roots during the lodging process for these treatments may have been more severe through more vigorous plant movement. A high incidence of barrenness for the control N treatment of Jubilee (Table 4.3), on the other hand, was probably due to N stress as found by Swank et al. (1982) rather than a direct effect of lodging.

Not only were the two highest N rates of Jubilee associated with greater barrenness but also depressed yields. Examining Figs. 4.10, 4.14, and 4.15 may initially suggest that high N rates caused a N toxicity, thereby inhibiting yield. However, a toxic effect would have reduced the weight of primary ears, cobs, and kernel recoveries. As these yield components increased with N rate (Figs. 4.11-4.13), the decreased yields observed for the 172 and 230 kg N/ha treatments are attributed to greater damage from lodging leading to barrenness rather than N toxicity.

Although ear and cob weights of Jubilee were consistent with the previous year's results (cf. Figs. 4.12 with 2.13a and 4.13 with 2.14a), kernel recoveries from primary cobs were about 13% lower (cf. Figs. 4.11 and 2.12a). A lower recovery may have resulted from kernels having a lower sink strength. Sink strength, which appears to be associated with zein accumulation (Russelle et al., 1983; Tsai et al., 1978a, 1980), may have been reduced due to a limited supply of N. With lodging damaging vascular bundles involved in the movement of absorbed nutrients (Yoshida, 1972), the supply of N for zein accumulation (Rendig and Broadbent, 1979; Schneider et al., 1952; Tsai et al., 1978a, 1980) may have been limited. Reduced zein accumulation may also explain the lower biomass of secondary ears. Further research would be required to test this hypothesis, however. As similar cumulative levels of incident radiation were received by Jubilee in each of the two experiments differences in kernel recoveries were not attributed to this variable.

The only yield variable for SS42 inconsistent with the previous study (Chapter 2) was kernel recovery from secondary ears. Depending on N rate, recoveries were up to 45% lower (cf. Section 4.3.1.3 and Fig. 2.5b), despite secondary ears and cobs being of similar weight with the previous study (cf. Section 4.3.1.4 with Figs. 2.6b and 2.7b) and a greater amount (20%) of solar radiation intercepted. Such low recoveries resulted in only 11% of secondary ears meeting marketability criteria, four-fold fewer than the previous study (cf. Sections 4.3.1.3 and 2.3.1.3). Lower recoveries in the current study may have resulted from moisture stress. Between R1 and R4 only 41 mm of rain fell, with only 5 mm falling during the two weeks prior to R1 (Fig. 4.1b). In contrast, 119 mm fell between R1 and R4 for SS42 in 1996, with a further 63 mm falling during the week prior to R1 (Fig. 2.1b). The correlation between reduced water availability and lower recoveries suggests that plants in the current study were moisture stressed between R1 and R4. Moreover, with moisture stress imparting an effect primarily on kernels suggests they are more sensitive to moisture stress than other ear components. Many workers have concluded that R1 is the most sensitive stage for moisture stress because this is when embryo fertilization and enlargement occur, both of which may be severely inhibited by moisture stress (Frederick et al., 1990; Herrero and Johnson, 1981; Shaw, 1974; Westgate and Boyer, 1986). Inhibited development leads to both reduced kernel number and biomass (Chotena et al., 1980; Claassen and Shaw, 1970; Frederick et al., 1990; Harder et al., 1982; Schussler and Westgate, 1994;

Thompson, 1988). However, with moisture stress reported to reduce the number of ears which 'silk' (Earley et al., 1974; Prine, 1971), yet the number of ears which silked was similar between the two studies (cf. Table 4.4 and Fig. 2.22b) suggests that any moisture stress influenced secondary ears during grain filling. Similarly, with silk delays for both primary and secondary ears of SS42 consistent with the previous study (cf. Table 4.4 with Fig. 2.20), despite reports that silk delay increases with moisture stress (Barnes and Woolley, 1969; Bennett et al., 1989; DuPlessis and Dijkhuis, 1967; Edmeades et al., 1993), further suggests that any moisture stress influenced grain filling rather than kernel set.

Due to the lack of replication of the commercial trial, inference from this data is limited. Nevertheless, data presented in Table 4.5 support the conclusion drawn in Chapter 2 that the density range of 69-77,000 plants per hectare is optimum for marketable yield of cobs and kernels. Support comes from both the actual and estimated kernel recoveries being highest with 68,350 plants per hectare. Further, with all 40 ears sampled meeting marketability criteria at this density indicates that marketable cob yield would also have been highest at this density. It also suggests that processors may be advantaged through reduced waste and, perhaps, a more consistent product. With kernels from secondary ears generally having a higher SMC than those from primary ears, a greater consistency would arise from their lower contribution to total yield within the 69-77,000 plants per hectare density range (Fig. 2.9).

This study has not only highlighted the need to further investigate the relationship between soil available N and yield, but raised important questions regarding the physiology associated with these responses. In particular, questions concerning sink strength in these genotypes and how this relates to N and DM partitioning to kernels remain unanswered. By further investigating source-sink relationships in these genotypes, hypotheses proposed in this discussion may be further elucidated.

Chapter 5

Nitrogen and dry matter partitioning in sweet corn

5.1 Introduction

High economic yield of grain depends on efficient translocation of assimilates to kernels (Koch et al., 1982). Thus, economic yield of a given corn genotype depends on sink size per plant, photoassimilate supply, and efficient partitioning of N and DM to kernels (Anderson et al., 1984a). Frequently, however, kernel sink strength for DM is limiting (Below et al., 1981, 1984; Cliquet et al., 1990b; Poneleit and Egli, 1979; Reed et al., 1988; Swank et al., 1982; Tollenaar, 1977). Such limitation is indicated by DM being partitioned to the stem and husks during reproductive growth (Campbell, 1964; Fairey and Daynard, 1978a, 1978b; Hume and Campbell, 1972; Uhart and Andrade, 1995a; Wilson and Allison, 1978b). The observation that DM was partitioned to the stem and husks of Jubilee and SS42 during reproductive growth (Chapter 3) therefore indicates that kernel sink strength was limiting in these cultivars. Source strength for newly assimilated N was also limiting for these cultivars. This conclusion was drawn from the observation that during reproductive growth N was remobilised from vegetative organs. Although numerous workers have reported similar source and sink limitations (Below et al., 1981, 1984; Cliquet et al., 1990b; Hanway, 1962a, 1962b; Lemcoff and Loomis, 1986; Maddonni et al., 1998; Poneleit and Egli, 1979; Reed et al., 1988; Swank et al., 1982; Tollenaar, 1977), most have considered the limitations as independent events. Chapter 3 provided evidence that the two events may be linked through what was termed an inhibitory cycle. This cycle stems from the premise that the reproductive organs (in particular, kernels and rachis) have a limited capacity to accumulate photoassimilate during early grain filling.

Maximum leaf area in maize and sweet corn is reached around R1 (Alofe and Schrader, 1975; Muchow, 1988; Uhart and Andrade, 1995b) and coincides with maximum carbon fixation (Prioul et al., 1990). However, at this ontogenetic stage, the ear is a relatively weak sink (Edmeades and Daynard, 1979a; Prioul et al., 1990; Setter and Meller, 1984; Schussler and Westgate, 1991a), and hence unable to accumulate all the photoassimilate being produced (Tanaka and Yamaguchi, 1972). Although the excess is partitioned to stems and husks, these organs can only accumulate a limited quantity before they become saturated. In Barnett and Pearce's (1983) study, stem reserves were saturated in only 6-12 days after ear removal. When the stem and husks become saturated, photoassimilate may accumulate in leaves (Farrar and Gunn, 1996; Thomas and

Stoddart, 1980), causing feedback inhibition of photosynthetic enzymes (Neales and Incoll, 1968) to reduce the supply of photoassimilate (Thomas and Stoddart, 1980). However, N assimilation rate is dependent on the rate of photoassimilate supply to roots (Pan et al., 1995). Thus, inhibited photosynthesis reduces N uptake (Karlen et al., 1988; Wild and Breeze, 1981), and as a consequence, remobilisation of N is stimulated (Hageman, 1986; Reed et al., 1988). Excessive remobilisation of N from leaves may impair photosynthetic activity (Hageman, 1986; Muchow, 1988; Sinclair and deWit, 1976; Swank et al., 1982), thereby restricting photoassimilate supply for root and shoot functions including grain filling (Hageman, 1986). Hence, an inhibitory cycle may evolve from the limited capacity of kernels and rachis to accumulate photoassimilate.

This proposed sequence of events is consistent with studies on sweet corn and maize (Fakorede and Mock, 1978; Geiger, 1976; Huelsen, 1954; Koch et al., 1982; Tanaka and Yamaguchi, 1972; Tollenaar, 1977; Treat and Tracy, 1994) as well as other crops (e.g., soybean (Clough et al., 1981; Mondal et al., 1978) and barley (Natr et al., 1974)) which suggest that the production, translocation, and partitioning of photoassimilate is influenced by the sink capacity of reproductive organs. Koch et al. (1982) suggested that decreased translocation of photoassimilate from leaves of endosperm mutants was due to starch accumulation (Geiger, 1979; Thorne and Koller, 1974) caused by an inadequate sink. Conversely, the low rate of starch accumulation and effective translocation out of source leaves of non-mutants was attributed to their higher sink strength (Tripathy et al., 1972), consistent with Greenwood's (1976) suggestion that bigger sinks demand more assimilate. In Chapter 3 the greater kernel sink strength of the *su1* mutant was speculated to result from photosynthetic rates being less inhibited by excess photoassimilate than for the *sh2* mutant.

Sink strength is associated with the level of the kernel storage protein zein (Tsai et al., 1978a, 1980). The contention that the level of zein may influence kernel sink strength is supported by observations that kernels of zein deficient mutants accumulate significantly less DM than wild types (Tsai et al., 1978b). In *su1* and *sh2* mutants kernel DM contents were reported by Tsai et al. (1978b) to be 27 and 57% lower than the wild type, respectively, corresponding to a 17 and 62% decrease in zein content, respectively.

As *sh2* and *su1* mutants substantially reduce zein content relative to their normal counterparts (Dalby and Tsai, 1975; Ma and Nelson, 1975; Mertz et al., 1964; Misra et al., 1972, 1975a; Nelson et al., 1965; Tsai et al., 1978b), they provide a valuable tool for elucidating the physiology of source-sink relationships. As Koch et al. (1982) pointed out, there are several advantages to using plants with mutations affecting sink metabolism. First, mechanical manipulation of source or sink tissues is avoided, thus avoiding atypical changes in the hormonal balance (Hew et al., 1967) or impaired phloem transport (Gersani et al., 1980). Second, inhibitors are not used, thus avoiding other secondary effects (Wardlaw, 1980). Third, the *sh2* mutation only affects the activity of *ADP-glucose pyrophosphorylase* in the endosperm (Preiss et al., 1981) and does not affect activity in the embryo, or sporophytic generation (Koch et al., 1982). For this reason, differences in photoassimilate partitioning for plants carrying the *sh2* mutation would result from reduced zein and starch synthesis in the endosperm, rather than a genetic change in the source leaf (Koch et al., 1982). While such localized activity has not been confirmed for *su1* mutants (Doehlert et al., 1993), localized activity was suggested in Treat and Tracy's (1994) study, and hence is assumed here.

Zein becomes increasingly abundant in the endosperm as soil N fertility increases (Rendig and Broadbent, 1979; Schneider et al., 1952; Singletary and Below, 1989; Tsai et al., 1978a, 1980, 1983, 1984; Wolfson and Shearer, 1981), and as a consequence, potential sink strength also increases (Tsai et al., 1980, 1984). However, an excessively strong sink may be detrimental to yield (Moll et al., 1994; Pan et al., 1984; Raper et al., 1978) because it reduces the photoassimilate available for N assimilation. As the rate of N assimilation is dependent on the rate of photoassimilate partitioning to roots (Pan et al., 1984) there is an inverse relationship between reproductive sink size and the quantity of photoassimilate partitioned to roots (Pan et al., 1995). Hence, N assimilation may be limited more by the amount of photoassimilate partitioned to roots than the availability of N in the soil (Pan et al., 1984; Reed et al., 1988). Allison (1984) showed that removal of laminae significantly reduced the photoassimilate supply and resulted in significantly less N being assimilated.

As zein accumulation is dependent on N supply (Tsai et al., 1990), continued N uptake during ear development is critical for maximising yield (Friedrich and Schrader, 1979; Moll et al.,

1982a; Pan et al., 1984). A deficiency of soil N, while restricting the amino acid supply for zein accumulation (Tsai et al., 1990), may also cause a premature termination of photosynthesis to affect kernel DM accumulation (Tsai et al., 1985). This termination may result from severe proteolysis of leaf proteins as N is remobilised (Tsai et al., 1986), and as such, will begin earlier under severe N deficiency (McClung et al., 1990; Weiland and Ta, 1992). Severe proteolysis may even stimulate an early onset of senescence (Pan et al., 1984; Sinclair and DeWit, 1976; Swank et al., 1982; Wolfe et al., 1988a). However, Hay et al. (1953) and Sayre (1948) found that hybrids continued to remobilise N despite high soil N fertility. Such a response may be consistent with the inverse relationship between reproductive sink size and the quantity of photoassimilate partitioned to roots (Pan et al., 1995). Palmer et al. (1973) found that by partially fertilizing the ear to reduce reproductive sink size that the translocation of photoassimilate to the root was enhanced. Thus, while N assimilated prior to R1 may later comprise most of the N in the ear (Anderson et al., 1984b; Crawford et al., 1982; Friedrich and Schrader, 1979; Pan et al., 1984, 1986; Reed et al., 1980) continued N assimilation during grain filling is fundamental to maximising yield.

The amount of corn grain produced per unit of fertiliser N depends not only on the accumulation of fertiliser- and soil-N in the plant but also on the utilization of this N in producing grain (Beauchamp et al., 1976; Pollmer et al., 1979). Together, these components determine how efficiently fertiliser N is used to produce grain (Kamprath et al., 1982; Moll et al., 1982a) and thus can be used to compare hybrids (Moll et al., 1987; Rhoads and Stanley, 1984). Chapter 3 demonstrated that Jubilee was significantly more efficient than SS42 at translating fertiliser N into kernel DM. While a higher sink strength and a larger root system were implicated as being responsible for Jubilee's greater efficiency, the inhibitory cycle theory may offer an alternative explanation. That is, the greater NUSE of a genotype may be a consequence of a higher uptake efficiency through greater DM partitioning to roots for N acquisition. The objective of this study was, therefore, to further elucidate the physiology of N and DM partitioning to kernels by understanding the influence of N nutrition on the source-sink relationships of a *sh2*, *su1*, and a normal maize genotype.

5.2 Materials and methods

5.2.1 Cultural

Data presented in this chapter were derived from the experiment described previously (Section 4.2). In addition, data from the maize cultivar Furio (*Zea mays* 'Furio'), which has a similar ontogeny to SS42 and Jubilee, were included. Furio was grown under the same conditions as Jubilee and SS42 until R4 (72% SMC), the ontogenetic stage at which kernels of sweet corn are generally considered 'too old' for processing.

5.2.2 Plant sampling

Three plants from each of the 0, 115, and 230 kg N/ha plots were removed at sequential ontogenetic stages (Table 5.1). Soil was shaken from roots and the remainder removed with water. Plants were fractioned immediately after harvesting into laminae, stem (including leaf sheaths and tassel), shank, husk, kernels, cobs, and roots. Roots were severed at the root crown. Fractioned material was stored at -18 C. At three specified stages (Table 5.1), only ears were harvested to permit a more detailed account of the ontogenetic changes in ear components.

5.2.3 Tissue analysis

Tissue was dried to constant weight in a forced air oven at 80 C. Dried cobs were fractioned into kernels and rachis. Tissue was weighed, sub-sampled, and a 15 g sub-sample ground to pass a 0.5 mm screen. The concentration of N in each fraction was determined from a 0.1 g sample using the semi-micro Kjeldahl method (Bremner, 1960).

Table 5.1. Relationship between accumulated GDD and ontogenetic stage.

SS42		Jubilee		Furio	
Ontogenetic stage	Accumulated GDD	Ontogenetic stage	Accumulated GDD	Ontogenetic stage	Accumulated GDD
V3	346	V4	412	V4	269
V7	530	V7	532	V7	464
V12	700	V13	727	V13	653
R1	877	R1	828	R1	846
R2[z]	939	R2[z]	956	R2	980
R2/R3	1061	R2/R3	1053	-	-
R3[z]	1172	R3[z]	1187	R3[z]	1072
R4	1323	R4	1242	R4	1253

[z] Only ears were harvested

5.2.4 Data analysis

Data for SS42, Jubilee, and Furio were combined to test genotypic differences. Pooling was possible because the cultivars were at a similar ontogenetic stage and GDD at each harvest (Table 5.1). However, a missing harvest for Furio at R2/R3 meant that the data set was incomplete. To achieve a complete data set, the harvest at R2 for Furio was reclassified as R2/R3. As reclassifying this harvest may have influenced results, data were analysed both with and without this harvest. When pooling the data sets, data for each cultivar were standardized to rate of N or DM accumulation per GDD. However, in doing this, genotypic differences become confounded with differences in incident radiation levels (2362 $MJ \cdot m^{-2}$ for SS42, 1925 $MJ \cdot m^{-2}$ for Jubilee, and 1788 $MJ \cdot m^{-2}$ for Furio). To determine the effect of this confounding influence, data were analysed using regression analysis with dummy variables as described in Sections 2.2.6 and 3.3.18. In addition, both raw and standardized data were analysed as a randomised complete block design (i.e., a factorial arrangement of three N rates and three cultivars in three blocks) by ANOVA. Both raw and standardized data were analysed to check whether differences in accumulated GDD influenced results. As analyses on raw and

standardised data provided similar results only results from analysis of raw data are presented. For ease of discussion, ontogenetic stages in Table 5.1 were classified as V3, V7, V13, R1, R2, R2/R3, R3, and R4 for the pooled data set.

Nitrogen use efficiency components, partitioning coefficients, and the source of DM or N within ontogenetic stages were calculated as previously described (Section 3.2.4). Partitioning coefficients were only calculated for harvests where entire plants were harvested (Table 5.1). Otherwise data analysis procedures were identical to those described in Section 3.2.4.

5.3 Results

5.3.1 Nitrogen use efficiency and component traits

Furio was significantly more efficient than both Jubilee and SS42 at using N fertiliser (Table 5.2). Compared to SS42, Furio was 49% more efficient at converting applied N into kernel DM, and 23% more efficient than Jubilee. Jubilee was also significantly more efficient (34%) than SS42 at using N fertiliser. As NUSE is a function of NUPE and NUTE, the greater efficiency of Furio was due to being both significantly more efficient at taking up N and translating this N into kernel DM. Furio was about 27% more efficient than SS42 at each of these tasks. Increasing N rate was, however, associated with significant declines in NUSE for all three cultivars (Table 5.2). Averaged across cultivars, NUSE declined 36% as N rate increased from 115 (1.64 g·plant^{-1}) to 230 kg N/ha (3.28 g.plant^{-1}). This decline was due to a significant decrease in uptake efficiency. Averaged across cultivars, plants in the 230 kg N/ha treatment took up fertiliser N 43% less efficiently than those in the 115 kg N/ha treatment. Nitrogen rate did not influence the efficiency with which endogenous N was translated in kernel DM.

Table 5.2. Effect of N rate on N use efficiency and efficiency components for Jubilee, SS42, and Furio.

Source of variation		NUSE[z]	NUPE[y]	NUTE[x]
			P > *F*	
Cultivar		**	*	*
N rate		**	***	NS
Cultivar × N rate		NS	NS	NS
Means	N rate (g·plant^{-1})	NUSE	NUPE	NUTE
SS42	1.64	19.8	1.78	11.6
	3.28	10.7	0.98	11.0
Jubilee	1.64	27.9	2.04	13.8
	3.28	18.3	1.37	13.5
Furio	1.64	35.9	2.38	15.1
	3.28	24.1	1.42	16.9
5% LSD		5.6	0.28	3.8

NS, *, **, ***; Nonsignificant or significant *F* test at $P \leq 0.05, 0.01, 0.001$, respectively.
[z] Nitrogen use efficiency
[y] Nitrogen uptake efficiency
[x] Nitrogen utilization efficiency

Variation in NUSE was due primarily to NUTE (Table 5.3), with the proportion of variability explained by NUTE increasing as N rate increased. With 115 kg N/ha, NUTE explained about 79% of the variability in NUSE, but over 89% with 230 kg N/ha. Although SS42 and Jubilee had a significantly lower NUSE than Furio (Table 5.2), the proportion of variability explained by NUTE at each N rate was similar among the cultivars. The 230 kg N/ha treatment of SS42 was an exception, however, as NUTE explained all of the variability in NUSE.

Table 5.3. Contribution of efficiency components to variation in N use efficiency for Jubilee, SS42, and Furio.

Cultivar	N rate ($g \cdot plant^{-1}$)	Efficiency trait		
		NUSE[z] (Y)	NUPE[y] (X_1)	NUTE[x] (X_2)
		---------- $\sum X_i Y / \sum Y^2$ ----------		
Jubilee	1.64	-	0.21	0.79
	3.38	-	0.11	0.89
SS42	1.64	-	0.19	0.81
	3.38	-	0.00	1.00
Furio	1.64	-	0.24	0.76
	3.38	-	0.11	0.89

[z] Nitrogen use efficiency
[y] Nitrogen uptake efficiency
[x] Nitrogen utilization efficiency

As N rate did not influence partitioning coefficients between R1 and R2/R3 or between R2/R3 and R4, data were pooled across N rates. Ontogenetic changes in the N and DM content of organs from which partitioning coefficients were calculated are presented later (Sections 5.3.5-5.3.13).

5.3.2 Dry matter and N partitioning between R1 and R2/R3

All organs, except leaves of SS42, were sinks for DM between R1 and R2/R3 (Figs. 5.1a-c). Although DM was remobilised from leaves of SS42, cultivar differences were not significant. Significant cultivar differences were, however, observed for the partitioning of DM to all other organs. Stems were the dominant sink for Furio, being partitioned about 50% of available DM. This was a significantly higher proportion than partitioned by either Jubilee or SS42. With SS42 partitioning twice the proportion of DM to stems than Jubilee, this difference was also significant. Husks were the dominant DM sink for SS42 being partitioned 38% of the available

DM. This proportion was significantly greater than the 25% partitioned to those of Jubilee and Furio. Jubilee partitioned a significantly greater proportion of DM to kernels than either SS42 or Furio. Both Jubilee and SS42 partitioned significantly more DM to shanks and rachis than Furio. Compared to Furio which partitioned about 8% of the available DM to rachis, SS42 and Jubilee partitioned about 18%. Roots of both Jubilee and Furio were partitioned a significantly greater proportion of DM than those of SS42. Whereas SS42 partitioned about 1.5% of the available DM to roots, Jubilee and Furio partitioned about 5%.

The cultivars differed significantly in their partitioning of N to stems and leaves. Whereas SS42 and Jubilee remobilised N from leaves, Furio partitioned N to leaves (Figs. 5.1d-f), SS42 also remobilised N from stems, which contrasted both Furio and Jubilee. Although all three cultivars partitioned N to husks between R1 and R2/R3, husks of SS42 were partitioned a significantly greater proportion of the available N. Husks of SS42 were partitioned about 53% of the available N, compared to about 21% for Jubilee and Furio. Kernels were the only other organ for which the partitioning of N differed significantly among the cultivars. While kernels of SS42 and Jubilee were partitioned about 51% of the available N, those of Furio were partitioned about 16% of the available N. Averaged across cultivars, roots, rachis and shanks were partitioned about -3.3, 8.8, and 27% of the available N, respectively.

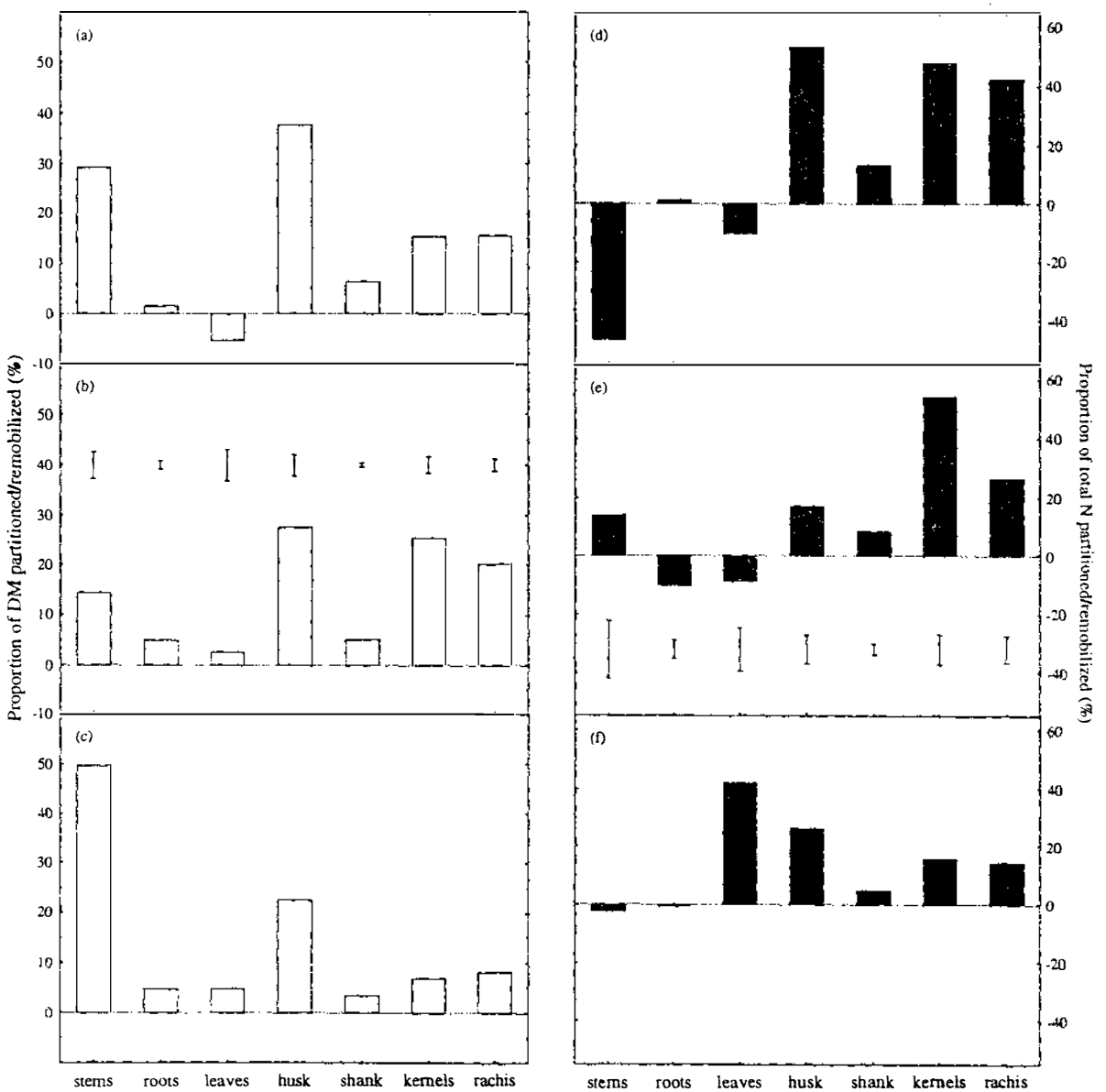

Fig. 5.1. Dry matter partitioning for (a) SS42, (b) Jubilee, and (c) Furio, and N partitioning for (d) SS42, (e) Jubilee, and (f) Furio between R1 and R2/R3. Vertical bars represent the pooled standard error for each organ (n=27).

5.3.3 Dry matter and N partitioning between R2/R3 and R4

While kernels were the dominant sink for DM between R2/R3 and R4 (Fig. 5.2a-c) the cultivars differed significantly in the proportions of DM partitioned to this organ. Whereas kernels of SS42 and Jubilee were partitioned about 84% of the available DM, those of Furio were partitioned 56%. Cultivar differences were also detected for DM partitioning to rachis, with SS42 partitioning a significantly greater proportion to this organ than either Jubilee or Furio. This high sink demand for SS42 was associated with greater remobilisation. Whereas Jubilee and Furio partitioned DM to stems, SS42 remobilised DM from this organ. The cultivars also differed for the partitioning of DM to roots. Unlike Furio which partitioned DM to roots, SS42 remobilised DM from this organ. Jubilee also remobilised DM from roots, although the proportion (about 1%) was not significantly different from either SS42 or Furio. Partitioning to leaves and shanks was also similar among the cultivars.

Kernels were also the dominant sink for N between R2/R3 and R4, with similar proportions (about 104%[5]) partitioned for all three cultivars (Fig. 5.2d-f). Partitioning to all other organs with the exception of shanks and stems was similar among the three cultivars. In contrast to SS42 and Jubilee which remobilised about 33% of the N partitioned within this period from stems, Furio neither partitioned nor remobilised N from this organ. A similar contrast was observed for shanks.

[5] Figure exceeds 100% as kernels accumulated more N than was assimilated during this period.

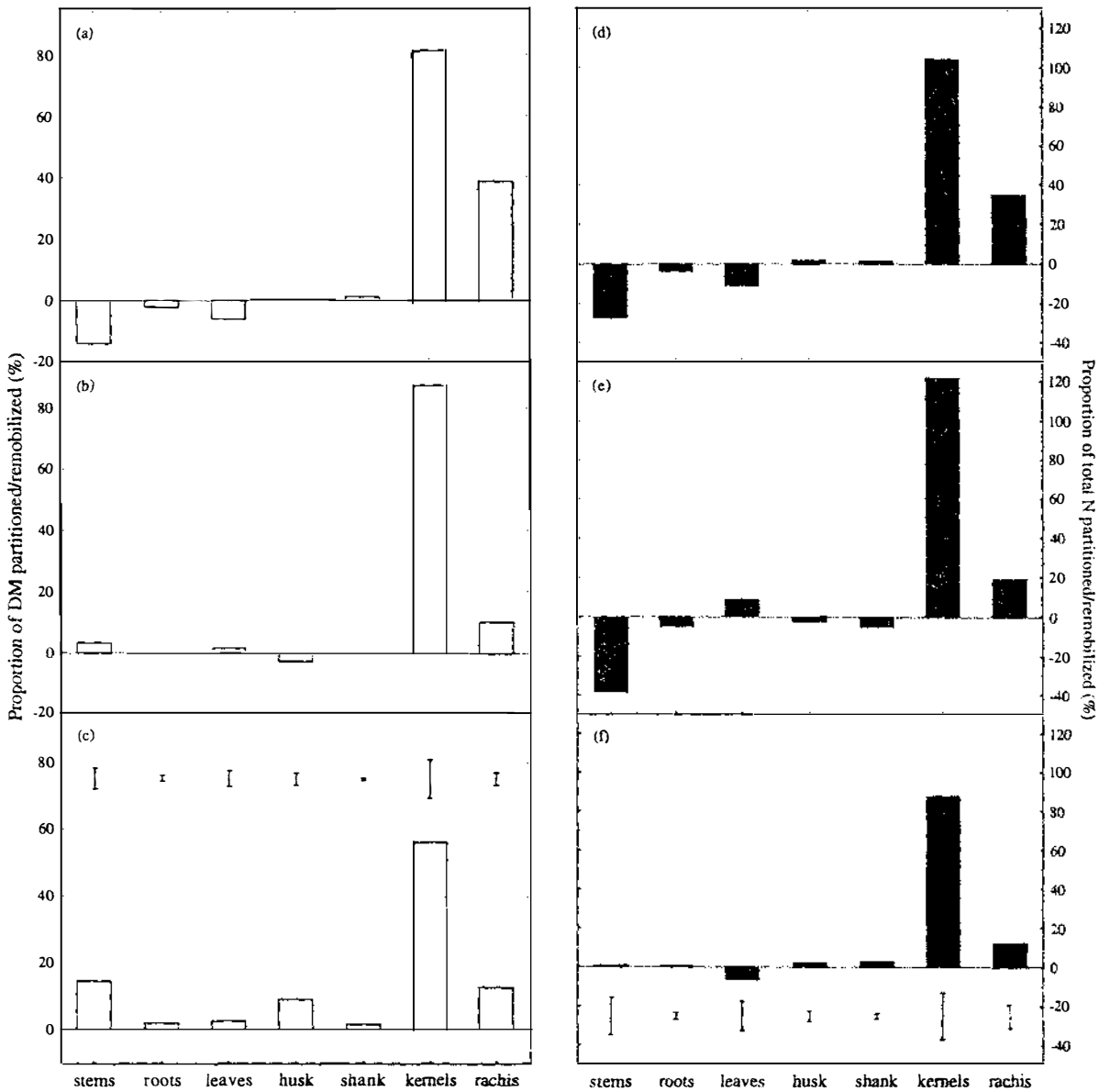

Fig. 5.2. Dry matter partitioning for (a) SS42, (b) Jubilee, and (c) Furio, and N partitioning for (d) SS42, (e) Jubilee, and (f) Furio between R2/R3 and R4. Vertical bars represent the pooled standard error for each organ (n=27).

5.3.4 Source of DM and N within ontogenetic periods

Current photoassimilate accounted for about 96% of the DM partitioned between R1 and R2/R3, irrespective of cultivar or N rate (Table 5.4). While the proportions were similar among the N rates, the actual quantities were not. Plants in the 230 kg N/ha treatment derived almost twice the quantity of DM from current photoassimilate as those of the control. Quantities of DM remobilised during this period were similar among the cultivars and were not influenced by N rate.

Table 5.4. Influence of cultivar and N rate on the quantities of DM derived from current photoassimilate and remobilisation between R1 and R2/R3.

N rate (kg/ha)	Quantity derived from remobilisation	Quantity derived from PS[z]	Proportion derived from PS
	---------- g·plant^{-1} ----------		(%)
0	1.9[y]	32.7	94.5
115	1.7	29.1	94.5
230	1.3	57.9	97.8
5% LSD	2.4	18.2	9.6
	---------- Significance levels ----------		
N rate	NS	**	NS
Cultivar	NS	NS	NS
Cultivar × N rate	NS	NS	NS

NS, *, **, ***; Nonsignificant or significant F test at $P \leq 0.05$, 0.01, 0.001, respectively.
[z] Current photoassimilate.
[y] Data were pooled across cultivars.

There was an inverse relationship between the quantity of DM remobilised and the quantity sourced from current photoassimilate between R2/R3 and R4 (Table 5.5). Generally, the higher the quantity of DM sourced from photoassimilate, the lower the quantity remobilised. However, only the quantities derived from current photoassimilate were significantly different among the

cultivars. When quantities were standardised by plant size, Furio remobilised less than 1% of DM during this period, compared to 16% for SS42. Jubilee remobilised a proportion similar to both SS42 and Furio during this period.

Table 5.5. Influence of cultivar and N rate on the quantities of DM derived from current photoassimilate and remobilisation between R2/R3 and R4.

Cultivar	Quantity derived from remobilisation	Quantity derived from PS[z]	Proportion derived from PS
	g·plant^{-1}		(%)
SS42	7.8[y]	39.8	83.6
Jubilee	4.2	50.0	92.2
Furio	1.7	110.5	99.3
5% LSD	5.7	22.4	13.7
	Significance levels		
N rate	NS	NS	NS
Cultivar	NS	***	*
Cultivar × N rate	NS	NS	NS

NS, *, **, *** Nonsignificant or significant F test at $P \leq 0.05$, 0.01, 0.001, respectively.

[z] Current photoassimilate.

[y] Data were pooled across N rates.

Newly assimilated N accounted for 91% of the N partitioned by Furio between R1 and R2/R3, significantly more than the 69% for SS42 (Table 5.6). The proportion of N derived from assimilation by Jubilee was similar to SS42 and Furio. Cultivars also differed for the quantity of N derived from newly assimilated N. Pooled across N rates, Jubilee and Furio assimilated 51% and 59% more N than SS42, respectively. The quantity of N derived from newly assimilated N also differed significantly among the N rates. Averaged across cultivars, 53% more N was derived from newly assimilated N with 230 kg N/ha than the control. Quantities of N remobilised were similar among cultivars and N rates.

Table 5.6. Influence of cultivar and N rate on the quantities of endogenous N derived from newly assimilated N and remobilisation between R1 and R2/R3.

Cultivar	N rate (kg/ha)	Quantity derived from remobilisation	Quantity derived from uptake	Proportion derived from uptake
		---------- mg·plant^{-1} ----------		(%)
SS42	0	180	324	64.3
	115	172	361	67.7
	230	153	451	74.7
Jubilee	0	125	533	81.0
	115	95	303	76.1
	230	4	1484	99.7
Furio	0	44	741	94.4
	115	152	577	79.1
	230	7	1450	99.5
5% LSD		111	390	20.5
		---------- Significance levels ----------		
N rate		NS	**	NS
Cultivar		NS	*	*
Cultivar × N rate		NS	NS	NS

NS, *, **, ***; Nonsignificant or significant F test at $P \leq 0.05, 0.01, 0.001$, respectively.

About 80% of the N partitioned between R2/R3 and R4 was from newly assimilated N (Table 5.7), regardless of cultivar or N rate. Quantities of N derived from remobilisation were also similar among the cultivars and N rates. Significant cultivar differences were, however, observed for the quantities derived from newly assimilated N. Compared to SS42, Furio assimilated 50% more N during this period. Jubilee assimilated similar proportions of N to SS42 and Furio.

Table 5.7. Influence of cultivar and N rate on the quantities of endogenous N derived from newly assimilated N and remobilisation between R2/R3 and R4.

Cultivar	Quantity derived from remobilisation	Quantity derived from uptake	Proportion derived from uptake
	mg·plant^{-1}		(%)
SS42	265[z]	818	75.5
Jubilee	363	1129	75.6
Furio	243	1638	87.1
5% LSD	251	625	22.5
	Significance levels		
N rate	NS	NS	NS
Cultivar	NS	*	NS
Cultivar × N rate	NS	NS	NS

NS, *, **, ***; Nonsignificant or significant F test at $P \leq 0.05$, 0.01, 0.001, respectively.
[z] Data were pooled across N rates.

5.3.5 Ontogenetic changes in total DM and N content

Dry matter accumulated in plants through ontogeny (Figs. 5.3a-c). Although the general pattern of DM accumulation was similar among the three cultivars, significant differences were observed from V7 onwards. At V7, SS42 contained significantly more (at least 60%) DM than either Jubilee or Furio. A varied response to N rate by the three cultivars contributed to the significant cultivar × N rate interactions observed at V13 and R1. At V13, Jubilee and SS42 contained significantly more DM than Furio. Unlike Jubilee and SS42, however, DM contents for Furio were not influenced by N rate. A similar contrast was observed at R1, but in this instance DM contents of the three cultivars were similar. The three cultivars also contained similar quantities of DM at R2/R3. At R4, on the other hand, Furio contained significantly more (at least 32%) DM than either SS42 or Jubilee. Dry matter contents at both R2/R3 and R4 were significantly increased by N rate, being about 28% higher with 230 kg N/ha than the control.

The pattern of N accumulation through the experiment was similar to that for DM (cf. Figs. 5.3a-c and 5.3d-f; r=0.79; $P<0.001$). Jubilee and SS42 contained similar quantities of N at V7, but both contained significantly more N than Furio. A similar response was observed at V13, although in this instance only Jubilee contained significantly more N than Furio. Significant cultivar × N rate interactions were detected at both R1 and R2/R3. At R1, the N contents of both Jubilee and SS42 were significantly increased with N fertiliser, while Furio showed no response. Significant increases in N content for SS42 occurred at both 115 and 230 kg N/ha, while only the 230 kg N/ha treatment significantly increased the N contents of Jubilee. This response was continued at R2/R3, although in this instance Furio exhibited a similar response to Jubilee. While the three cultivars contained similar quantities of N at R2/R3, significant differences were detected at R4. At this ontogenetic stage, both Jubilee and Furio contained at least 27% more N than SS42. The N contents at R4 were also significantly enhanced with N fertiliser, being about 32% higher (averaged across cultivars) with 230 kg N/ha than the control.

5.3.6 Pre- and post-anthesis DM and N accumulation

Both pre-anthesis N and DM accumulation for SS42 and Jubilee increased with N rate (Table 5.8). For Furio, on the other hand, greatest accumulations occurred with 115 kg N/ha. Such varying response to N rate by the three cultivars for both pre-anthesis N and DM accumulation resulted in significant cultivar × N rate interactions.

Accumulation of both N and DM during the post-anthesis period differed significantly among the cultivars (Table 5.8). In both instances Furio accumulated significantly more N and DM than either SS42 or Jubilee. While SS42 and Jubilee accumulated similar quantities of DM during the post-anthesis period, Jubilee accumulated significantly more N (about 37%) during this period. Nitrogen rate also increased post-anthesis N and DM accumulation for all three cultivars, increasing 39% and 34%, respectively as N rate increased from 0 to 230 kg N/ha.

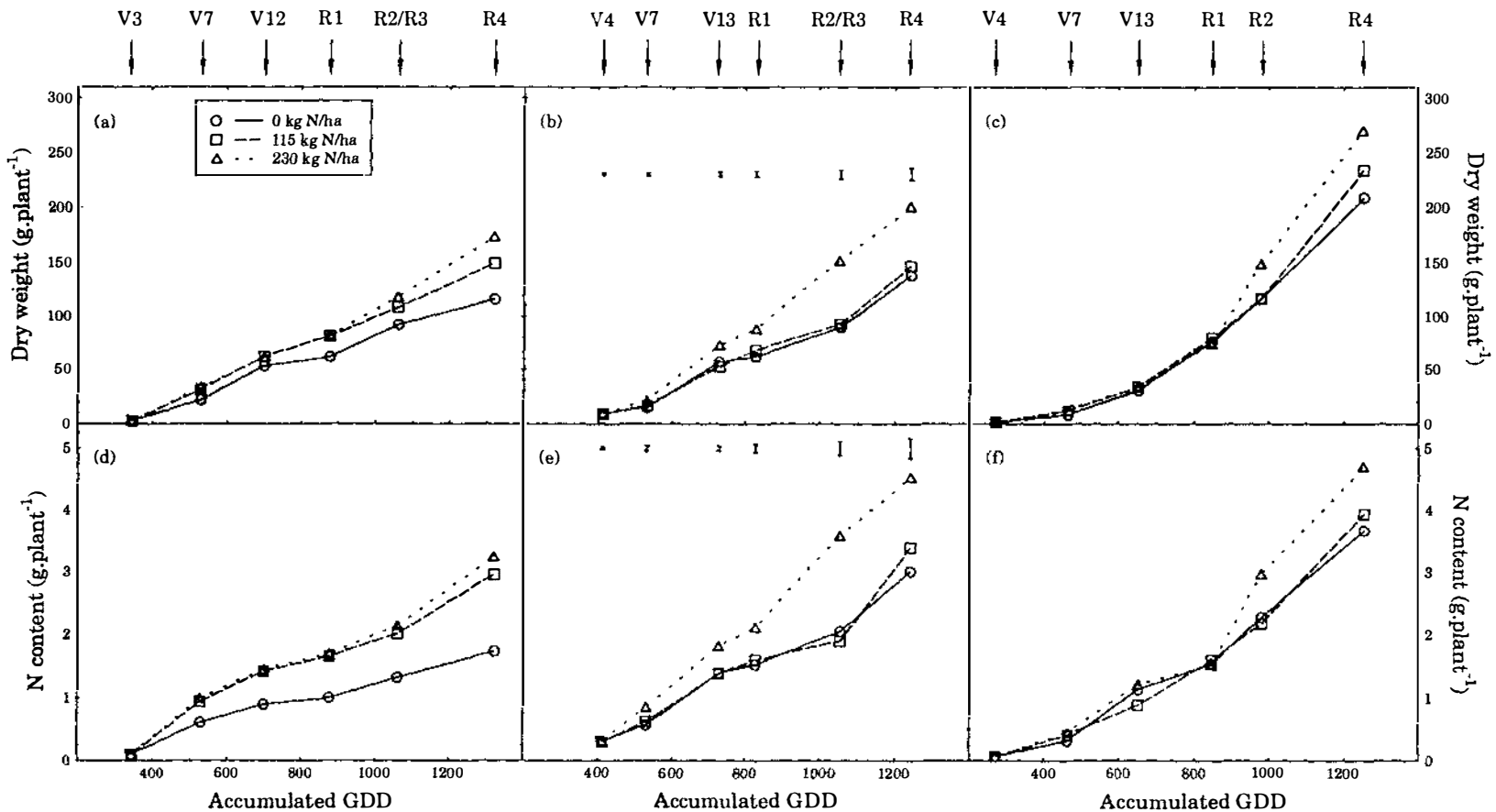

Fig. 5.3. Effect of N rate on total DM accumulation for (a) SS42, (b) Jubilee, and (c) Furio, and total N accumulation for (d) SS42, (e) Jubilee, and (f) Furio. Vertical bars represent the pooled standard error for each harvest (n=27).

Table 5.8. Effect of N rate on pre- and post-anthesis DM and N accumulation for Jubilee, SS42, and Furio.

Cultivar	N rate (kg/ha)	DM accumulated (g·plant^{-1})		N accumulated (mg·plant^{-1})	
		pre-anthesis	post-anthesis	pre-anthesis	post-anthesis
Jubilee	0	62	76	1522	1492
	115	68	78	1597	1793
	230	88	112	2115	2421
SS42	0	62	54	1000	735
	115	82	67	1654	1307
	230	83	90	1692	1548
Furio	0	76	132	1534	2141
	115	80	155	1596	2350
	230	74	196	1519	3191
5% LSD		8.3	20	212	479
		Significance levels			
Cultivar		NS	***	*	***
N rate		**	***	**	**
Cultivar × N rate		*	NS	*	NS

NS, *, **, ***; Nonsignificant or significant F test at $P \leq 0.05$, 0.01, 0.001, respectively.

Pre-anthesis DM accumulation was highly correlated with pre-anthesis N uptake (r=0.77; $P<0.001$), but not with post-anthesis N uptake. Similarly, post-anthesis DM accumulation was highly correlated with post-anthesis N uptake (r=0.86; $P<0.001$), but not with pre-anthesis N accumulation.

5.3.7 Ontogenetic changes in DM, N concentration, and N content of stems

There was a sigmoidal increment in stem DM accumulation (Figs. 5.4a-c). Although DM contents were similar among the cultivars at V3, significant differences were observed at V7. By this stage, stems of SS42 contained similar quantities of DM to Jubilee, but 64% more DM than those of Furio. The cultivars differed in their response to N rate at both V13 and R1. At V13, stems of Jubilee and SS42 contained significantly more DM than those of Furio, but only for Jubilee were the DM contents significantly increased with N fertiliser. At R1, the DM contents of both SS42 and Jubilee increased with N rate, unlike Furio. Additionally, DM contents for Furio were significantly higher than for Jubilee, but similar to SS42. At R2/R3 and R4, stems of Furio contained significantly more DM than either SS42 or Jubilee. Dry matter contents at R2/R3 and R4 were also significantly influenced by N rate with stems in the 230 kg N/ha treatment containing at least 25% more DM than those of the control.

The concentration of N in stems generally declined with ontogeny before plateauing around 8-12 mg·g DM^{-1} at R2/R3 (Figs. 5.4d-f). Despite the three cultivars exhibiting a similar response, significant differences were detected at several stages during ontogeny. The first was at V13 whereby stems of Furio contained a significantly higher concentration of N than either Jubilee or SS42. Further, at this ontogenetic stage Furio was the only cultivar which responded to N rate. Varying response to N rate among the cultivars was also observed at R2/R3 and R4. At R2/R3, stems of SS42 contained a significantly higher concentration of N than either Furio or Jubilee, but only for Jubilee were concentrations significantly improved with N fertiliser. At R4, Jubilee had highest concentrations of N, significantly higher than SS42. At this ontogenetic stage, concentrations for Jubilee with 115 kg N/ha were significantly higher than the either the control or 230 kg N/ha treatments. For SS42, on the other hand, the 230 kg N/ha treatment resulted in a significantly higher concentration than the control.

The N content of stems increased to R1, plateaued to R2/R3, then either declined (Jubilee and SS42; Figs. 5.4g and 5.4h) or remained constant (Furio; Fig. 5.4i) between R2/R3 and R4. Significant cultivar differences were detected at all ontogenetic stages except V3 and R1. At V7, stems of SS42 contained significantly more N than those of either Jubilee or Furio. Varied

response to N rate by the three cultivars was observed at V13. Unlike SS42 where N contents were significantly higher with 115 or 230 kg N/ha, only the 230 kg N/ha significantly increased the N concentration of Jubilee. The N concentration for Furio in the 115 kg N/ha treatment, on the other hand, was significantly lower than both the control and 230 kg N/ha treatments. Similar responses were observed at R2/R3 and R4. At each of these ontogenetic stages, both Jubilee and Furio contained significantly more N than SS42.

Dry matter content was positively correlated with N content (r=0.78; $P<0.001$), but negatively correlated with N concentration (-0.79; $P<0.001$). Nitrogen content was only moderately associated with N concentration (r=0.61; $P<0.01$).

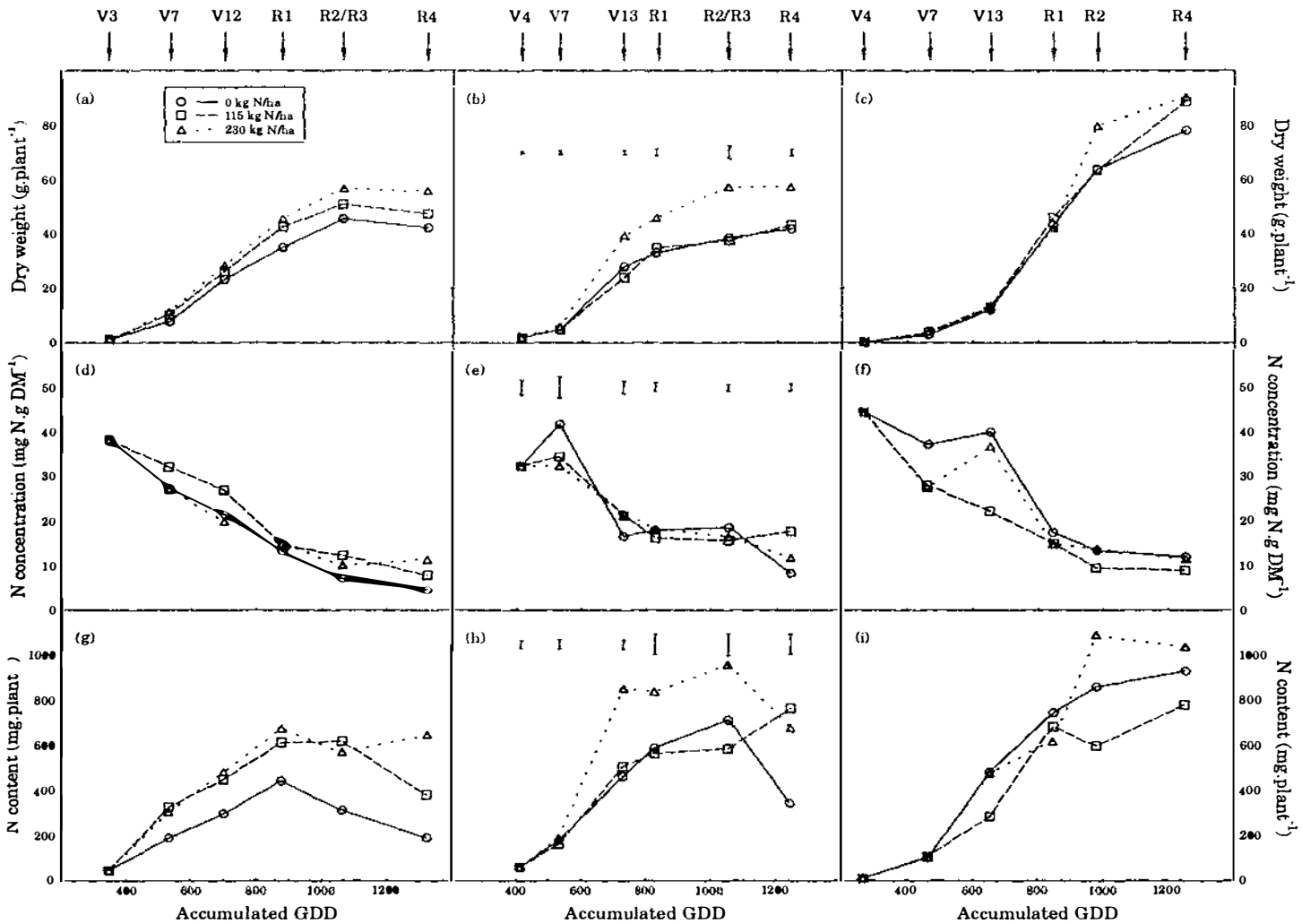

Fig. 5.4. Effect of N rate on DM accumulation in stems of (a) SS42, (b) Jubilee, and (c) Furio, N concentration in stems of (d) SS42, (e) Jubilee, and (f) Furio, and N accumulation in stems of (g) SS42, (h) Jubilee, and (i) Furio. Vertical bars represent the pooled standard error for each harvest (n=27).

5.3.8 Ontogenetic changes in DM, N concentration, and N content of roots

While roots of Jubilee and Furio accumulated DM with a sigmoidal pattern (Figs. 5.5b and 5.5c), those of SS42 accumulated DM with a curvilinear pattern (Figs. 5.5a). Significant cultivar differences for the quantity of DM accumulated were detected from V7 onwards. At V7, roots of SS42 contained significantly more DM than those of either Furio or Jubilee. A similar response was observed at V13, although by this stage roots of Jubilee also contained significantly more DM than those of Furio. Dry matter contents at V13 also differed significantly among the N rates, being 21% higher with 230 kg N/ha than the control. As roots of Furio continued to accumulate DM between R1 and R4 unlike either SS42 or Jubilee, they contained significantly more DM at R1 and subsequent ontogenetic stages. At R4, roots of Furio contained about 53% more DM than those of either SS42 or Jubilee. Roots of SS42 and Jubilee contained similar quantities of DM between R1 and R4. Further significant increases in the DM content of roots with N fertiliser were recorded at both R2/R3 and R4. At R2/R3, DM contents were 55% higher with 230 kg N/ha than the control, and 28% higher at R4.

The N concentration in roots generally declined with ontogeny (Figs. 5.5d-f). Only at V7 and R1 were the concentrations significantly different among the cultivars. Furio had highest concentrations at V7. At R1, the N concentration of Jubilee was highest, being 35% higher than either SS42 or Furio. At R4, roots of the three cultivars contained N at a concentration of 12 mg·g DM^{-1}. Nitrogen concentrations were similar among the N rates at all ontogenetic stages.

Roots of the three cultivars contained similar quantities of N at all ontogenetic stages except R4 (Figs. 5.5g-i). At this ontogenetic stage, roots of Furio contained over twice the quantity of N as those of either Jubilee or SS42. Increasing N rate significantly increased the N content of roots at both R2/R3 and R4. Averaged across cultivars, the N content of roots at each of these ontogenetic stages was 50% higher with 230 kg N/ha than the control.

Despite a highly significant correlation, the N content of roots was only weakly associated with N concentration ($r=-0.25$; $P<0.002$). In contrast, DM content was highly correlated with N content ($r=0.78$; $P<0.001$), but negatively associated with N concentration ($r=-0.59$; $P<0.001$).

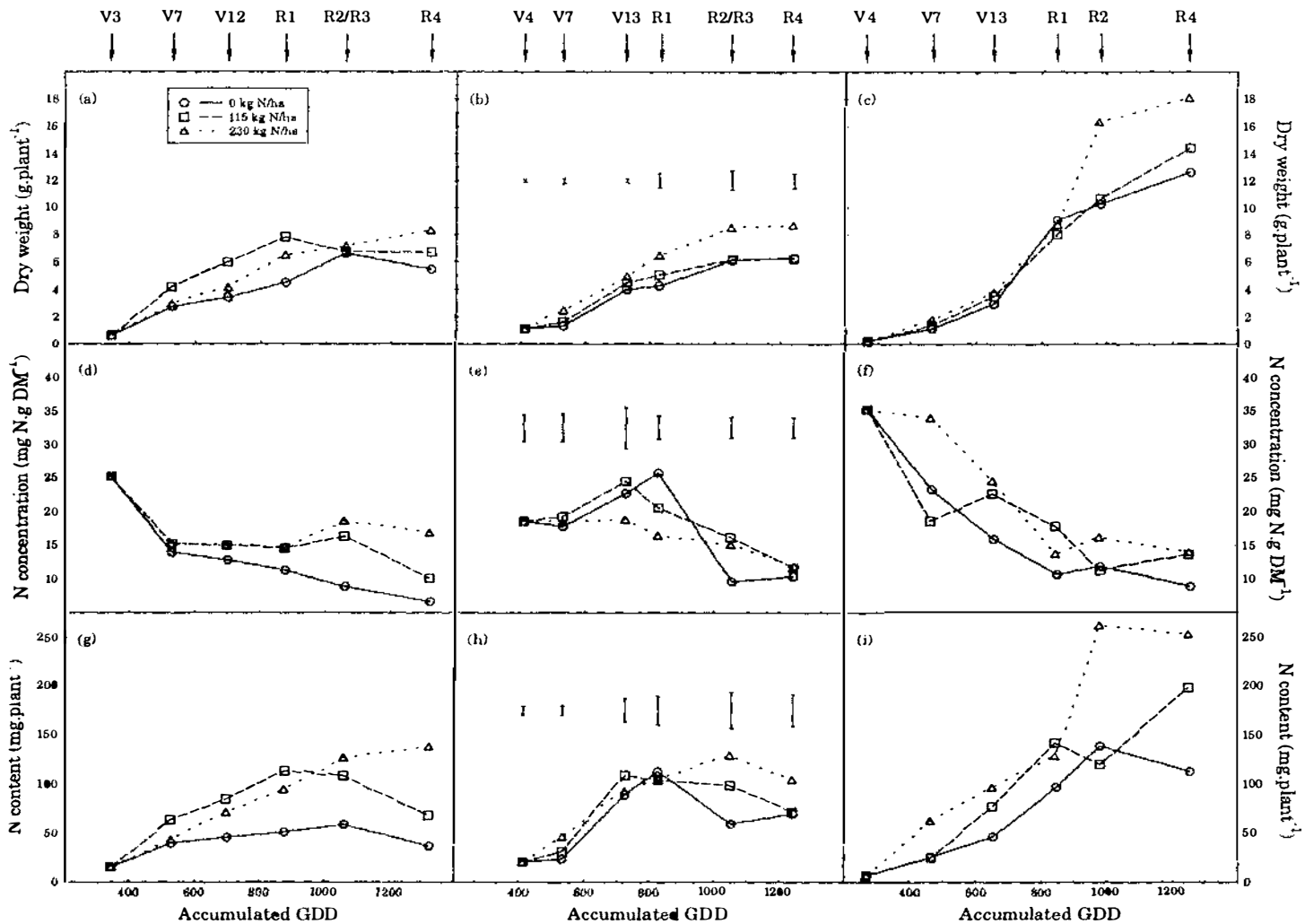

Fig. 5.5. Effect of N rate on DM accumulation in roots of (a) SS42, (b) Jubilee, and (c) Furio, N concentration in roots of (d) SS42, (e) Jubilee, and (f) Furio, and N accumulation in roots of (g) SS42, (h) Jubilee, and (i) Furio. Vertical bars represent the pooled standard error for each harvest (n=27).

5.3.9 Ontogenetic changes in DM, N concentration, and N content of leaves

Leaves of both Jubilee and Furio accumulated DM with a sigmoidal pattern (Figs. 5.6b and 5.6c). While DM accumulation in leaves of SS42 followed a similar pattern, the relationship was more curvilinear (Fig. 5.6a). Leaves of Jubilee contained significantly more DM than those of either SS42 or Furio at V3. At V7, however, leaves of Jubilee contained similar quantities to those of SS42, but only leaves of SS42 contained significantly more (60%) DM than those of Furio. At V13, leaves of Jubilee contained greatest quantities of DM, significantly more than Furio, but similar to SS42. While the DM content of leaves was similar among the three cultivars at both R1 and R2/R3, leaves of Furio contained significantly more DM at R4. At this ontogenetic stage, leaves of Furio contained 28% more DM than those of SS42, but quantities similar to Jubilee. Significant increases in leaf DM were achieved with N fertiliser at all ontogenetic stages except V3 and R1. Depending on ontogenetic stage, increasing N rate from 0 to 230 kg/ha increased DM contents 23-31%.

As with roots and stems, the N concentration in leaves declined with ontogeny (Figs. 5.6d-f). At V3, leaves of Furio and SS42 contained similar concentrations and these concentrations were significantly higher than for Jubilee. Concentrations for Jubilee increased between V3 and V7 such that at V7, leaves of Jubilee contained significantly more N than SS42. Significant cultivar differences were also observed at V13. At this ontogenetic stage, leaves of Furio contained highest concentrations of N, 16% higher than SS42. At R1 and later ontogenetic stages, leaves of the three cultivars contained N at similar concentrations. Nitrogen rate did not influence N concentrations at any ontogenetic stage.

Increases in leaf N content followed a pattern similar to that for DM accumulation (cf. Figs. 5.6a-c and 5.6g-i; r=0.91; $P<0.001$). Significant cultivar differences were observed at all ontogenetic stages, with a significant cultivar × N rate interaction detected at R4. While N contents were highest for Jubilee at V3, N contents for both Jubilee and SS42 were highest at V7. Leaves of Jubilee contained a significantly higher quantity of N than those of either Furio or SS42 at both V13 and R1. By R2/R3 the N content of leaves of Furio had increased such that leaves of both Jubilee and Furio contained similar quantities of N, but significantly more than

SS42. The cultivar x N rate interaction detected at R4 resulted from Jubilee and Furio continuing to have a significantly higher N content than SS42, but with a variable response to N rate among the three cultivars. For example, significant increases in N content above the control were observed for both the 115 and 230 kg N/ha treatments for SS42 and Furio, but only for the 230 kg N/ha treatment of Jubilee were N contents significantly higher. Moreover, the 230 kg N/ha treatment of Jubilee gave a N content significantly higher than the 115 kg N/ha treatment. Significant increases in leaf N content with N fertiliser were also detected at V7, R1, and R2/R3. Averaged across cultivars, N contents with 230 kg N/ha at these ontogenetic stages were 39, 16, and 47% higher than the control, respectively.

Nitrogen concentration was negatively associated with both DM (r=-0.67; $P<0.001$) and N content (r=-0.48; $P<0.001$).

5.3.10 Ontogenetic changes in DM, N concentration, and N content of kernels

Depending on cultivar, kernels comprised 21-30% of total plant DM at R4 (Fig. 5.7a-c). Although the three cultivars accumulated DM with a similar curvilinear pattern, significant cultivar differences were observed from R2/R3 onwards. A significant cultivar x N rate interaction at R2/R3 resulted from kernels of Jubilee containing significantly more DM than those of SS42 and, unlike SS42, being responsive to N fertiliser[6]. Both Jubilee and Furio contained significantly more DM than those of SS42 at both R3 and R4. At R4, however, kernels of Furio contained significantly more DM than those of Jubilee. Compared to Jubilee and SS42, Furio contained 23% and 52% more DM, respectively. Kernels of Jubilee, on the other hand, contained significantly (38%) more DM than those of SS42 at this ontogenetic stage. Kernel DM was significantly increased with N fertiliser at R2/R3 and later ontogenetic stages with kernels in the 230 kg N/ha treatment containing 33% more DM than those of the control at R4.

[6] Recall that no data was available for ear components of Furio at R2/R3.

The similarity of kernel DM (Fig. 5.7a-c) and N accumulation (Fig. 5.7g-i) was reflected in a highly significant correlation ($r=0.93$; $P<0.001$). Significant differences among the cultivars for kernel N content were observed at all ontogenetic stages except R1. At R2, kernels of both Jubilee and Furio contained significantly more (at least 57%) N than those of SS42. A significant cultivar × N rate interaction was detected at R2/R3. At this ontogenetic stage kernels of Jubilee contained significantly more DM than those of SS42, but unlike SS42, DM contents were significantly enhanced with N fertiliser. Kernels of both Jubilee and Furio contained significantly more (at least 42%) N than those of SS42 at both R3 and R4. With the exception of R2/R3, N rate did not significantly influence kernel N contents.

While the N concentration of kernels generally declined with ontogeny, increases were noted for the 230 kg N/ha treatment of Jubilee between R1 and R2/R3 (Figs. 5.7d-f). This variable pattern contributed to the significant cultivar × N rate interaction observed at R1. Aside from R1, concentrations at other ontogenetic stages were similar among N rates and cultivars. Nitrogen concentration in kernels was negatively correlated with both DM ($r=-0.68$; $P<0.001$) and N content ($r=-0.56$; $P<0.001$).

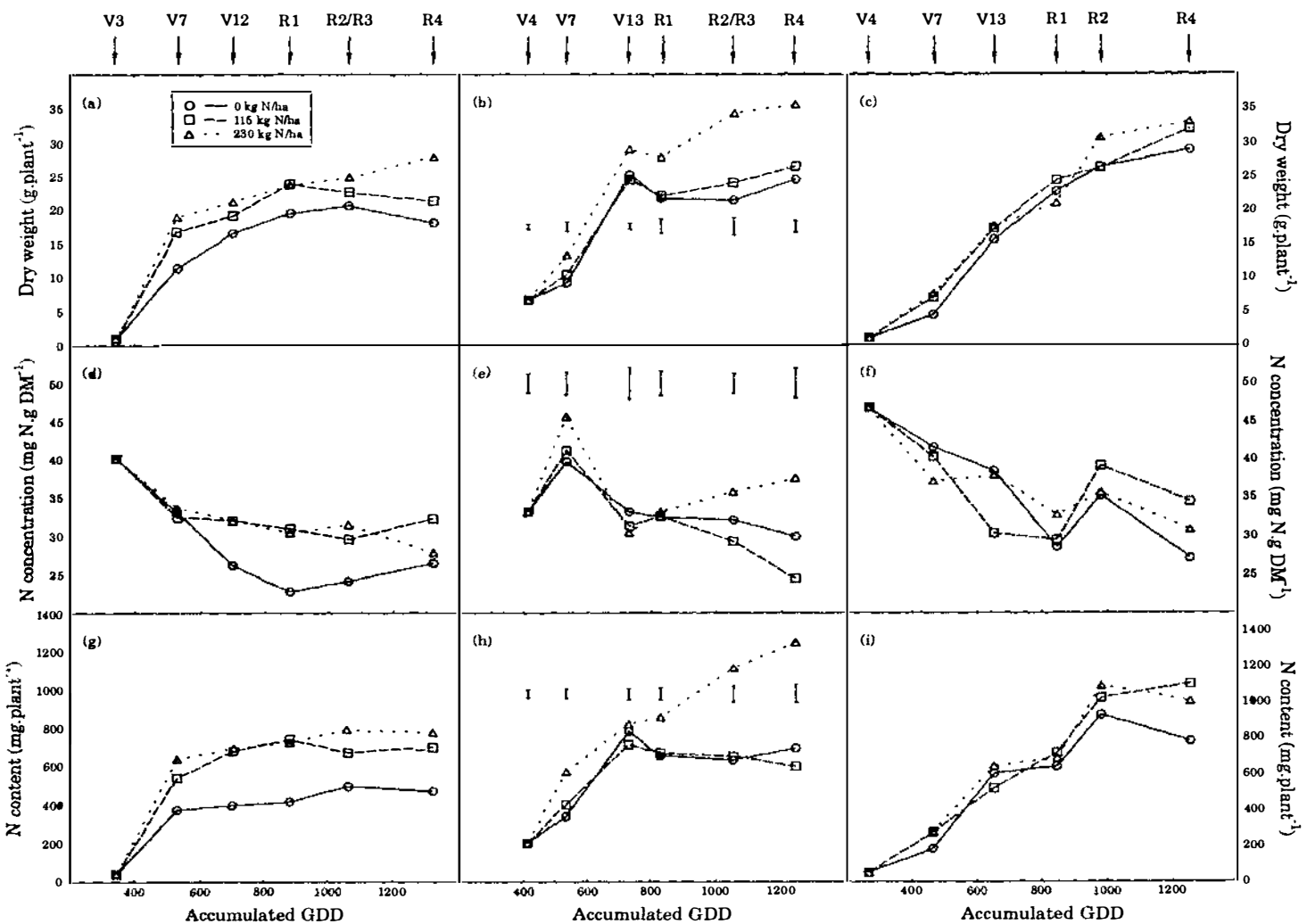

Fig. 5.6. Effect of N rate on DM accumulation in leaves of (a) SS42, (b) Jubilee, and (c) Furio, N concentration in leaves of (d) SS42, (e) Jubilee, and (f) Furio, and N accumulation in leaves of (g) SS42, (h) Jubilee, and (i) Furio. Vertical bars represent the pooled standard error for each harvest (n=27).

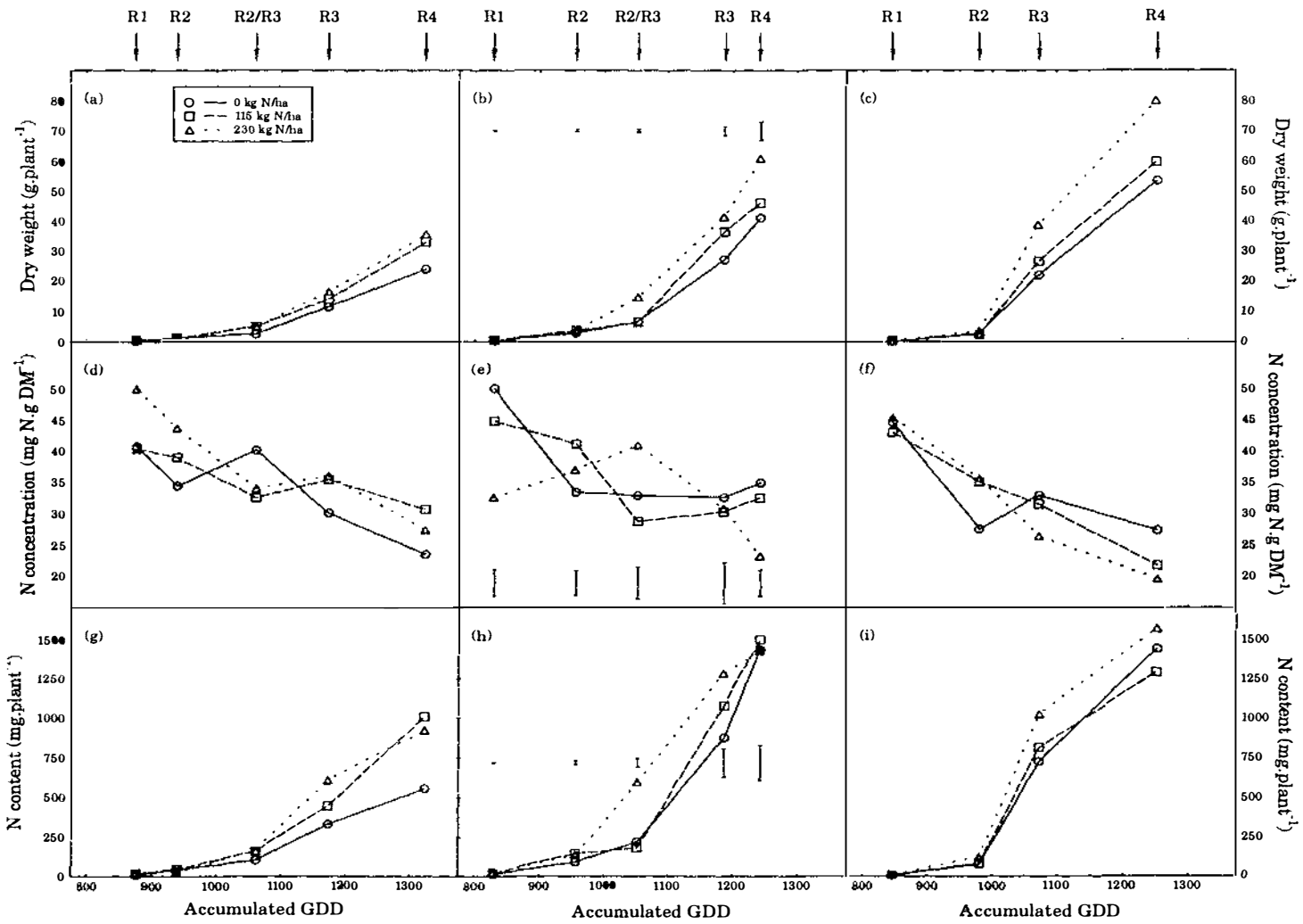

Fig. 5.7. Effect of N rate on DM accumulation in kernels of (a) SS42, (b) Jubilee, and (c) Furio, N concentration in kernels of (d) SS42, (e) Jubilee, and (f) Furio, and N accumulation in kernels of (g) SS42, (h) Jubilee, and (i) Furio. Vertical bars represent the pooled standard error for each harvest (n=27).

5.3.11 Ontogenetic changes in DM, N concentration, and N content of rachis

Increases in rachis DM with ontogeny generally followed a sigmoidal pattern (Figs. 5.8a-c). An exception to this pattern was the 115 kg N/ha treatment of Jubilee, for which, DM contents declined between R3 and R4. Despite the similarity of patterns, significant cultivar differences were observed from R2 onwards. At R2, rachis of Furio contained significantly more (36%) DM than those of SS42, but quantities similar to Jubilee. A significant cultivar × N rate interaction at R2/R3 resulted from rachis of Jubilee containing significantly more DM than those of SS42, but unlike SS42, responded positively to N fertiliser. SS42 had highest DM contents at R3 and R4. While the DM contents for SS42 were significantly higher at these ontogenetic stages (at least 24%), they were only significantly higher than Furio at R3 and Jubilee at R4. Dry matter contents at R3 and R4 were significantly increased with N fertiliser, being 30-33% higher with 230 kg N/ha than the control.

A sigmoidal pattern was noted for N accumulation in rachis (Figs. 5.8g-i). With rachis also accumulating DM with a sigmoidal pattern, N and DM accumulation were highly correlated (r=0.82; P<0.001). Only at R1 were the N contents significantly different among the cultivars. At this ontogenetic stage, rachis of SS42 contained 73% more N than those of Furio, but quantities similar to Jubilee. Significant increases in the N content of rachis with N fertiliser were achieved at both R2/R3 and R4. With 230 kg N/ha, N contents at R2/R3 were 41% higher than the control, and 51% higher at R4. Nitrogen contents at other ontogenetic stages were similar among the N rates.

Nitrogen concentrations steadily declined between R1 and R4, although increases for the 230 kg N/ha treatment of Jubilee between R1 and R2, and again between R3 and R4 were noted (Fig. 5.8d-f). The lower N concentration of rachis in the 230 kg N/ha treatment of Jubilee at R1 compared to the other cultivars and N treatments contributed to a significant cultivar × N rate interaction at this ontogenetic stage. Concentrations for Jubilee at R2 were significantly higher than Furio, but similar to SS42. A further significant interaction was recorded at R2/R3. At this ontogenetic stage SS42 had a significantly higher concentration of N in rachis than Jubilee, but unlike SS42, concentrations were not influenced by N rate. Nitrogen concentrations at both R3

and R4 were similar among the cultivars and not influenced by N rate. Dry matter and N content were both negatively associated with N concentration (r=-0.79; $P<0.001$ and r=-0.49; $P<0.001$, respectively).

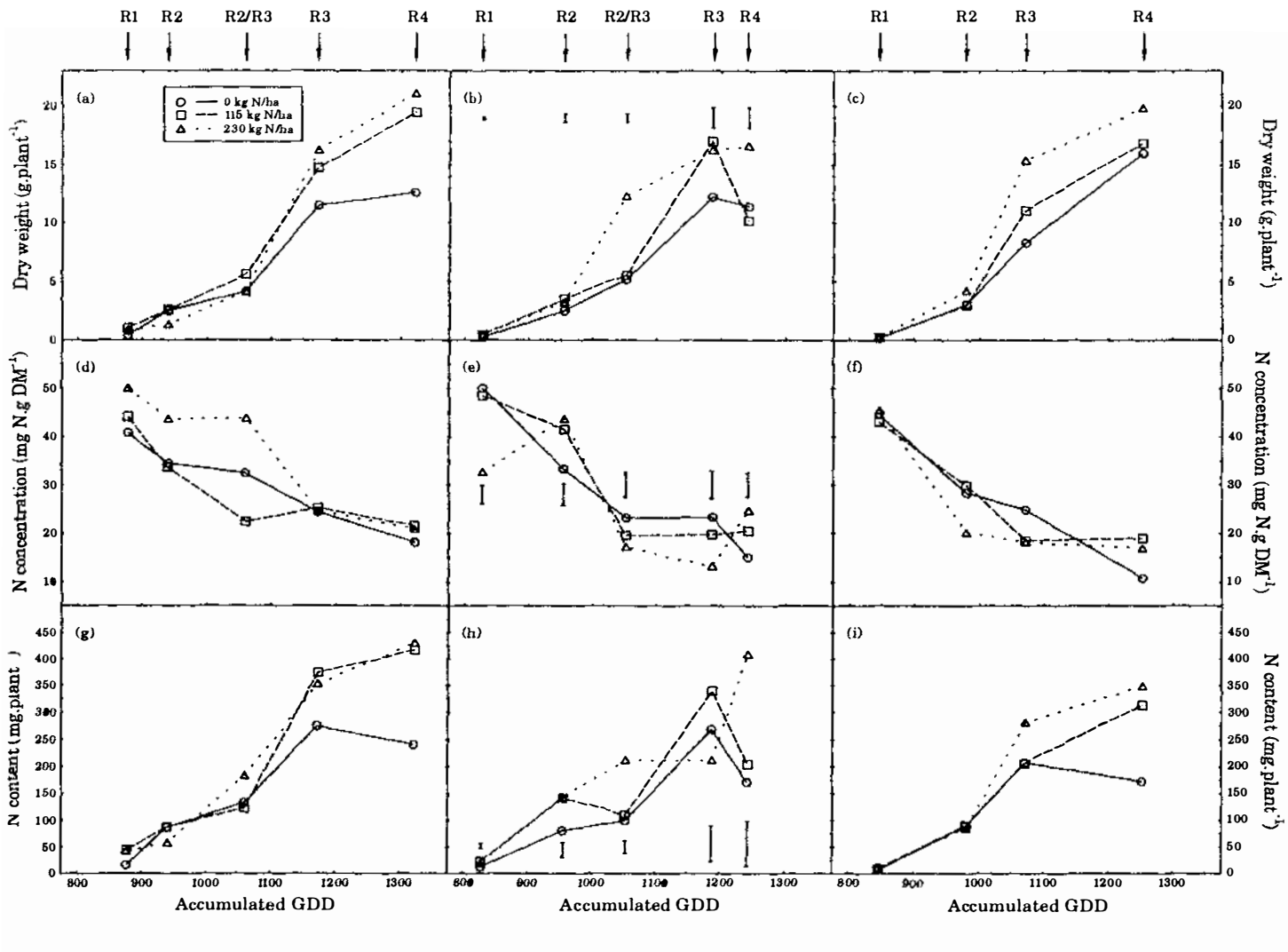

Fig. 5.8. Effect of N rate on DM accumulation in rachis of (a) SS42, (b) Jubilee, and (c) Furio, N concentration in rachis of (d) SS42, (e) Jubilee, and (f) Furio, and N accumulation in rachis of (g) SS42, (h) Jubilee, and (i) Furio. Vertical bars represent the pooled standard error for each harvest (n=27).

5.3.12 Ontogenetic changes in DM, N concentration, and N content of the shank

While shanks of SS42 and Jubilee accumulated DM with a curvilinear pattern, those of Furio accumulated DM with a linear pattern (Figs. 5.9a-c). Such different accumulation patterns resulted in significant cultivar differences at R1, R2, and R3. At each of these ontogenetic stages, shanks of Jubilee contained significantly more (at least 40%) DM than those of Furio, but quantities similar to those of SS42. Significant increases in shank DM with N fertiliser were achieved from R2/R3 onwards with shanks in the 230 kg N/ha treatment containing 42% more DM than those of the control at R4.

The N concentration of shanks for all three cultivars generally declined between R1 and R4, although control N treatments were an exception to this pattern as concentrations increased between R3 and R4 (Figs. 5.9d-f). Nitrogen concentrations at each ontogenetic stage were similar among the cultivars. With the exception of R3, N concentrations at each ontogenetic stage were also similar among the N rates. Averaged across cultivars, the N concentration of shanks at R3 was 47% higher with 230 kg N/ha than the control.

Nitrogen accumulated in shanks of both SS42 and Furio with a curvilinear pattern (Figs. 5.9g and 5.9i). Large variability among the N rates for Jubilee made it difficult to characterise an overall response, although a curvilinear pattern was noted for the control (Fig. 5.9h). At R1, both Jubilee and SS42 contained significantly more DM than those of Furio. At R2, however, only those of Jubilee contained significantly more N than for Furio, but quantities similar to those of SS42. Jubilee and SS42 differed in their response to N rate at R2/R3. Compared to Jubilee where N contents increased significantly with 230 kg N/ha, N contents for SS42 were not influenced. Jubilee continued to have the highest N contents at R3, being significantly higher (54%) than for Furio, but similar to SS42. Shanks of the three cultivars contained similar quantities of N at R4. Aside from R2/R3, R1 and R3 were the only ontogenetic stages where N contents were significantly improved with N fertiliser, being at least 50% higher with 230 kg N/ha than the control.

Dry matter accumulation was highly correlated with N accumulation ($r=0.77$; $P<0.001$). Nitrogen concentration was negatively associated with both DM and N content ($r=-0.30$; $P<0.001$).

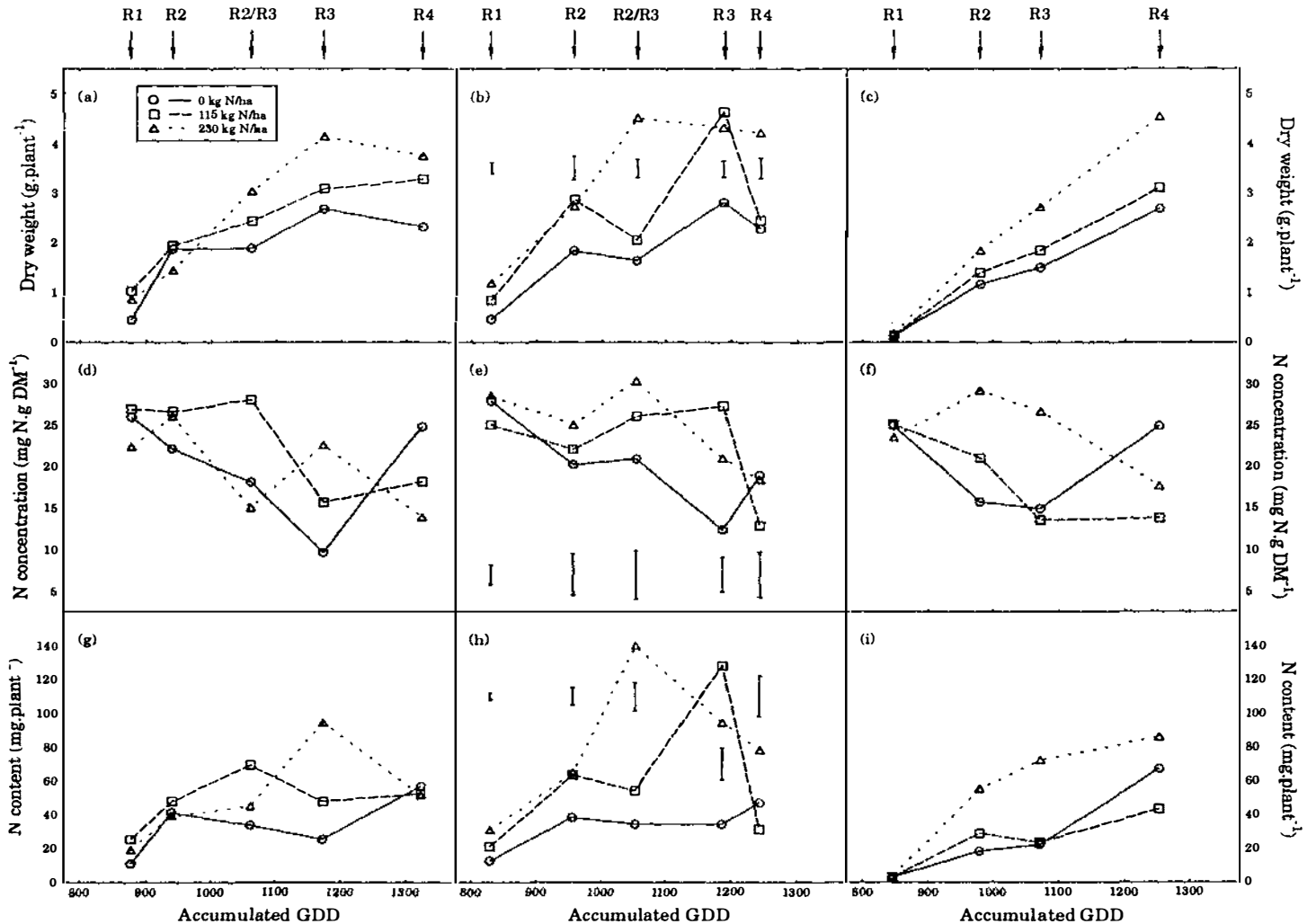

Fig. 5.9. Effect of N rate on DM accumulation in shank of (a) SS42, (b) Jubilee, and (c) Furio, N concentration in shank of (d) SS42, (e) Jubilee, and (f) Furio, and N accumulation in shank of (g) SS42, (h) Jubilee, and (i) Furio. Vertical bars represent the pooled standard error for each harvest (n=27).

5.3.13 Ontogenetic changes in DM, N concentration, and N content of the husk

Husks of SS42 and Jubilee accumulated DM with a curvilinear pattern (Figs. 5.10a and 5.10b). While husks of Furio also accumulated DM with a curvilinear pattern (Fig. 5.10c), there was no obvious plateauing as observed for SS42 and Jubilee. Husks of both SS42 and Jubilee contained significantly more DM than those of Furio at R1. Highest quantities were also accumulated by Jubilee at R2, significantly more (32%) than for SS42. While DM contents were similar between SS42 and Jubilee at R2/R3, significant cultivar differences were detected at R3. At this ontogenetic stage husks of SS42 and Furio contained significantly less DM than those of Jubilee. At R4, on the other hand, husks of Furio contained greatest quantities of DM, containing about 36% more than those of Jubilee. Significant increases in husk DM were achieved with N fertiliser at R1, R3, and R4. At each of these ontogenetic stages husk DM was at least 38% higher with 230 kg N/ha than the control.

After initial increases, N contents generally plateaued from R2 (Figs. 5.10g-i). Increases were, however, noted for the 115 and 230 kg N/ha treatments of Jubilee between R2/R3 and R4. Significant cultivar differences were detected at R1 where husks of Jubilee contained significantly more (at least 55%) N than those of both Furio and SS42. Although the three cultivars contained similar quantities of N in husks at R4, they varied in their response to N fertiliser. Whereas the 115 kg N/ha gave a significantly higher N content than the control for SS42, the 230 kg N/ha treatments gave a significantly higher N content for both Furio and Jubilee. A significant influence of N rate was also recorded at both R1 and R3. Averaged across cultivars, N contents at these ontogenetic stages were about 56% higher with 230 kg N/ha than the control.

The N concentrations of husks were significantly different among the cultivars only at R3 (Figs. 5.10d-f). At this ontogenetic stage, husks of Jubilee contained N at a concentration of 23 mg·g DM^{-1} compared to 13 and 16 mg·g DM^{-1} for SS42 and Furio, respectively. Nitrogen rate did not influence N concentrations at any ontogenetic stage.

Whereas D M content was negatively correlated with N concentration ($r=-0.58$; $P<0.001$), it was positively correlated with N content ($r=0.63$; $P<0.001$). Nitrogen content and concentration were not correlated.

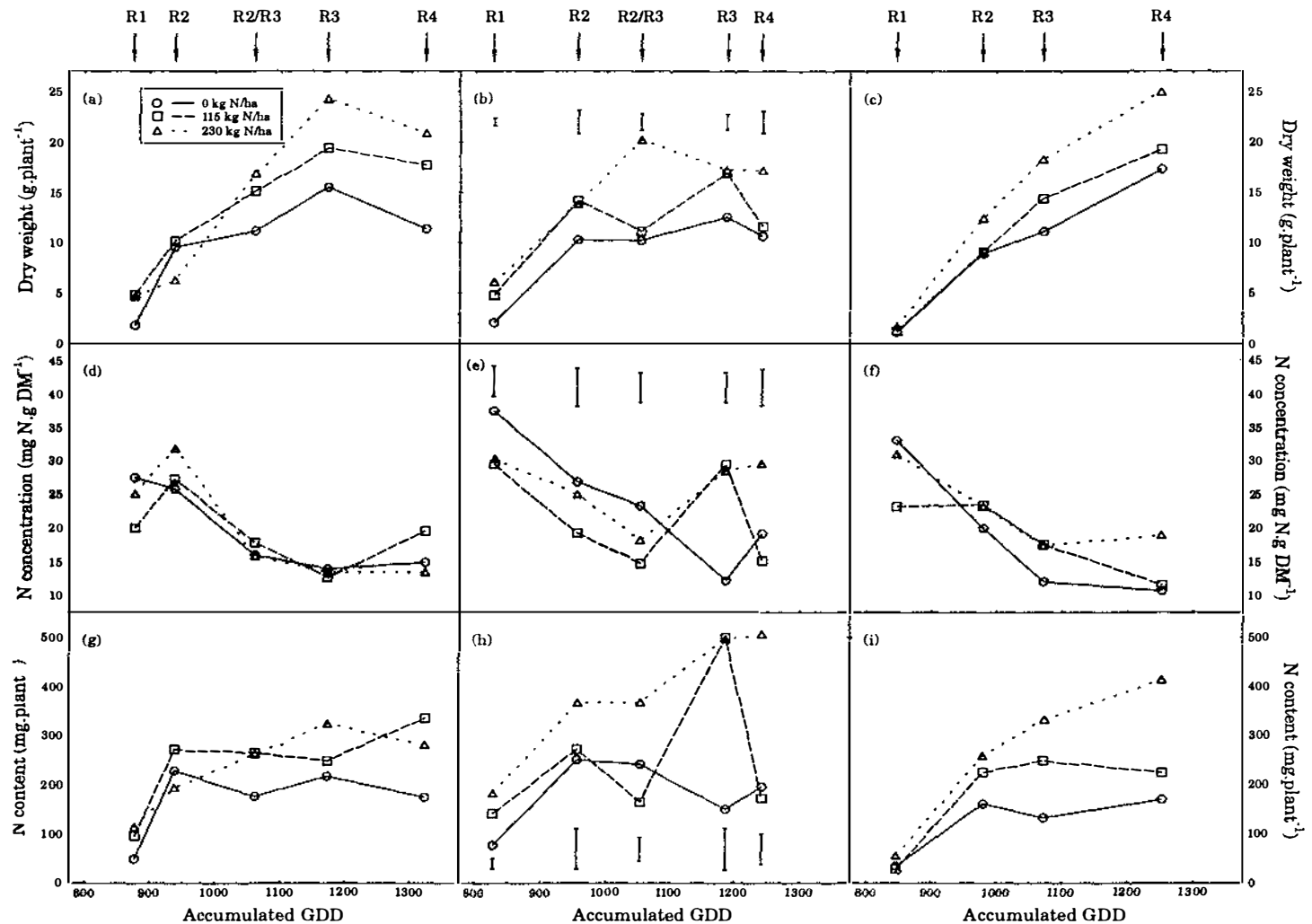

Fig. 5.10. Effect of N rate on DM accumulation in husk of (a) SS42, (b) Jubilee, and (c) Furio, N concentration in husk of (d) SS42, (e) Jubilee, and (f) Furio, and N accumulation in husk of (g) SS42, (h) Jubilee, and (i) Furio. Vertical bars represent the pooled standard error for each harvest (n=27).

5.3.14 Results from additional data analysis using data from Stone et al. (1998)

About 24% more incident radiation was potentially available to SS42 than Furio in the current study. Similarly, SS42 potentially had 18% more incident radiation available than Jubilee. The consequence of these differences was estimated using data from Stone et al. (1998) in conjunction with data from the current study as described in Section 3.3.18. That is, maximum leaf area (which occurred at R1) was determined from Stone et al. (1998) and then again with 18% and 24% less incident radiation for Jubilee and Furio, respectively. The proportionate difference in leaf area was then used as a basis to adjust data in the current study in conjunction with regression analysis using dummy variables. In the case of Stone et al. (1998), 18% less incident radiation corresponded to leaf area decreasing from 3.9 m^{-2} per plant to 3.1 m^{-2} per plant (i.e., a 21% reduction) while a 24% reduction corresponded to a 26% reduction. Analysis was confined to DMPCs and NPCs from R1 onwards as these were the most important variables.

Following data adjustment and re-analysis the significance of several variables was changed, but only for the period R1 to R2/R3. In this instance, cultivar differences for partitioning of both N and DM to the shank and leaves were not observed following re-analysis. Although partitioning of N and DM to other organs was also altered the significance of cultivar differences was not altered.

5.4 Discussion

This study provides further evidence to support the speculated inhibitory cycle. The sequence of events leading to an inhibitory cycle apparently begins with the limited sink strength of kernels and rachis during early grain filling. Negative correlations between DM partitioning to kernels and partitioning to husks and stems (r=-0.87; $P<0.001$; Figs. 5.1a-c and 5.2a-c) indicates that there was an excess of photoassimilate at low sink strength. Thus, with kernels and rachis of Furio having a combined sink strength of only 15% between R1 and R2/R3, stems and husks were partitioned 72% of the available DM. In contrast, the significantly higher sink strength of kernels and rachis of Jubilee resulted in only 42% of the available DM being partitioned to these

organs. SS42 partitioned about 67% of the available DM to husks and stems, consistent with having a significantly lower kernel sink strength than Jubilee. Other studies (e.g., Campbell, 1964; Fairey and Daynard, 1978a, 1978b; Hume and Campbell, 1972; Palmer et al., 1973; Uhart and Andrade, 1995a; Wilson and Allison, 1978b) have similarly concluded that photoassimilate not used in reproductive growth is partitioned to the stem and husks.

The stem can only accumulate a limited quantity of DM before it becomes saturated (Barnett and Pearce, 1983). In their study, 6-12 days of photosynthesis after ear removal saturated the stem with photoassimilate. When the stem and husks become saturated, photoassimilate may accumulate in leaves (Farrar and Gunn, 1996; Thomas and Stoddart, 1980), causing feedback inhibition of photosynthetic enzymes (Barnett and Pearce, 1983; Kalt-Torres and Huber, 1987; Neales and Incoll, 1968; Tollenaar and Daynard, 1982) and may even trigger protein and chlorophyll degradation (Jeannette, 1993). Thus, a high concentration of leaf photoassimilate is associated with a decreased photosynthetic rate (Chatterton et al., 1972; Early et al., 1967; Foyer, 1987; Habeshaw, 1973; Nafziger and Koller, 1976; Rufty and Huber, 1983) and may even repress the transcription of photosynthetic genes (Sheen, 1990). Inhibited photosynthesis leads to the next stage of the inhibitory cycle - a restricted supply of newly assimilated N.

The rate of N assimilation depends on the rate of photoassimilate supply to roots (Neyra and Hageman, 1976; Pan et al., 1995). Photoassimilate provides energy for active uptake of N (Jackson et al., 1980, 1986; Pate, 1973), for maintenance processes (Veen, 1981), and enables more extensive root growth (Mackay and Barber, 1986; Pan et al., 1986). With inhibited photosynthesis reducing the availability of photoassimilate, N uptake is reduced (Jackson et al., 1980; Karlen et al., 1988; Wild and Breeze, 1981). While there was no data collected to show that photosynthesis in any of the three hybrids was repressed between R1 and R4 in the current study, the observation that Jubilee and Furio partitioned a significantly greater proportion of DM to roots than SS42 between R1 and R2/R3 (cf. Figs. 5.1a-c) may indicate photosynthetic inhibition in the *sh2* mutant. Further, work by Koch et al. (1982) suggests that plants carrying the *sh2* mutation may have a lower photosynthetic rate during grain filling than wild types. Both Jubilee and Furio assimilated significantly more N than SS42 between R1 and R2/R3 (Table 5.6). By continuing to partition DM to roots between R2/R3 and R4, unlike either Jubilee or SS42

(cf. Figs. 5.2a-c), Furio assimilated significantly more N than SS42 during this period (Table 5.7). The similar quantities of N assimilated by Furio and Jubilee during this period may reflect the earlier DM partitioning to roots by Jubilee between R1 and R2/R3 (Fig. 5.2b).

Furio partitioned DM to roots between R1 and R4 despite having a significantly lower kernel sink strength than either SS42 or Jubilee (Figs. 5.1 and 5.2). This response suggests that photosynthesis for Furio was not inhibited, and thus, stem and husks did not become saturated with photoassimilate between R1 and R4. This result is consistent with the observation that plants of Furio were notably taller than those of SS42 and Jubilee and therefore probably had a greater capacity to store photoassimilate.

Low post-anthesis N uptake places more demand on vegetative organs to supply N (Hageman, 1986; McClung et al., 1990; Ta and Weiland, 1992; Uhart and Andrade, 1995a; Weiland and Ta, 1992), particularly when the N sink is large (Anderson et al., 1984b). Thus, by assimilating significantly less N than Furio between R1 and R2/R3 (Table 5.6) and yet having a significantly larger sink strength for N (cf. Figs. 5.1e and 5.1g), SS42 remobilised significantly more N from stems during this period. Jubilee also remobilised N during this period, sourcing it from leaves and roots (Fig. 5.1b), despite partitioning DM to roots for N uptake between R1 and R2/R3. Such remobilisation by Jubilee is consistent with the large N sink of this cultivar (Fig. 5.1e). Further, N is often remobilised from leaves and stems as they hold one of the largest reserves of N (Chandler, 1960; Friedrich et al., 1979; Millard, 1988; Novoa and Loomis, 1981). Tsai et al. (1991) reported that leaves may contribute 25-60% to grain N with greatest remobilisation generally occurring as maturity approaches (Hanway, 1962b). However, most N in leaves is associated with chloroplasts (Hageman, 1986; Morita, 1980; Stocking and Ongun, 1962) and photosynthetic enzymes (Crafts-Brandner and Poneleit, 1987b; Evans, 1983; Kawashima and Wildman, 1970; Prioul et al., 1990; Sugiyama et al., 1984; Wolfe et al., 1988b), which serve as prominent sources of N (Crafts-Brandner and Poneleit, 1987a). As remobilising N from leaves negatively impacts on photosynthetic rates (Dwyer et al., 1995; Edwards, 1986; Hunt and Van der Poorten, 1985; Muchow, 1988; Sinclair and deWit, 1976; Sinclair and Horie, 1989; Wong et al., 1985), the supply of photoassimilate for SS42 and Jubilee between R1 and R2/R3 would likely have been reduced. As a consequence, less photoassimilate would have been available for

N uptake, thereby placing more demand on vegetative organs to supply N (i.e., an inhibitory cycle; Fig. 5.11).

This sequence of events fits with the general observation made by Thomas and Stoddart (1980) that the removal of sink organs with high demand for current photoassimilate leads to accumulation of carbohydrate in source leaves which may induce senescence. It also fits with observations that maximum amounts of nonstructural carbohydrate accumulate in stems 3-4 weeks after R1 (Asanuma et al., 1967; Daynard et al., 1969; Johnson et al., 1966; Manters and Arny, 1967; Van Reen and Singleton, 1952; Welton et al., 1930; Williams et al., 1968) and that these levels decline as the ear sink increases in size (Daynard et al., 1969; Hanway, 1962a; Jones and Simmons, 1983; Jordan et al., 1950; Kiesselbach, 1950). It is also consistent with observations that shading around R1 decreases nonstructural carbohydrate levels in the stem (Schussler and Westgate, 1991b, 1994; Uhart and Andrade, 1995a; Westgate and Boyer, 1985).

Although no measures of photosynthesis were taken to qualify steps two and three in the proposed cycle, data from other studies on leaf enzyme activity and quantity (e.g., *RUBISCO*, *sucrose synthase*), as well as carbohydrate concentrations in leaves are consistent with the theory. Prioul et al. (1990), using an *sh2* mutant and a normal maize genotype, reported significant declines in *RUBISCO* activity from 11 DAP, but only significant declines in quantity from 40 DAP. Associated with this decline in activity were maximum carbohydrate levels (primarily sucrose; > 90%) in the ear leaf between 10 and 40 DAP. Crafts-Brandner and Poneleit (1987a) observed a similar pattern of events. As grain filling continued, leaf sucrose pools in both studies declined, but increased again as grain filling slowed during late ontogeny. Fairey and Daynard (1978a) observed sugar concentrations in the plant to increase up to 17 DAP and then decline from 31 DAP. Similar observations were made by Below et al. (1984b) and Christensen et al. (1981) with carbohydrate levels in leaves highest at 18 DAP, then declining between 20 and 25 DAP, and increasing again subsequent.

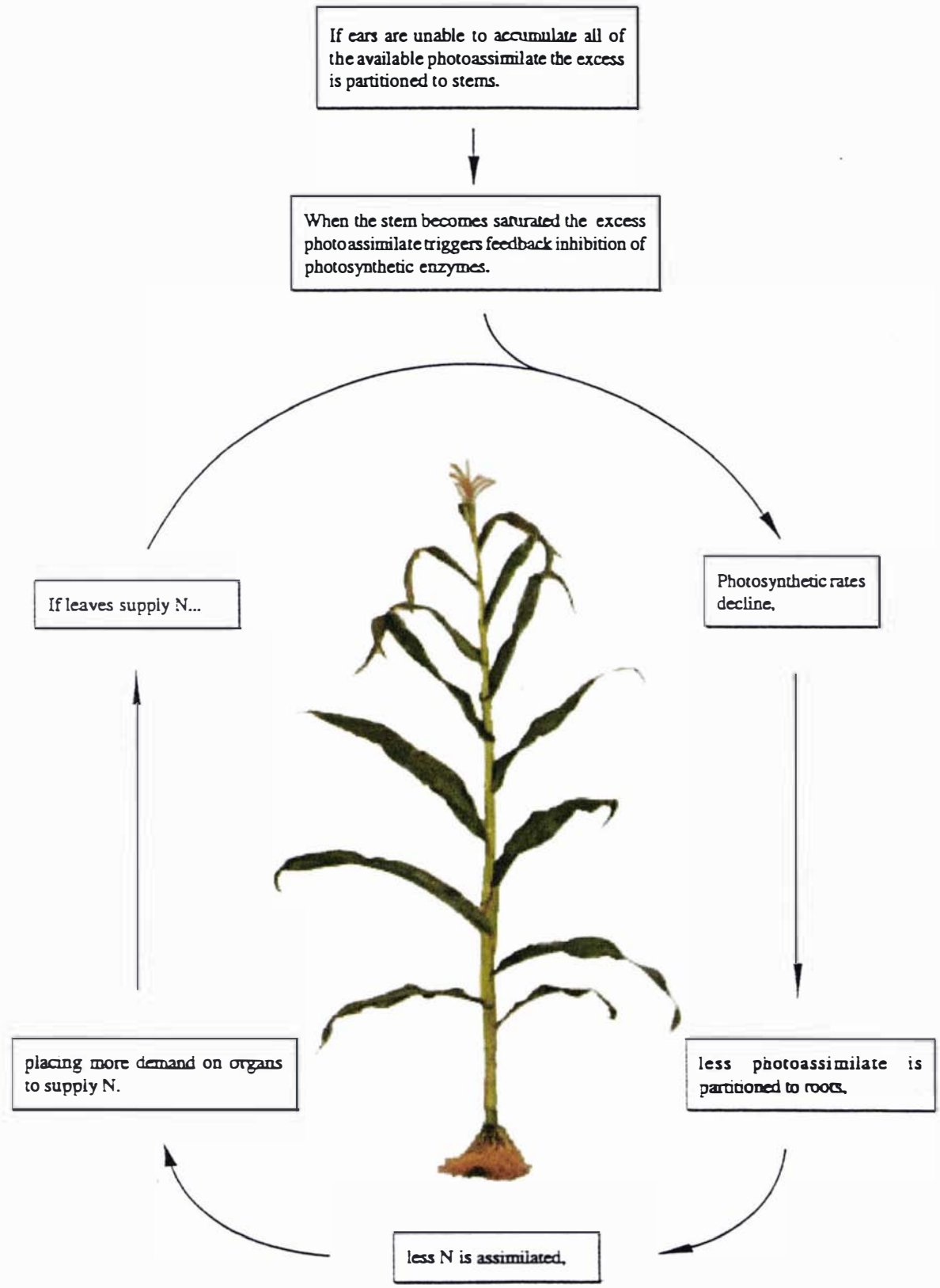

Fig. 5.11. Summary of the proposed inhibitory cycle.

With excess photoassimilate being partitioned to husks and stems, one may question why roots were not partitioned a greater quantity, particularly as the supply of newly reduced N was apparently limiting. Partitioning of excess photoassimilate may relate to both proximity and organ size (Brouwer, 1962; Ho, 1988; Tripathy et al., 1972; Wardlaw, 1990). Cook and Evans (1983) suggested that the proximity of the sink to the source was critical for the sink to receive or attract photoassimilate. Furthermore, with shank and root fractions being smaller than husk, stem, or leaf fractions, their capacity to store photoassimilate is limited. Studies by Raper et al. (1976, 1978) and Fairey and Daynard (1978a) show that soluble carbohydrate concentrations in roots remain within the range of 5%-9%. Thus N uptake is dependent on a continued supply of photoassimilate. To what extent decreased photosynthetic supplies influence N acquisition is unknown.

Limited photoassimilate partitioning to roots is a probable cause of the reduced N uptake observed in the current study. During the experiment it was observed that lower leaves of SS42 were chlorotic, with obvious senescence. Such chlorosis was less apparent for Jubilee, and almost non-existent for Furio. Other studies have similarly noted the senescence of lower leaves during ontogeny (e.g., Feller et al., 1977; Rendig and Crawford, 1985; Wolfe et al., 1988b) and attribute this senescence to these leaves being physiologically older and receiving a lower photosynthetic photon flux density (PPFD) (Allison, 1969; Hoyt and Bradfield, 1962; Lizaso and Ritchie, 1997). However, chlorosis and senescence are associated with reduced chlorophyll concentrations and declining photosynthetic rates (Eik and Hanway, 1965; Girardin et al., 1985; Thimann, 1980; Tollenaar and Daynard, 1978d; Wolfe et al., 1988b). Lower leaves partition DM to roots and lower stem, whereas higher leaves partition photoassimilate predominantly to ears and upper stem (Criswell et al., 1974; Eastin, 1969, 1970; Fairey and Daynard, 1978a, 1978b; Hoyt and Bradfield, 1962; Tripathy et al., 1972). Therefore, reduced partitioning of DM to roots of SS42 (cf. Figs. 5.1a and 5.1b) may be attributed to reduced photoassimilate supply from lower leaves during grain filling. Large sinks will often dominate the overall supply of photoassimilate with smaller sinks relying on local supplies and storage (Pan et al., 1995; Wardlaw, 1990; Zink and Michael, 1985). Consequently, the sugar concentration in roots is generally less than 5% and declines during grain filling (Conrad, 1937; Fairey and Daynard, 1978a). Furthermore, the transport of ^{14}C from lower leaves may be directed towards the ear as it becomes the dominant

sink (Tripathy et al., 1972) or even cease (Gardner et al., 1985) with lower leaves becoming parasitic (Prine, 1962). Thus, even though excess photoassimilate was available, a weak concentration gradient below the ear may have limited photoassimilate supplies to roots (Cliquet et al., 1990b; Edmeades et al., 1979; Fairey and Daynard, 1978a; Palmer et al., 1973).

If sink strength, sink size, or both do not increase, the sequence of events proposed in the inhibitory cycle would result in premature senescence (Hageman, 1986; Moll et al., 1994; Tollenaar and Daynard, 1982). In studies where sink strength is either altered through ear removal or naturally through barrenness, senescence is not only initiated earlier, but hastened (Allison and Weinmann, 1970; Christensen et al., 1981; Crafts-Brandner et al., 1984a, 1984b; Kiniry et al., 1992; Prioul and Schwebel-Dugué, 1992; Uhart and Andrade, 1995a). Accelerated leaf senescence is shown by a loss of chlorophyll and leaf N (Crafts-Brandner et al., 1984b; Crafts-Brandner and Poneleit, 1987a; Feller et al., 1977; Reed et al., 1988), a loss of photosynthetic enzymes (Christensen et al., 1981; Millard, 1988; Prioul, 1996; Tsai et al., 1986), and a significant decline in the net assimilation rate (Barnett and Pearce, 1983; Fujita et al., 1994; Moss, 1962; Thiagarajah et al., 1981). However, consistent with the inhibitory cycle theory (Fig. 5.11), the onset of enzyme degradation is preceded by soluble sugar accumulation in leaves and stems (Allison and Watson, 1966; Allison and Weinmann, 1970; Setter and Flannigan, 1986; Verduin and Loomis, 1944).

As plants bearing ears generally do not senesce until the end of grain filling (Pan et al., 1995), other responses must override the inhibitory cycle as grain filling continues. An overriding response is consistent with the development of kernels and rachis, and their ability to accumulate more photoassimilate (cf. Figs. 5.1a-c and 5.2a-c). The concentration of photoassimilate in the stem rapidly declines during the grain filling period (Daynard et al., 1969; Hanway, 1962a; Kiesselbach, 1950) due to the enlarged sink capacity of the ear (Daynard et al., 1969). As a consequence, the inhibition of photosynthetic enzymes would be alleviated (Barnett and Pearce, 1983; Neales and Incoll, 1968) and chlorophyll concentrations may again increase (Natr, 1972; Vesk et al., 1965). However, effects of the proposed cycle may still be evident as indicated by continued remobilisation of N from stems of both SS42 and Jubilee. Continued remobilisation of N from leaves between R2/R3 and R4 (Fig. 5.2d; Table 5.7) with possible reductions in

photosynthetic rates, may explain why SS42 remobilised DM from stems between R2/R3 and R4, in contrast to Jubilee and Furio (cf. Figs. 5.2a and 5.2b-c). As a decline in stem DM during ear development indicates that less photoassimilate is available for N acquisition by roots (Pan et al., 1984), this observation may indicate a greater influence of the inhibitory cycle as compared to Jubilee.

The significantly lower kernel sink strength of Furio compared to Jubilee and SS42 between R1 and R2/R3 (Fig. 5.1) contrasts other reports. Other workers have reported that normal maize genotypes should have a higher sink strength than either *su1* or *sh2* mutants (Glover et al., 1975; Goldman and Tracy, 1994; Ma and Nelson, 1975; Mertz et al., 1964; Misra et al., 1972, 1975a; Paulis et al., 1978; Tsai et al., 1983; Tsai and Dalby, 1974). This lower sink strength may have resulted from differences in prolificacy. At 70,000 plants per hectare (the density used in the current study), Jubilee and SS42 carried at least 1.7 ears (Table 4.4), in contrast to Furio which carried only one. Prolific hybrids have a greater sink strength than non-prolific hybrids (Anderson et al., 1984a) and translocate a greater proportion of photoassimilate to kernels than non-prolific hybrids (Anderson et al., 1984a; Sato et al., 1978). As a consequence they may compete for photoassimilate that would otherwise be translocated to the roots (Eastin, 1970; Palmer et al., 1973), resulting in impeded N uptake and greater remobilisation (Pan et al., 1995). Differences in prolificacy may therefore explain the lower sink strength of Furio.

Lower kernel sink strength of Furio compared to either SS42 or Jubilee may alternatively have resulted from differences in the ontogenetic interval over which the coefficients were calculated. The coefficients for SS42 and Jubilee were calculated for the periods R1 to R2/R3 and R2/R3 to R4, but for the periods R1 to R2 and R2 to R4 for Furio (Table 5.1). As kernels accumulate DM with a sigmoidal fashion (Figs 5.7 and 3.7; Frey, 1981; Johnson and Tanner, 1972; Jones and Simmons, 1983), less DM would have accumulated in kernels between R1 and R2 than between R1 and R2/R3. Even though more kernel DM would have accumulated between R2 and R4 than between R2/R3 and R4, the ontogenetic interval over which the result is standardised is greater. The consequence of the wider interval is to reduce the magnitude of the coefficient. Therefore, directly comparing partitioning coefficients for Furio, particularly kernels, with those of SS42 and Jubilee between R1 and R4 may be misleading.

Evidence exists in the current study, however, to suggest that Furio had a higher kernel sink strength than either SS42 or Jubilee. At R4, kernels of Furio contained 23 and 52% more DM than those of Jubilee and SS42, respectively (Fig. 5.7). In finding that endosperm DM was highly correlated (r=0.98) with the level of zein in the endosperm, Tsai et al. (1980) concluded that zein was associated with kernel DM accumulation, and hence, kernel sink strength. However, genetic mutations influence levels of zein and therefore the accumulation of kernel DM (Boyer and Shannon, 1984). Therefore, the significantly lower quantities of DM accumulated by Jubilee and SS42 may be associated with having a lower level of zein. Numerous studies with maize have found similar differences in DM accumulation between wild types and endosperm mutants, with all reporting significantly lower zein accumulation in these mutants (Dalby and Tsai, 1975; Doehlert and Kuo, 1994; Glover et al., 1975; Lee and Tsai, 1985; Misra et al., 1972, 1975a; Tsai et al., 1978b; Wilson, 1992). Thus, while the partitioning coefficients indicate that Furio had a lower kernel sink strength than SS42 and Jubilee, particularly between R2/R3 and R4 (Fig. 5.2), the coefficients appear to underestimate the kernel sink strength of Furio.

The result that kernels of Jubilee contained 38% more DM than those of SS42 (Fig. 5.7) was not only consistent with the previous study (Section 3.3), but also with other similar studies using these genotypes (e.g., Dalby and Tsai, 1975; Tsai et al., 1978b). Despite kernels of Jubilee accumulating significantly more DM than SS42 from R2/R3 onwards (cf. Figs. 5.7a and 5.7b), both cultivars had a similar sink strength for N and DM between R2/R3 and R4 (Fig. 5.2). Yet between R1 and R2/R3, Jubilee had a significantly higher kernel sink strength (Fig. 5.1). This pattern was also noted in the previous study (Chapter 3) and was speculated to result from Jubilee reaching maximum levels of zein faster than SS42. Zein would have accumulated until physiological mechanisms slowed transcription (Tollenaar and Daynard, 1978b). Slowing transcription would therefore have allowed SS42 to 'catch up', thus explaining the similar sink strength of SS42 and Jubilee between R3 and R4 (assuming that zein is a measure of sink strength). To my knowledge, zein accumulation in *su1* or *sh2* mutants with ontogeny has not been investigated.

Significant cultivar differences in NUSE (Table 5.2) were associated with significant cultivar differences in kernel DM accumulation at R4 (Fig. 5.7). Compared to SS42, Furio was twice as efficient at translating fertiliser N into kernel DM and 23% more efficient at uptake than Jubilee. Jubilee, on the other hand, was 34% more efficient than SS42, a result comparable with the previous experiment (Table 3.3). In that study, the greater NUSE of Jubilee resulted from being significantly more efficient at both taking up N (NUPE) and translating that N into kernel DM (NUTE). However, in the current study Jubilee was only significantly more efficient at taking up N. As both SS42 and Jubilee had a similarly sized root system (based on DM content; Fig. 5.5), the greater NUPE of Jubilee cannot be argued in terms of size of the root system as in the previous study. Rather, the higher NUPE may have resulted from Jubilee partitioning significantly more DM to roots for N assimilation as discussed earlier. This possibility may also explain the higher NUPE observed for Jubilee in the previous study. Furio, on the other hand, had both a significantly higher NUPE and NUTE than SS42. The higher NUPE is consistent with Furio continuously partitioning DM to roots between R1 and R2/R3 (Fig. 5.1c). It is also consistent with Furio having a significantly larger root biomass than SS42 (cf. Figs. 5.5a and 5.5c), which would potentially have enabled it to extract more N from the soil (Eghball and Maranville, 1993; Reed and Hageman, 1980). The significantly higher NUTE was consistent with kernels of Furio potentially having a significantly higher sink strength as discussed earlier. Hence, the combination of a greater uptake efficiency and a greater kernel sink strength at R4 equated to Furio being significantly more efficient at using fertiliser N than either SS42 or Jubilee.

Nitrogen use efficiency for the three cultivars declined significantly as N application rate increased (Table 5.2). This decline was predominantly due to a decrease in the efficiency with which the cultivars took up N, as also observed in both the previous study (Table 3.3) and other studies (Eichelberger et al., 1989; Kamprath et al., 1982; Moll et al., 1982a; Sabata and Mason, 1992; Salardini et al., 1992; Tsai et al., 1992). A decreased uptake efficiency results from the fraction of fertiliser N taken up declining as N rate increases. Consequently, at any given fertility level, the smaller the quantity of fertiliser N applied, the higher the probability that an equivalent amount will be taken up by the plant. Hence, the NUPE × N rate function would be a negative exponential. NUTE, while following a similar trend, declines with increasing N rate (Albus and

Moraghan, 1995; Anderson et al., 1984a, 1985; Bundy and Carter, 1988; Kamprath et al., 1982; Salardini et al., 1992). This trend occurs because plants produce grain DM more efficiently with declining N rates as a greater proportion of N is remobilised with increasing N stress (Crawford et al., 1982; Thom and Watkin, 1978).

Although the three cultivars differed in the efficiency with which they took up N (Table 5.2), the contribution of NUPE to variability in NUSE was similar among the cultivars when grown with 115 kg N/ha. With this N rate, NUTE contributed about 20% to the variability in NUSE (Table 5.3). However, there was 92 kg N/ha available to plants from the soil (Table 4.1), to which a further 115 kg N/ha was added, yet NUPE still explained 20% of the variability in NUSE. This suggests that the three cultivars are inefficient at N uptake. If these cultivars were efficient at N uptake, then NUPE would have explained none of the variability in NUSE, consistent with Kamprath et al.'s (1982) hypothesis that under high N fertility differences in NUSE would be due to genetic differences in the plant's ability to utilise accumulated N. When 230 kg N/ha was applied, NUPE still explained 11% of the variability in NUSE for Jubilee and Furio (Table 5.3), further suggesting that Jubilee and Furio are inefficient at N uptake.

The result that NUPE explained none of the variation in NUSE for SS42 with 230 kg N/ha compared with 11% for Jubilee and Furio (Table 5.3) is consistent with the significantly greater N uptake by Jubilee and Furio (Table 5.8). As over 28% more N was removed from soil by Jubilee and Furio, soil N reserves in the root zone would have been more depleted than for SS42, in accord with Lafitte and Edmeades's (1994b) suggestion that extensive N acquisition may exhaust N supplies. With 115 kg N/ha, Jubilee and Furio accumulated only 12% more N than SS42, corresponding to less marked differences in the proportion of variability explained by NUPE between the cultivars.

A consequence of high N fertility in the current study was a general lack of cultivar response to N rate. Comparison of total N accumulation (*Nt*; Table 5.8) with fertiliser N (*Ns*; Table 5.2) shows that almost half the N accumulated in plants of SS42 grown with 115 kg N/ha was supplied by the soil as $Nt \approx 1.8(Ns)$. Even greater quantities were supplied for Furio and Jubilee.

As discussed in Chapter 4, roots may have penetrated further than the 150 mm depth to which soil was sampled.

Data for this study were generated from the experiment described in Chapter 4. However, in that study lodging and water stress were suggested to influence results. To what extent these variables influenced results in the current study is unclear. There was also a confounding influence of different levels of total radiation intercepted by the three cultivars as evidenced by altered statistical significance of some cultivar differences. However, even with these confounding influences, results of both the current and previous study (Chapter 3) suggest that the limited sink strength of endosperm mutants impedes N uptake, placing more demand on vegetative organs to supply N. However, this discussion, and that of previous chapters has hinged around sink strength, yet no attempt has been made to quantify sink strength in any of the genotypes investigated. Relating sink strength with partitioning coefficients is vital if credibility is to be provided for hypotheses raised in these discussions.

Chapter 6

Relationship between zein accumulation and sink strength in sweet corn

6.1 Introduction

Understanding the factors that limit kernel sink strength is fundamental to identifying opportunities to increase future yields of sweet corn and maize crops. The N storage protein, zein, has been implicated as a regulator of sucrose movement into kernels (Singletary and Below, 1989; Tsai et al., 1980, 1983), and hence, kernel sink strength. Evidence supporting this role comes from studies which have shown that sucrose movement into kernels and starch accumulation is severely reduced when zein synthesis terminates (Tsai et al., 1978a, 1980). Furthermore, the increased sucrose movement into kernels as soil N fertility increases (Singletary et al., 1990; Tsai et al., 1980, 1983) is associated with an increasing abundance of zein in the endosperm (Rendig and Broadbent, 1979; Schneider et al., 1952; Tsai et al., 1980, 1984; Wolfson and Shearer, 1981). Further evidence to suggest that zein regulates kernel DM accumulation is provided from studies with zein-deficient mutants. Kernels of *su1* and *sh2* mutants contain 23-42% and 42-62% less zein than wild types, respectively, and their kernel DM contents are reduced by similar proportions (Dalby and Tsai, 1975; Doehlert and Kuo, 1994; Glover et al., 1975; Lee and Tsai, 1985; Misra et al., 1972, 1975a; Nass and Crane, 1970; Tsai et al., 1978a, 1978b; Wilson, 1992). This latter evidence indicates the high association between zein level and kernel DM (Tsai et al., 1978a).

The zein family consists of a mixture of alcohol-soluble polypeptides, resolved by SDS-polyacrylamide gel electrophoresis (SDS-PAGE) into seven components (Tsai et al., 1978b) with apparent molecular masses of 28, 22, 20, 16, 14, and 10 kDa (Gianazza et al., 1976; Lee et al., 1976). Based on molecular weight, solubility, and structure, Esen (1987) divided the proteins into classes designated α-, β-, and γ- zeins that correspond to the 22 and 20, the 16 and 14, and the 28 kDa components, respectively. The 10 kDa protein is structurally different from the others (Kirihara et al., 1988) and constitutes a fourth class, δ-zein (Wallace et al., 1990). In normal maize genotypes (i.e., wild types) zein may account for as much as 60% of the total endosperm protein (Hansel et al., 1973; Tsai, 1979b) comprising about 75-85% α-zein, 10-15% β-zein, 5-10% γ-zein, and less than 5% δ-zein (Burr and Burr, 1976; Esen, 1986, 1987; Larkins et al., 1989; Lee et al., 1976; Misra et al., 1976; Wilson, 1991).

While it is known that *sh2* and *su1* mutants have lower total zein content than wild types, the zein classes reduced or omitted in these mutants have received little attention. Knowledge of any preferential loss is important to understanding the mechanism by which total zein accumulation is reduced. For example, reduced levels of α-zein may interfere with zein translation (Jones et al., 1977a) and the organisation of zeins into protein bodies (Lending and Larkins, 1992). Other zeins may affect polypeptide folding (Lending and Larkins, 1989, 1992). Although two major zein protein classes (α- and β-zein; Burr and Burr, 1976; Esen, 1986; Wilson, 1991) are reported as being preferentially reduced in *sh2* and *su1* mutants (Doehlert and Kuo, 1994; Paulis et al., 1992), other studies have found to the contrary. For example, Wilson (1992) reported that only α-zein was reduced in the *su1* mutant, while Misra et al. (1976) and Tsai et al. (1978b) reported no loss of any zein components in their *sh2* mutants. Conflicting reports of preferential increases in zein components with N fertiliser (cf. Singletary et al., 1990 with Tsai, 1979a) further confuse the situation.

Developmental studies show that zein synthesis begins about 10-12 days after pollination (DAP) (Tsai et al., 1978a), the time at which protein body formation is initiated (Jones et al., 1977b), and is most active between 16 and 35 DAP (Khoo and Wolf, 1970; Kodrzycki et al., 1989; Oaks et al., 1979; Tsai and Dalby, 1974; Tsai et al., 1978a). However, in some endosperm mutants (e.g., *o2* (Tsai, 1979a; Tsai et al., 1984)), zein synthesis is not only delayed but terminates earlier than wild types with severe consequences to kernel DM accumulation (Dalby and Tsai, 1975; Jones et al., 1977b).

The ontogeny of zein accumulation in *su1* or *sh2* mutants does not appear to have been studied. Understanding the pattern of zein accumulation is important to support hypotheses raised in previous chapters. One of these hypotheses proposed that limited sink strength during early grain filling led to an inhibitory cycle (Chapter 5). This cycle resulted from the inability of kernels to accumulate all the photoassimilate produced during early grain filling, the excess being partitioned to stems and husks. Once stems and husks become saturated with photoassimilate, photosynthetic rates may become impaired through feedback inhibition of photosynthetic enzymes (Neales and Incoll, 1968), resulting in reduced N assimilation by roots (Hageman, 1986; Swank et al., 1982) and further impaired photosynthetic rates. Studies with near-isogenic

endosperm mutants that affect starch, protein synthesis, or both, indicate an involvement of sink regulation as manipulating source activities alters the zein concentration in the kernel (Glover and Mertz, 1987; Jones and Simmons, 1983; Remison and Omueti, 1982; Zink, 1980). However, with much of the evidence for this inhibitory cycle reliant on the assumption that SS42 (*sh2* mutant) has a lower kernel sink strength than Jubilee (*su1* mutant), the magnitude of sink strength differences must be quantified to validate this suggestion. One possible way to do this is to quantify levels of zein in kernels, which due to its high association with kernel DM, should be a reliable indicator of sink strength. A second hypothesis (Sections 2.4-5.4) regarded the different response of SS42 and Jubilee to N rate; yield of Jubilee responded to N fertiliser while yield of SS42 was not influenced (e.g., cf. Figs. 2.4a and 2.11a). This response difference may be explained by Jubilee accumulating significantly more zein than SS42 and in doing so, requiring more N for zein synthesis. However, an alternative explanation is provided by Tsai et al. (1984). They suggested that hybrids which synthesise zein rapidly reach their maximum genetic level with only small amounts of N fertilizer, and thus grain yields do not increase with additional N due to zein saturation. The first objective of this experiment was therefore to quantify the influence of N nutrition on zein accumulation in kernels of a *sh2*, *su1*, and a wild type with ontogeny. The second objective was to relate zein accumulation at defined ontogenetic stages with DM and N partitioning to various organs. The third objective was to compare how zein proteins for the three genotypes are influenced by N rate.

6.2 Materials and methods

6.2.1 Cultural

Data presented in this chapter were derived from the experiment previously described (Section 4.2). The maize hybrid Furio (*Zea mays* 'Furio') was included as the wild type in this study because of its similar ontogeny to SS42 and Jubilee.

6.2.2 Plant sampling

Primary ears from 15 plants in each plot were periodically harvested (Table 6.1) and immediately frozen (-18 C). Ears were harvested until 72% SMC, the maturity at which kernels are generally 'too mature' for processing.

Table 6.1. Cob harvests for SS42, Jubilee, and Furio as related to accumulated GDD.

Cob harvest	SS42		Jubilee		Furio	
	DAP[z]	GDD[y]	DAP	GDD	DAP	GDD
1	10	114	8	115	13	133
2	15	183	13	165	19	188
3	21	257	18	225	26	251
4	-	-	24	292	34	319
5	27	343	30	359	-	-
6	35	446	36	414	42	407

[z] Days after pollination.
[y] Accumulated GDD from T_{50} silking (Fig. 4.1a).

As there was limited response to N rate in the previous studies (Sections 4.3 and 5.3) and with data in the current study being generated from these same set of treatments, only cobs from the 0, 115, and 230 kg N/ha treatments were used in this study.

6.2.3 Tissue analysis

Fifteen kernels midway between the tip and butt of the cob were dissected from each of five randomly selected cobs from each treatment. Kernels were dried in a forced air oven at 80 C until constant weight, weighed, and then ground to pass a 0.1 mm screen. Nitrogen concentrations were determined from a 0.1 g sample using the semi-micro Kjeldahl method (Bremner, 1960).

Defatted meal was prepared by stirring 1 g of ground kernel DM in cold acetone (40 ml/g) for two hours, as described by Lending et al. (1988). Samples were washed with anhydrous ether before air-drying and further drying at 60 C for 1 hour. The method of Wallace et al. (1990) was used for zein extraction because of its superior extraction (Hamaker et al., 1995). This procedure involved completely solubilizing 100 mg of defatted meal in a 1.0 ml solution of 0.0125 M sodium borate (pH 10.0), 1% sodium dodecyl sulphate (SDS), and 2% 2-mercaptoethanol. After incubation with agitation at 20 C overnight, samples were centrifuged for 15 minutes at 12,000 rpm in an Eppendorf microcentrifuge, and supernatants extracted. Following second, third, and fourth extractions of the pellet, the supernatants were pooled and ethanol added to a final concentration of 70% containing 2% 2-mercaptoethanol. Samples were agitated overnight at 60 C and again centrifuged. The supernatant, which comprises the zein fraction, was taken to dryness before determining the N concentration of the residue by the semi-micro Kjeldahl method (Bremner, 1960).

A check was made to ensure complete zein extraction by extracting the pellets of 10 randomly selected samples a fifth time. In this instance, only the final cob harvests (Table 6.1) were sampled. Following agitation and centrifuging as discussed above, 100 µl samples were loaded onto a SDS-polyacrylamide gel for electrophoresis (SDS-PAGE). Following electrophoresis the gel was stained with Coomassie blue before being destained with 70% ethanol. An absence of banding indicated that zein was completely extracted with four extractions. Samples for separating and partially characterizing zein fractions using SDS-PAGE were prepared, loaded, and stained as just described although samples had been extracted four times in this instance. The known standards for SDS-PAGE, supplied by Sigma® under the product name Dalton Mark VII-L, were bovine serum albumin (66 kDa), oval-albumin (45 kDa), glyceraldehyde-3-phosphate dehydrogenase (36 kDa), carbonic andhydrase (29 kDa), trypsinogen (24 kDa), soybean trypsin inhibitor (20.1 kDa), and α-lactalbumin (14.2 kDa).

6.2.4 Data analysis

The quantity of zein determined by Kjeldahl digestion is often converted to zein protein using a conversion factor (e.g., Dalby and Tsai, 1975; Tsai et al., 1980) ranging from 5.7 to 6.25 (Mosse, 1990). Conversion factors were not used in the current study because of discrepancies in the value of the conversion factor and the potential that values may differ among endosperm mutants. Zein was, therefore, reported as $\mu g\ N \cdot kernel^{-1}$ and for ease of discussion is simply referred to as zein.

The experiment was a two-factor factorial analysed as a randomised complete block design with three blocks. Nitrogen rates were 0, 115, or 230 kg/ha with genotypes SS42 (*sh2*), Jubilee (*su1*), or Furio (wild type). The data sets for SS42, Jubilee, and Furio were combined to test genotypic differences. As accumulated GDD were similar for each genotype (Table 6.1), pooling the data across genotypes was valid. However, in doing this, genotypic differences became confounded as SS42, Jubilee, and Furio had each experienced different amounts of incident radiation (2362 $MJ \cdot m^{-2}$, 1925 $MJ \cdot m^{-2}$, and 1788 $MJ \cdot m^{-2}$, respectively). In Chapter 5 the influence of this confounding influence was tested using regression analysis with dummy variables adjusted using leaf area measurements. In that analysis, the significance of cultivar differences for partitioning of N and DM to kernels was unchanged. Similar results were observed in Chapter 3 using the same adjustment. Based on these findings, data in the current study were not adjusted to determine the magnitude of the confounding influence of different incident radiation levels.

Data for each genotype were standardized to rate of DM or N accumulation per GDD in order to eliminate possible influences of differences in the accumulated GDD for each cultivar. As the extra cob harvest of Jubilee created an unbalanced data set, cob harvest four of Jubilee was deleted for the ANOVA. Following analysis with cob harvest four of Jubilee omitted, data were again analysed, but with this harvest included and cob harvest three deleted. As both analyses provided similar results, only ANOVA results with cob harvest four omitted are presented. Similarly, as analyses using both raw and standardised data provided similar results, only analyses on raw data are presented. For convenience of discussion the cob harvests in Table 6.1

for the pooled data set were reclassified as harvests 1 through 5 and the average GDD taken for each harvest (Table 6.2).

Table 6.2. Cob harvests for SS42, Jubilee, and Furio for the pooled data set.

Cob harvest	SS42	Jubilee	Furio	Average for the three cultivars
	GDD[z]			
1	114	115	133	121
2	183	165	188	179
3	257	225	251	244
4	343	359	319	340
5	446	414	407	422

[z] Accumulated GDD from T_{50} silking (Fig. 4.1a).

No cob harvest data were omitted when modelling trends using regression. However, during regression modelling a high degree of similarity was noted between the 115 and 230 kg N/ha treatments. To determine whether these treatment differences were significant, data were analysed using the SAS procedure TTEST (SAS Institute, 1989). In all instances, differences among these N rates were not significant, therefore these data were pooled and are presented as 115 kg N/ha. As there were no significant effects of N rate on DM, N, or zein accumulation in SS42 all data for SS42 were pooled across N rates.

Non-linear regression

Sigmoidal trends were modelled using the Boltzman function (Graybill and Iyer, 1994; Equation 6.1) which gave lowest RSS compared with other models in the sigmoidal family.

$$y = \frac{a - b}{1 + e^{\frac{(x - c)}{d}}} + b \qquad (6.1)$$

To account for non-constant variance, models were weighted by the inverse of the SE of the mean for each harvest. Coefficients of determination were calculated using Equation 6.2.

$$R^2_{adj} = 1 - \left(\frac{n-1}{n-p} \times \frac{RSS}{TSS} \right) \qquad (6.2)$$

where R^2_{adj} is the adjusted coefficient of determination; n is the total degrees of freedom; p is the number of parameters in the model; RSS and TSS are the residual and total sums of squares for the model, respectively.

Correlation analysis

Partitioning coefficients for each organ for the periods R1 to R2/R3 (Fig. 5.1) and R2/R3 to R4 (Fig. 5.2) were correlated against the quantity of zein accumulated at R2/R3 and R4 (i.e., harvests 3 and 5 in Table 6.2, respectively). However, non-constant variance, apparent in many of the correlations, violated an assumption of the analysis (Mead et al., 1993). Rather than transform the data or use weighted regression (which would have obscured important information), lines were tentatively drawn between the groups of data for each genotype.

6.3 Results

6.3.1 Dry matter accumulation in kernels through ontogeny

Dry matter accumulated in kernels of the three cultivars in a sigmoidal pattern (Fig. 6.1). While similar quantities of DM accumulated in kernels of all cultivars up to 179 GDD (i.e., the second cob harvest; Table 6.2), significant cultivar differences in response to N rate were detected at later harvests. Kernels of Furio contained significantly more DM than those of SS42 from 244 GDD onwards for the 115 kg N/ha treatment and from 340 GDD for the control. At 422 GDD (the final harvest), kernels of Furio in the 115 kg N/ha treatment contained 167 mg DM (SE 3.0), 49% more than the 85 mg (SE 1.6) for those of SS42. While kernels of Jubilee contained similar quantities of DM as SS42 at 244 GDD, kernels in both the control and 115 kg N/ha treatments contained significantly more DM from 340 GDD onwards. At 422 GDD, kernels of Jubilee in the 115 kg N/ha treatment contained 136 mg DM (SE 1.8), 37% more than those of SS42, but less than those of Furio. Whereas kernels in the control N treatment of Furio contained 151 mg DM (SE 1.1), those of Jubilee contained 124 mg (SE 2.3), corresponding to a 18% difference. A similar significant difference was observed between the 115 kg N/ha treatments for these cultivars. Differences in kernel DM between Jubilee and Furio at earlier harvests were not significant.

Differences between the N rates for kernel DM content of Jubilee and Furio were significant from 244 GDD onwards (Fig. 6.1). At 244 GDD kernels of Jubilee in the control N treatment contained 28 mg DM (SE 1.7), 22% less than the 35 mg (SE 1.5) contained by those in the 115 kg N/ha treatment. Similarly, Furio kernels in the control N treatment contained 39 mg DM (SE 1.0), 29% less than the 55 mg (SE 2.6) for those in the 115 kg N/ha treatment. The magnitude of this difference declined with ontogeny such that at 422 GDD the difference was only 8% for Jubilee, and 9% for Furio. Nitrogen rate did not influence DM contents for SS42.

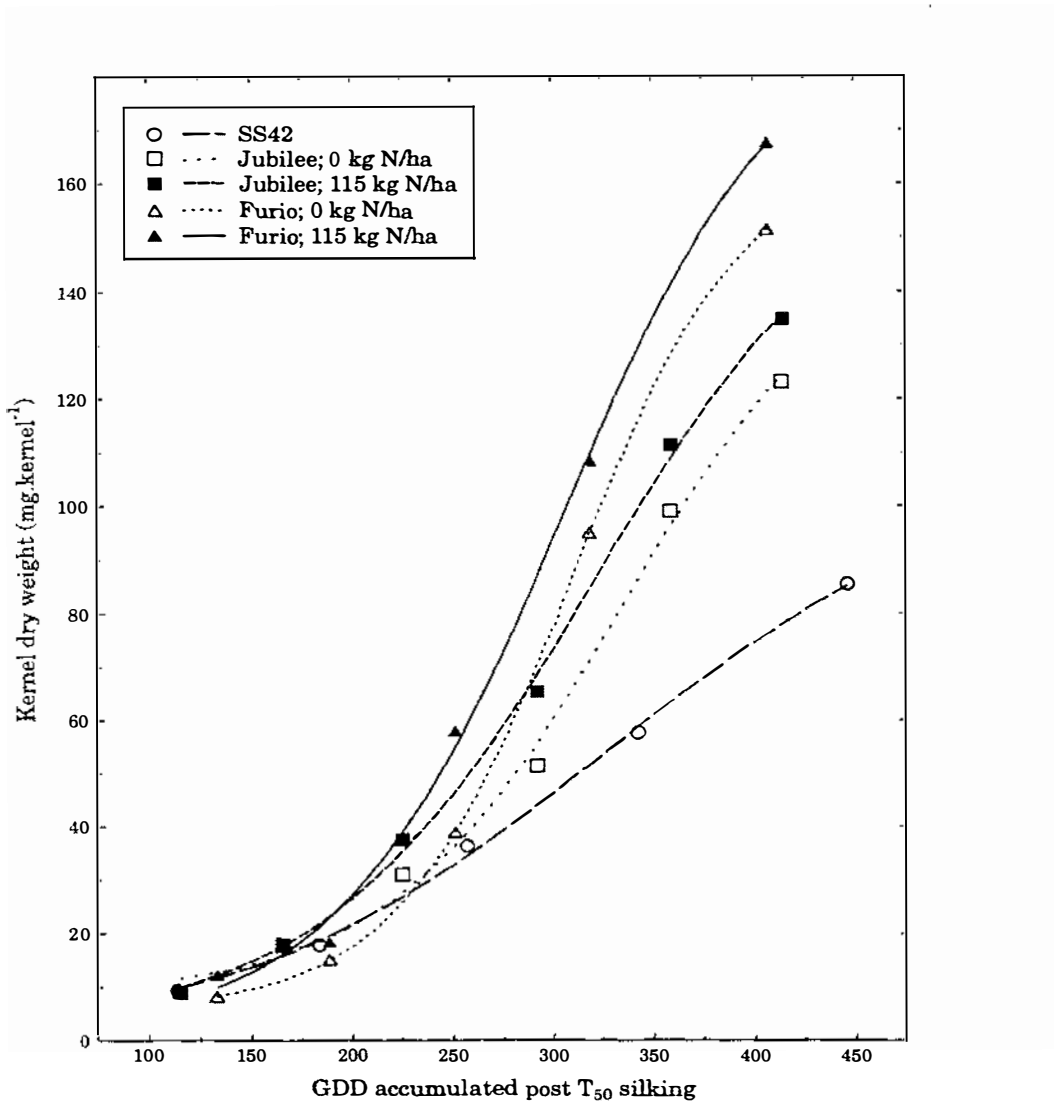

Fig. 6.1. Dry matter accumulation in kernels of SS42, Jubilee, and Furio as influenced by N rate. Each data point represents the mean for each harvest, pooled across blocks after analysis for clarity. Data for SS42 were pooled across N rates. Fitted functions are: SS42, $Y=-108.8/(1+e^{(X-327.4)/92.0})+108.8$ ($R^2_{adj}=0.93$); Jubilee, 0 kg N/ha, $Y=8.3-145.9/(1+e^{(X-334.7/58.5)})+145.9$ ($R^2_{adj}=0.96$); Jubilee, 115 kg N/ha, $Y=2.0-168.8/(1+e^{(X-321.5/68.8)})+168.8$ ($R^2_{adj}=0.98$); Furio, 0 kg N/ha, $Y=5.5-161.3/(1+e^{(X-309.4/43.6)})+161.3$ ($R^2_{adj}=0.92$); Furio, 115 kg N/ha, $Y=1.1-193.5/(1+e^{(X-305.0/56.7)})+193.5$ ($R^2_{adj}=0.91$).

6.3.2 Zein accumulation in kernels through ontogeny

Zein accumulated in kernels in a sigmoidal fashion (Fig. 6.2). While levels of zein for the three cultivars were similar up to 179 GDD, significant differences were detected from 244 GDD onwards. At these harvests, largest quantities of zein accumulated in kernels of Furio. At 244 GDD, kernels of Furio contained at least 453 μg zein (SE 13), 22% more than the 353 μg (SE 15) in those of SS42. The quantity of zein contained in kernels of Jubilee was similar to that of Furio and SS42 at this harvest. The cultivars responded to N rate differently at 340 GDD with a significant increase in levels of zein for both Jubilee and Furio with N fertiliser and a negligible response for SS42. Kernels of both Jubilee and Furio contained significantly more zein than those of SS42 at this harvest. Although levels of zein were similar between the control N treatments of Furio and Jubilee at this harvest, significant differences were detected among the cultivars for the 115 kg N/ha treatment. Whereas kernels of Jubilee in the 115 kg N/ha treatment contained 789 μg zein (SE 13) those of Furio contained 984 μg (SE 21) with this N rate. Differences among the N rates for both Furio and Jubilee were significant at this harvest. Further significant cultivar differences were observed at 422 GDD. At this harvest, kernels of Furio in the 115 kg N/ha treatment contained 1251 μg zein (SE 21), significantly more than the 932 μg (SE 17) and 643 μg (SE 19) in those of Jubilee and SS42, respectively. Kernels in the control N treatment of Furio contained 1164 μg zein (SE 17), significantly more than those of Jubilee at either N rate. Furthermore, both the control and 115 kg N/ha treatments of Jubilee contained significantly more (at least 20%) zein than SS42 at this harvest. Differences among the N rates for Jubilee and Furio were also significant at 422 GDD. Compared to the controls, levels of zein for Furio and Jubilee were 7 and 13% higher with 115 kg N/ha, respectively. The cultivar × N rate interaction was not significant for this harvest.

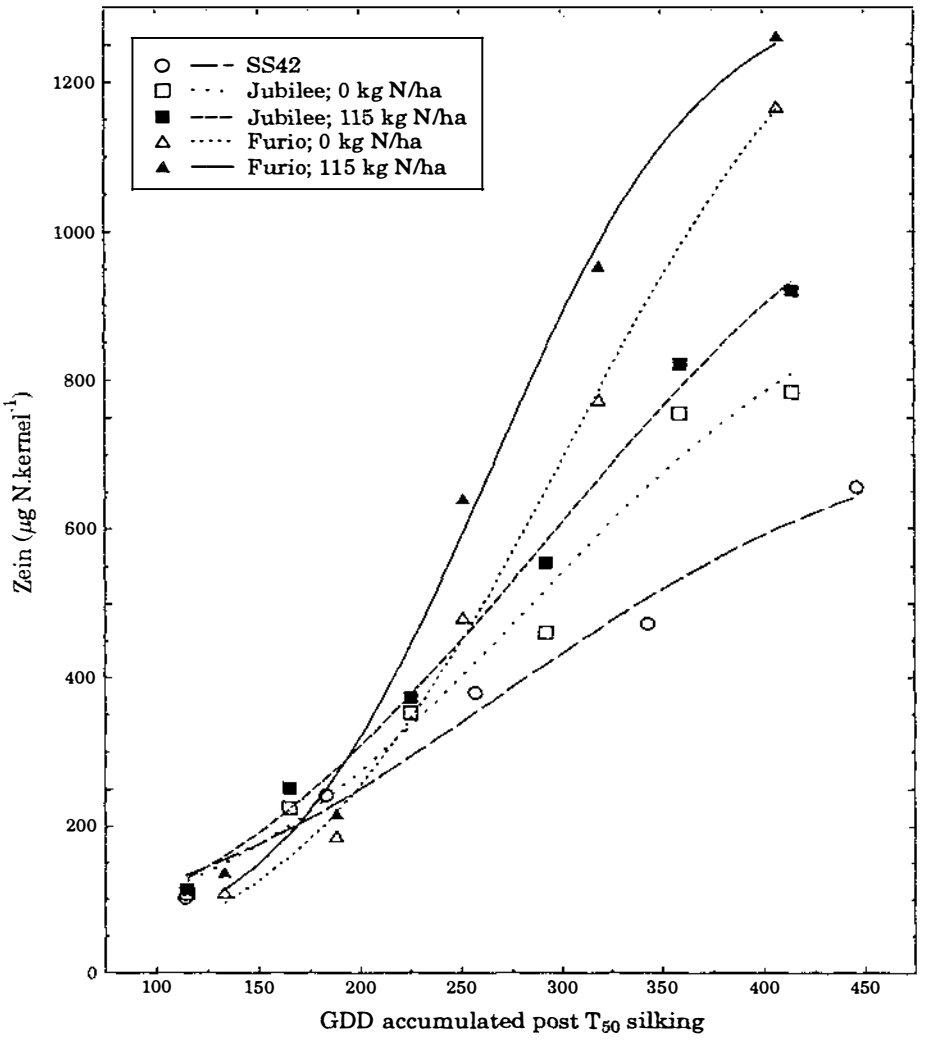

Fig. 6.2. Zein accumulation in kernels of SS42, Jubilee, and Furio as influenced by N rate. Each data point represents the mean for each harvest, pooled across blocks after analysis for clarity. Data for SS42 were pooled across N rates. Fitted functions are: SS42, $Y=-757.5/(1+e^{(X-271.1/101.5)})+757.5$ ($R^2_{adj}=0.97$); Jubilee, 0 kg N/ha, $Y=-2.7-995.5/(1+e^{(X-283.7/88.1)})+995.5$ ($R^2_{adj}=0.95$); Jubilee, 115 kg N/ha, $Y=-68.5-1315.3/(1+e^{(X-294.2/105.3)})+1315.3$ ($R^2_{adj}=0.93$); Furio, 0 kg N/ha, $Y=-41.1-1505.3/(1+e^{(X-304.0/74.2)})+1505.3$ ($R^2_{adj}=0.92$); Furio, 115 kg N/ha, $Y=0.3-1342.7/(1+e^{(X-263.7/54.8)})+1342.7$ ($R^2_{adj}=0.94$).

The relationship between DM accumulation and zein accumulation was non-linear (Fig. 6.3) with the fitted function strongly influenced by the six data points for Furio (top right in Fig. 6.3) as evidenced by large DEFITS values (SAS Institute, 1989; data not presented). Non-linearity was

apparent even when individual functions for each cultivar were fitted. Moreover, as the coefficients for these functions were similar among the cultivars, there was no benefit from fitting individual functions. Clearly, further data at later ontogenetic stages for each cultivar are required to confirm the appropriateness of this function.

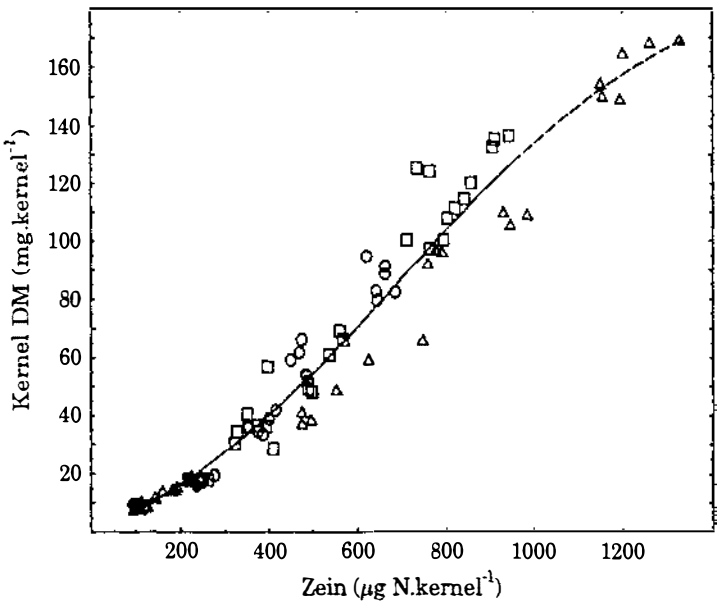

Fig. 6.3. Relationship between kernel DM accumulation and the level of zein in the kernel. □ = Jubilee, Δ = Furio, ○ = SS42. Postulated function is $Y=-23.0-219.3/(1+e^{(X-696.6)/327.7})+219.3$ ($R^2_{adj}=0.91$).

6.3.3 Separation of zein proteins at R4

Distinct differences in zein protein banding were observed between SS42 and the other two cultivars. Whereas Jubilee and Furio exhibited distinct banding of 24 and 22 kDa proteins (i.e., α-zein; Esen, 1986, 1987; Wilson, 1991), only trace amounts were observed for SS42. Similarly, banding observed for Furio and Jubilee at 45 kDa was also negligible for SS42. No obvious differences in banding patterns and apparent densities of these bands were observed between

Jubilee and Furio. Furthermore, as banding patterns were similar between the control and 230 kg N/ha treatments, only the 230 kg N/ha treatments are presented (Fig. 6.4).

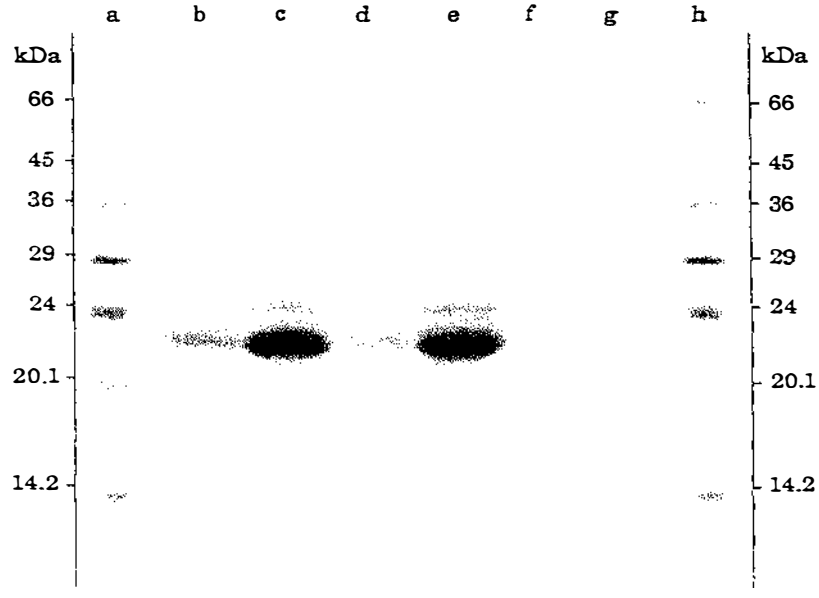

Fig. 6.4. Separation of zein fractions from kernels harvested at R4 by SDS-PAGE. Lanes a and h are the standards with lanes b-g the samples. Lanes b and c correspond to Furio, d and e to Jubilee, and f and g to SS42. The first lane for each cultivar was loaded with 50 µl of sample and the second with 100 µL. All samples were from kernels in the 230 kg N/ha treatments.

6.3.4 Nitrogen accumulation in kernels through ontogeny

The sigmoidal pattern observed for DM and zein accumulation in kernels (Figs. 6.1 and 6.2, respectively) was also detected for N accumulation (Fig. 6.5). While the three cultivars contained similar quantities of N at the first two harvests, significant differences were detected from 244 GDD onwards through cultivar x N rate interactions. These interactions resulted from the lack of response of SS42 to N rate, which contrasted both Jubilee and Furio. Regression analysis revealed that only kernels in the 115 kg N/ha treatment for Furio and Jubilee contained

significantly more N than those of SS42 at 244 GDD, containing 11 and 35% more N, respectively. Similarly, only for the 115 kg N/ha treatments were differences between Jubilee and Furio significant at 244 GDD. Kernels of Furio in the 115 kg N/ha treatment contained 1.44 mg N (SE 0.07), 27% more than the 1.05 mg (SE 0.03) contained by those of Jubilee. Differences among the N rates for both Jubilee and Furio were not only significant at this harvest but also at subsequent harvests. At 446 GDD, kernels of Jubilee in the control N treatment contained 2.34 mg N (SE 0.05), 14% less than the 2.73 mg (SE 0.03) for those in the 115 kg N/ha treatment. Kernels of Furio in the control N treatment contained 2.77 mg N (SE 0.05) and those of the 115 kg N/ha treatment contained 3.40 mg N (SE 0.09) at this harvest. Regression analysis confirmed the significance of cultivar differences at this harvest with kernels of Furio in the 115 kg N/ha treatment containing 3.40 mg N (SE 0.09) and those of Jubilee containing 2.73 mg N (SE 0.04). Similar significant differences were observed for the control N treatments. All these treatments contained significantly more N than the 1.87 mg (SE 0.03) contained by kernels of SS42 at this harvest. Kernels of SS42 also contained significantly less N than the other cultivars and N rates at the previous harvest (340 GDD). Kernels in the 115 kg N/ha treatments of Jubilee and Furio contained similar quantities of N at this earlier harvest as did the control N treatments.

With zein and DM also accumulating in kernels with a sigmoidal pattern (Figs. 6.1 and 6.2) they were both highly correlated with N accumulation ($r=0.98$; $P<0.001$). In these instances, non-linearity was not detected.

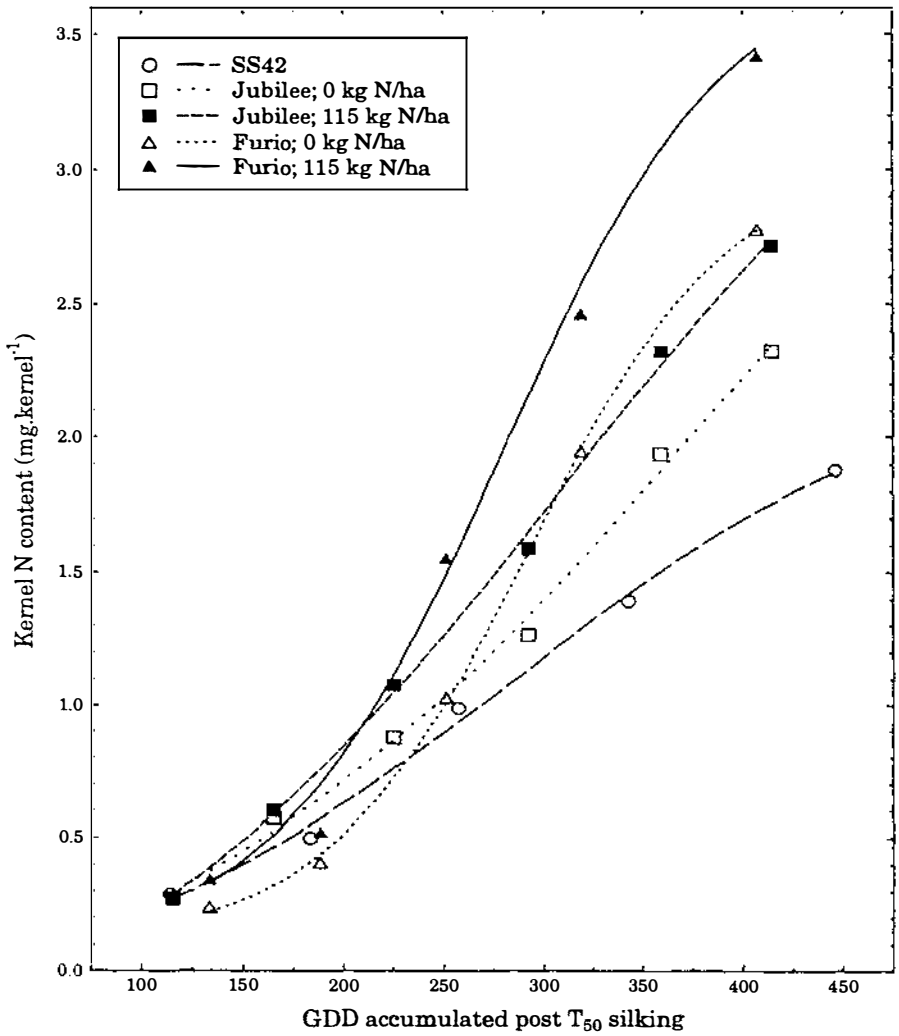

Fig. 6.5. Nitrogen accumulation in kernels of SS42, Jubilee, and Furio as influenced by N rate. Each data point represents the mean for each harvest, pooled across blocks after analysis for clarity. Data for SS42 were pooled across N rates. Fitted functions are: SS42, $Y=-0.16-2.47/(1+e^{(X-281.7/107.1)})+2.47$ ($R^2_{adj}=0.95$); Jubilee, 0 kg N/ha, $Y=-0.41-5.20/(1+e^{(X-396.6/15\ .1)})+5.20$ ($R^2_{adj}=0.91$); Jubilee, 115 kg N/ha, $Y=-0.51+4.61/(1+e^{(X-307.4/123.1)})+4.61$ ($R^2_{adj}=0.94$); Furio, 0 kg N/ha, $Y=0.10-2.96/(1+e^{(X-292.2/51.0)})+2.96$ ($R^2_{adj}=0.97$); Furio, 115 kg N/ha, $Y=0.01-3.75/(1+e^{(X-278.3/57.4)})+3.75$ ($R^2_{adj}=0.96$).

6.3.4 Ontogenetic changes in kernel N concentration

Kernel N declined in concentration with ontogeny (Fig. 6.6) in contrast to concurrent increases in N (Fig. 6.5), zein (Fig. 6.2), and DM (Fig. 6.1). Most rapid declines for Jubilee and Furio coincided with the linear phase of DM, N and, zein accumulation (cf. Figs. 6.1, 6.2, and 6.5 with 6.6). As DM, N, and zein accumulation plateaued, the rate of decline in N concentration decreased for these cultivars with concentrations for Jubilee and Furio plateauing around 19.7 mg.g DM^{-1} (SE 0.6) at 422 GDD. Although concentrations for SS42 also declined with ontogeny, similar plateauing was not detected. While the influence of N rate at each harvest was similar, significant cultivar differences were detected. A N concentration of 31.5 mg·g DM^{-1} (SE 0.6) was detected at the first harvest (121 GDD) for kernels of Jubilee, significantly higher than the 28.2 mg.g DM^{-1} (SE 0.4) for those of Furio, but similar to the 30.4 mg.g DM^{-1} (SE 0.3) in those of SS42. At the second harvest (179 GDD), kernels of Jubilee contained N at a significantly higher concentration than both Furio and SS42. Although kernels of the three cultivars contained N at similar concentrations at the third harvest (244 GDD), further significant cultivar differences were detected at the final two harvests. At these harvests, SS42 had a significantly higher concentration of N (22.1 mg.g DM^{-1} (SE 0.4)) than either Jubilee or Furio.

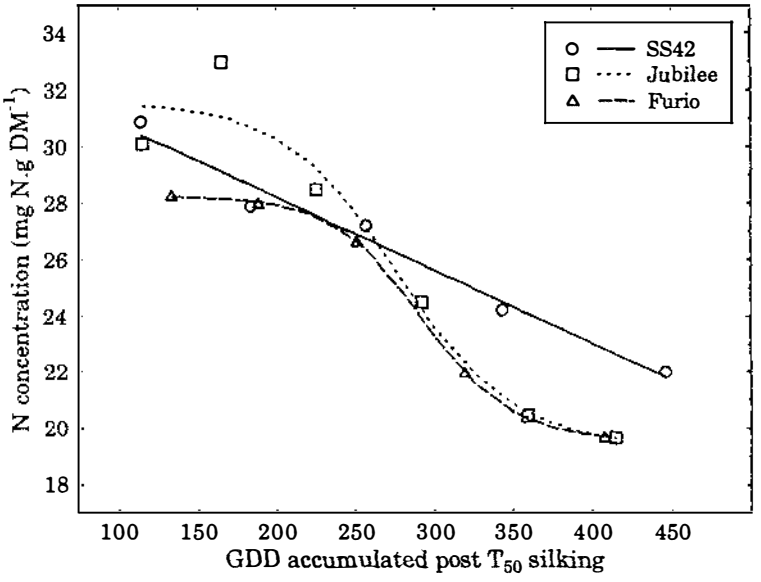

Fig. 6.6. Ontogenetic changes in kernel N concentration for (a) SS42, (b) Jubilee, and (c), Furio. Each data point represents the mean for each harvest, pooled across N rates. For clarity, data were also pooled across blocks after analysis. Fitted functions are: SS42, $Y=33.4-2.6\times10^{-2}X$ ($r^2=0.94$); Jubilee, $Y=31.6+12.2/(1+e^{(X-277.0/35.9)})-12.2$ ($R^2_{adj}=0.92$); Furio, $Y=28.3+8.6/(1+e^{(X-292.1/27.8)})-8.6$ ($R^2_{adj}=0.94$).

6.3.5 Relationship between the level of zein and N and DM partitioning to kernels

The overall correlation between the level of zein and kernel sink strength for DM was 0.72 ($P<0.001$). However, a plot of the two variables (Fig. 6.7) indicates heterogeneous variance; a violation of an assumption of this analysis (Mead et al., 1993). Variance increased as the concentration of zein increased. As discussed in Section 6.2.4, data were not transformed as a transformation would have obscured important information. Rather, groups of data for each genotype were identified in the following graphs (Figs. 6.7-6.9) for comparison.

At low levels of zein (i.e., 150-400 μg·kernel^{-1}) kernel sink strength for DM was similar amongst the three cultivars. Moreover, at these low levels there appeared a trend for increased kernel sink strength with increased zein content. At high levels of zein, however, this trend was not evident with Furio kernels containing significantly more zein than either SS42 or Jubilee yet having a significantly lower kernel sink strength.

The association between the level of zein and kernel sink strength for N was similar to that between the level of zein and kernel sink strength for DM (data not presented). Such similarity is consistent with the high association (r=0.80; P<0.001) between kernel DMPCs and NPCs.

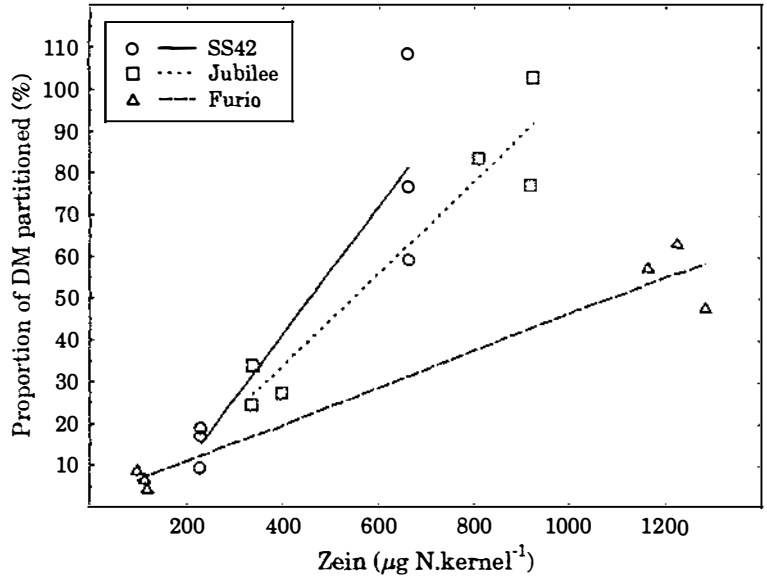

Fig. 6.7. Relationship between the level of zein in the kernel and kernel sink strength for DM. Overall correlation was 0.72 (P<0.001).

6.3.6 Relationship between the level of zein and N and DM partitioning to stems and husks

Partitioning of DM to both stems and husks was negatively associated with the level of zein ($r=-0.57$; $P<0.01$ and $r=-0.69$; $P<0.002$, respectively). As with kernel sink strength, however, the assumption of constant variance was not met in these analyses (Figs. 6.8 and 6.9). When data for each cultivar are identified, the heterogeneous variance is seen to be attributable to cultivar differences at high levels of zein.

At low levels of zein, higher partitioning to stems was associated with lower zein content (Fig. 6.8). At higher levels, on the other hand, this trend was reversed; the higher the level of zein, the higher the proportion of DM partitioned to stems. In contrast, the three cultivars partitioned similar proportions of DM to husks at low levels of zein, but not at higher levels (Fig. 6.9). Jubilee remobilised DM from husks at the higher level of zein, while Furio partitioned DM to husks. These differences in partitioning occurred despite Furio kernels containing a significantly higher level of zein than Jubilee.

The association between husk NPCs and level of zein ($r=-0.69$; $P<0.002$) was almost identical to that presented in Fig. 6.9 for husk DMPCs and zein. Such similarity is consistent with husk DMPCs and NPCs being highly correlated ($r=0.84$; $P<0.001$). Nitrogen partitioning to stems was not correlated with the level of zein.

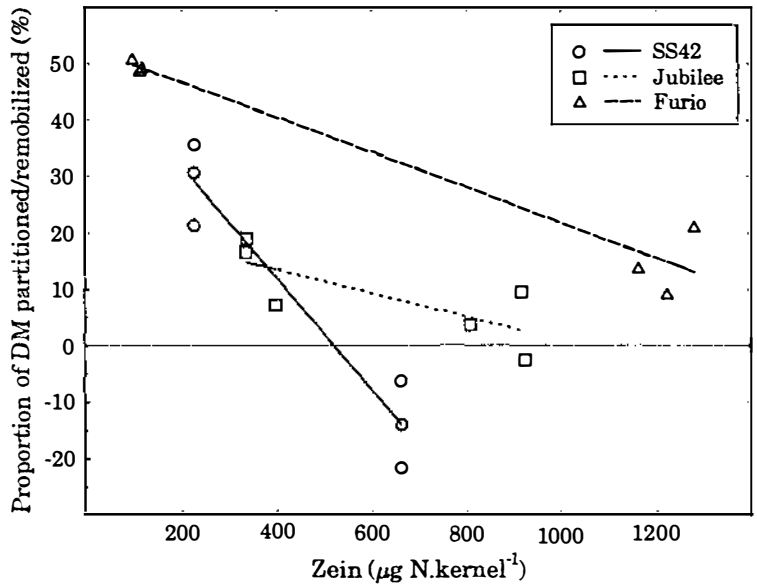

Fig. 6.8. Relationship between the level of zein in the kernel and DM partitioning to stems. Overall correlation was -0.57 (P<0.01).

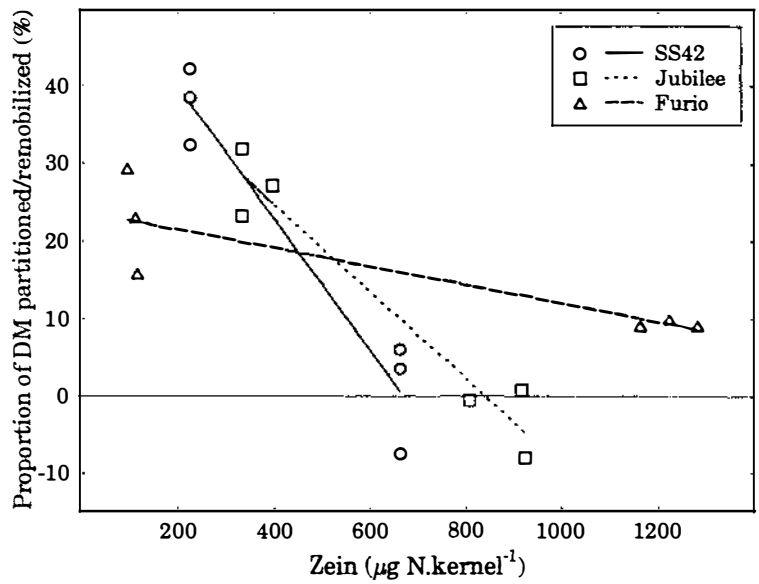

Fig. 6.9. Relationship between the level of zein in the kernel and DM partitioning to husks. Overall correlation was -0.69 (P<0.002).

6.4 Discussion

High correlations between kernel DM accumulation and zein content in both the current study (Fig. 6.3) and in studies with maize (Cully et al., 1984; Misra and Oaks, 1981; Tsai et al., 1978a, 1978b, 1980, 1983) strongly suggests that zein is associated with kernel sink strength. Further evidence is provided by the significantly lower zein accumulation in kernels of endosperm mutants (Fig. 6.2) and their correspondingly lower DM contents (Fig. 6.1). Compared to the *su1* and *sh2* mutants, the wild type contained about 25% and 49% more zein at R4, respectively, and accumulated 18% and 49% more DM, respectively. Similarly, kernels of the *su1* mutant, which contained 31% more zein than those of the *sh2* mutant, accumulated 38% more DM. Similar results have been reported in other studies (Figs. 3.7 and 5.7; Dalby and Tsai, 1975; Doehlert and Kuo, 1994; Glover et al., 1975; Goldman and Tracy, 1994; Ma and Nelson, 1975; Mertz et al., 1964; Misra et al., 1972, 1975a; Nelson, 1980; Nelson et al., 1965; Paulis et al., 1978; Tsai and Dalby, 1974; Tsai et al., 1978b).

A positive association between the level of zein and apparent kernel sink strength for DM ($r=0.72$; Fig. 6.7) further supports the hypothesis that zein may influence kernel sink strength. However, heterogeneous variance meant that the calculated coefficient was an incorrect statistic (Mead et al., 1993). Examining Fig. 6.7 indicates that this variation was due to cultivar differences in the proportion of DM partitioned, particularly at high levels of zein. Jubilee and SS42 partitioned large proportions (about 80-90%) of their available DM to kernels at the high level of zein, notably more than the 60% partitioned by Furio. Such lower partitioning by Furio is not consistent with the hypothesis that a higher level of zein translates into a higher kernel sink strength. However, as discussed in Section 5.4, the wider ontogenetic interval over which the partitioning coefficients were calculated for Furio (Table 5.1) apparently reduced the size of the coefficients. The effect was to make it difficult to compare partitioning coefficients between R1 and R4 for Furio with those of either Jubilee or SS42 as is possibly the case here. There is also the possibility that the lower DM partitioning to Furio compared to the other cultivars may have resulted from Furio receiving less incident radiation (*ca.* 24% compared to SS42). However, analysis in Chapters 3 and 5 failed to detect differences in DM or N partitioning to kernels when different incident radiation levels were taken into account.

Dry matter, zein, and N accumulated in kernels with the sigmoidal pattern (Figs. 6.1, 6.2, and 6.5) observed in other studies (Dalby and Tsai, 1974; Da Silva and Arruda, 1979; Jones et al., 1977a; Lee and Tsai, 1985; Misra and Oaks, 1981; Tsai et al., 1983). The observation that cultivar differences in accumulation generally became apparent from 244 GDD onwards (i.e., from R2/R3) implies that zein synthesis was similar among the genotypes during early grain filling. This contrasts work with other mutants (e.g., *o2*, *fl2*) where quantities of zein were not only significantly lower during this period but the synthesis of zein was delayed (Dalby and Tsai, 1974; Misra et al., 1975b; Tsai, 1979a; Tsai et al., 1978a, 1978b; Tsai and Dalby, 1974). Further data at lower GDD are required to confirm this finding.

The higher sink strength for DM by kernels of Jubilee compared to SS42 between R1 and R2/R3 (Figs. 3.13 and 5.1) was earlier hypothesised (Sections 3.4 and 5.4) to result from a greater rate of zein accumulation. The observation that kernels of Jubilee contained similar quantities of zein as SS42 at 121 GDD (Fig. 6.2) but significantly more (about 28%) at 244 GDD (i.e., R2/R3) supports this hypothesis. However, Jubilee continued to accumulate DM at a faster rate between R2/R3 and R4, yet cultivar differences in kernel sink strength for DM between R2/R3 and R4 (Figs. 3.14 and 5.2) were not detected. Such a response is consistent with the hypothesis that zein reaches physiologically maximum levels for each cultivar during this period. However, as a plateau phase for zein accumulation (which would signal termination of zein synthesis) was not identified for any of the genotypes, this latter hypothesis is not supported by these results.

Levels of zein increased significantly with increased N fertility from 244 GDD for Jubilee and Furio (Fig. 6.2). This response, consistent with studies on maize (Keeney, 1970; Prince, 1954; Rendig and Jimenez, 1978; Sauberlich et al., 1953; Tsai et al., 1978a, 1980) is attributed to zein becoming increasingly abundant in the endosperm with ontogeny (Rendig and Broadbent, 1979; Schneider et al., 1952; Tsai et al., 1980, 1984; Wolfson and Shearer, 1981). Moreover, under high N fertility the increased supply of amino acids (Balconi et al., 1991, 1993; Keeney, 1970; MacGregor et al., 1961; Shinano et al., 1991) enables more N to be partitioned to kernels (Anderson and Kole, 1975; Balconi et al., 1991, 1993; Barlow et al., 1983; Manther and Giese, 1984), presumably for zein synthesis. However, unlike either Jubilee or Furio, levels of zein in SS42 did not respond to increased N fertility. This lack of response is consistent with the limited

response to N rate by SS42 observed elsewhere in this study (e.g., Chapters 2-5). While these observations may, in part, be explained by the high levels of residual- and mineralizable-N (Tables 2.1 and 4.1) masking any effect of increased N fertility, they may also be attributable to the lower levels of zein bought about by the *sh2* mutation. As discussed above, zein levels in the *sh2* mutant at R4 were 28 and 49% lower than the *su1* mutant and wild type, respectively (Fig. 6.2). Despite these lower levels, total endogenous N levels were only 21 and 28% lower at this ontogenetic stage than the *su1* mutant and wild type, respectively (Figs. 5.3d-f; Table 5.8). With zein accumulation dependent on an adequate supply of N (Tsai et al., 1980, 1984) it is conceivable that zein accumulation would be less limited by endogenous N levels in the *sh2* mutant than in either the *su1* mutant or the wild type, and hence less likely to respond to additional fertiliser N under moderate to high soil N fertility. This hypothesis is supported by the correlation between levels of zein for the *su1* mutant increasing significantly with N fertiliser from 340 GDD compared to 244 GDD for the wild type and the significantly higher zein accumulation by the wild type at 244 GDD (Fig. 6.2).

Negative correlations between zein quantity and DMPCs for both husks and stems (Figs. 6.8 and 6.9) further support the hypothesis that these organs accumulate photoassimilate not consumed in reproductive growth (Sections 3.4 and 5.4). Kernels with a low sink strength accumulate less photoassimilate than would otherwise be accumulated with a high sink strength. Hence, increased zein content, and thus kernel sink strength, was associated with decreased partitioning of DM to stems and husks for all three cultivars. Similar observations were made by Walker et al. (1988). Partitioning to husks and stems declined with increases in the level of zein and partitioning to these organs essentially ceased at levels of 600-1000 μg zein·kernel^{-1}. At higher levels, DM was remobilised from these organs, consistent with the hypothesis that increased kernel sink strength reduces photoassimilate availability. The greater remobilisation of DM from stems of SS42 compared to Jubilee between R2/R3 and R4, despite a lower level of zein (Fig. 6.8) is consistent with the suggestion that photosynthetic rates were impaired for this cultivar (Section 5.4).

Separation of zeins clearly indicates that SS42 was deficient in α-zein (Fig. 6.4). While this observation is consistent with Doehlert and Kuo's (1994) and Paulis et al.'s (1992) studies, it

contrasts work by Misra et al. (1976) and Tsai et al. (1978b). Such preferential loss of α-zein was not observed for the *su1* mutant, and in this instance contrasts Wilson's (1992) study. Aside from α-zein, the only other zein detected was a 45 kDa protein for both Jubilee and Furio. With no other studies to my knowledge having reported such a class of zein, the significance of this protein in unknown. The apparent absence of other zeins (i.e., β-, γ-, or δ-zeins; Esen, 1987) may reflect their relatively low abundance compared to α-zein (Esen, 1986, 1987; Larkins et al., 1989; Lee et al., 1976; Misra et al., 1976; Wilson, 1991), particularly if the size of sample loaded was insufficient. Nevertheless, further research is clearly required if these conflicting results are to be clarified and functional roles assigned to these zeins.

In conclusion, this study has provided further evidence to support hypotheses proposed throughout Chapters 2-5 that differences in physiological responses among genotypes were related to differences in kernel sink strength, which in turn may be related to zein accumulation. In doing so, further evidence to support the hypothesis that an inhibitory cycle stems from the limited sink strength of kernels during early grain filling has been provided. Similarly, this study has further supported the hypothesis that the limited yield response of SS42 to N fertiliser compared to Jubilee was due to physiologically lower levels of zein, and hence a lower requirement for N.

Chapter 7

General discussion

7.1 Agronomic and physiological importance

A primary goal of this research was to increase grower profit by identifying means of increasing yield, reducing input costs, or both. Achieving this goal required critical evaluation of the original cropping regime. Under this regime, crops of Jubilee and SS42 are sown at 55,000 plants per hectare with up to 150 kg/ha of fertiliser N. With suggestions that growers commonly apply more fertilizer N than is economically optimal (Morris and Blackmer, 1989; El-Hout and Blackmer, 1990) and numerous studies reporting ear yield increases in the order of 3-12 t/ha with higher densities than currently used (Andrew and Weis, 1974; Bailey, 1941; Bowers, 1943; Moss and Mack, 1979; Roberts et al., 1980a; Warren and Kelly, 1963), doubt was cast as to whether this regime maximized yield and used fertiliser N efficiently. The suitability of this regime for both Jubilee and SS42 (the cultivars which currently dominate sweet corn plantings at Gisborne) is further questioned by studies showing hybrid differences in response to both density and N rate (Balko and Russell, 1980a; Sabata and Mason, 1992; Smicklas and Below, 1990; Tsai et al., 1984).

The first experiment (Chapter 2) showed that yield of both SS42 and Jubilee was maximised at densities greater than 100,000 plants per hectare (Figs. 2.4a and 2.11a). However, such densities would unlikely maximise grower profit due to yield at high densities containing an increased proportion of cobs unsuitable for factory processing (Sections 2.3.1.3 and 2.3.2.3) with these cobs deducted from payments to growers. Rather, densities which maximise grower profit by maximising 'processable' (or marketable) ear yield are 80,800 and 100,660 plants per hectare for SS42 and Jubilee, respectively (Figs. 2.8a and 2.15a). However, as yield for both cultivars at each of these densities was statistically similar to that at 55,000 plants per hectare, it is likely that growers are currently planting within the density range for maximum yield.

There is little value in maximising marketable ear yield if the processor's saleable products (i.e., kernels and cobs) are not also maximised; although marketable ear yield maximises grower profit, processors may not be advantaged and therefore reluctant to increase payments for crops. Marketable kernel and marketable cob yield for both SS42 and Jubilee were maximised in the range 69-77,000 plants per hectare (Figs. 2.9a, 2.10a, 2.16a, and 2.17a). As with marketable ear

yield, however, yield within this density range was statistically similar to that at 55,000 plants per hectare. This again suggests there is no yield advantage from growers increasing densities to 69-77,000 plants per hectare. However, these higher densities may offer a significant advantage to processors. Kernels derived from secondary ears generally had a higher SMC and were less mature than those from primary cobs (Chapter 2). Thus, their lower contribution to total marketable yield in the density range of 69-77,000 plants per hectare (Figs. 2.9c, 2.10c, 2.16c, and 2.17c) should increase the consistency of the saleable product.

As density increases, interplant competition for N also increases (Donald, 1963), and as a consequence, the level of N required for maximum yield also increases (Bray, 1954; Chipman and MacKay, 1960; Colyer and Kroth, 1968; Downey, 1971; Duncan, 1954; Lang et al., 1956). Hence, ear yield increases of 4-11 t/ha may be achieved with N fertiliser (Balko and Russell, 1980b; Fox; 1973; Lang et al., 1956; Sanmaneechai et al., 1984; Steele et al., 1982). Despite such reports, the first experiment (Section 2) failed to generate such large yield increases with N fertiliser. Yield responses were either negligible or did not follow a trend consistent with incremental increases in N rate (e.g., Figs. 2.4 and 2.11). Further investigation revealed that high levels of soil available N (259 kg/ha; Table 2.1) probably negated the yield response in this experiment. A second experiment, designed to investigate yield response to N on a soil with low available N, also found limited response. Despite an apparently low level of soil available N (92 kg N/ha; Table 4.1), yield response to N rates above 74 kg/ha in the second experiment was also negligible (Figs. 4.3 and 4.10). Combining the two years' results suggests that maximum yield may be achieved when levels of soil available N are $\geq$ 213 kg N/ha (i.e., the average of the levels of N above which no further significant response to N rate was recorded in the two studies). This result is consistent with Tsai et al.'s (1992) suggestion that when soil available N is $\geq$ 175 kg/ha, yield response to fertiliser N will be limited. More importantly, however, these results suggest that by not accounting for soil available N levels when determining fertiliser regimes, some growers in Gisborne may be applying fertiliser N in excess of crop requirements for maximum yield.

High levels of soil available N may result from carryover of nitrates from previous crops (Jokela, 1992; Guillard et al., 1995; Kimble et al., 1972; Lory et al., 1995b; Olsen et al., 1970; Russelle

et al., 1981), a source which may be considerable in continuous sweet corn production (Herron et al., 1971; Roberts et al., 1980a; Taber and Peterson, 1979). While carryover (i.e., residual N) was identified as a source of N, the largest contributor to soil available N was mineralizable N, contributing up to 66% (Tables 2.1 and 4.1). Despite the apparent importance of mineralizable N, few growers use mineralizable N levels when estimating fertiliser N requirements. Failing to take mineralizable N into account is a result of most growers being unfamiliar with the concept of mineralizable N (Davis, pers. comm.). These studies therefore highlight two important areas on the N nutrition of sweet corn. First, the need for grower education on the importance of mineralizable N to cropping. In the two experiments conducted (Chapters 2 and 4), the $NZ 75 per sample for the comprehensive soil information obtained (e.g., Table 2.1) would easily have been recovered in savings in fertiliser and application costs. Second, to obtain maximum benefit from soil analyses (Jungk and Wehrmann, 1978; Stanford, 1973) further research is required, particularly on the relationship between soil available N and yield. Better understanding this relationship is essential if fertiliser N requirements are to be better estimated.

Under the conditions of soil available N experienced in these studies, Jubilee was more responsive to fertiliser N than SS42 (e.g., cf. Figs. 2.4 and 2.11). This finding may have important ramifications for the management of these cultivars. For example, if soil available N levels are high, SS42 may be cropped without the need for N fertiliser. This finding may be particularly important to growers of organic sweet corn as they are largely reliant on soil available N levels. Only with further research and perhaps 'cropping out' residual soil N in the year before the experiment (Tsai et al., 1992) can this suggestion be confirmed.

Different responses between Jubilee and SS42 to N fertiliser was associated with kernels of Jubilee accumulating significantly more (about 31%) zein than those of SS42 (Fig. 6.2). Zein, the primary N storage protein in kernels of sweet corn and maize (Tsai et al., 1980, 1983), becomes increasingly abundant as soil N fertility increases (Keeney, 1970; Prince, 1954; Rendig and Jimenez, 1978; Sauberlich et al., 1953; Tsai et al., 1978a, 1980). Significant increases in levels of zein with N fertiliser for Jubilee, unlike SS42 are therefore consistent with SS42 (*sh2* mutant) accumulating significantly less zein than Jubilee (*su1* mutant). Thus, Jubilee would be expected to require more N for maximum yield than SS42. Further, as total endogenous N levels

for SS42 at R4 were only 21% lower than Jubilee (Figs. 5.3d-f; Table 5.8), zein accumulation in kernels of SS42 would be less limited by endogenous N levels than those of Jubilee. As a consequence, SS42 would be less likely to respond to additional fertiliser N under moderate to high soil N fertility. Observations that zein levels for Furio (wild type) responded to N fertiliser at an earlier ontogenetic stage than Jubilee and had a significantly higher zein level at this ontogenetic stage (Fig. 6.2) support this hypothesis.

While it is known that zein serves as a N storage protein in kernels (Geraghty et al., 1981; Jones et al., 1977a; Tsai et al., 1978a, 1978b), results presented in Chapter 6 and in studies with maize (Cully et al., 1984; Misra and Oaks, 1981; Tsai et al., 1978a, 1978b, 1980, 1983) show that zein is associated with kernel sink strength. Zein may therefore be a reliable indicator of sink strength or perhaps even play a role in determining kernel sink strength. Evidence to suggest that zein may be a determinant of sink strength is indicated by studies showing that zein deficient mutants accumulate significantly less DM than wild types (Dalby and Tsai, 1975; Doehlert and Kuo, 1994; Goldman and Tracy, 1994; Ma and Nelson, 1975; Nelson et al., 1965; Tsai et al., 1978b). Chapter 6 showed that the wild type contained 25 and 49% more zein at R4 than the *su1* and *sh2* mutants, respectively (Fig. 6.2), and accumulated 18 and 49% more DM, respectively (Fig. 6.1). Similarly, kernels of the *su1* mutant, which contained 31% more zein than those of the *sh2* mutant, accumulated 38% more DM. Collectively, these results provide compelling evidence that zein level is associated with kernel sink strength, and therefore grain yield (Tsai and Tsai, 1990).

Kernel growth and development is dependent on being partitioned N and DM. However, the observation that DM was partitioned to vegetative organs in contrast to N being remobilised from these organs (Figs. 3.13, 3.14, 5.1, and 5.2) indicates that both SS42 and Jubilee were sink limited for current photoassimilate, yet source limited for newly assimilated N. Similar source and sink limitations have been shown in many studies (Below et al., 1981, 1984; Cliquet et al., 1990b; Goldsworthy et al., 1974; Hay et al., 1953; Prioul et al., 1990; Tollenaar, 1977; Yamaguchi, 1974). With roots requiring photoassimilate for active uptake of N (Hatrick and Bowling, 1973; Pan et al., 1995), it is unclear why roots were partitioned so little DM when photoassimilate was in excess. This source limitation is further surprising given that soil N

fertility was apparently high (Tables 2.1 and 4.1). Hay et al. (1953) and Sayre (1948) similarly observed N remobilisation from vegetative organs, regardless of soil N fertility. While there may be many theories to explain these phenomena, evidence from two experiments (Chapters 3 and 5) suggests that the two events are linked and are initiated by limited kernel sink strength. This link is discussed below and summarised in Fig. 7.1.

When maximum leaf area in maize and sweet corn is reached (around R1; Alofe and Schrader, 1975; Muchow, 1988; Uhart and Andrade, 1995b), ears are relatively small sinks (Figs. 3.13 and 5.1; Edmeades and Daynard, 1979a; Prioul et al., 1990; Setter and Meller, 1984; Schussler and Westgate, 1991a) and unable to accumulate all the photoassimilate being produced (Tanaka and Yamaguchi, 1972). Although the excess is partitioned to stems and husks (Figs. 3.13, 3.14, 5.1, and 5.2; Barnett and Pearce, 1983; Campbell, 1964; Huelsen, 1954), these organs can only accumulate a limited quantity before becoming saturated (Barnett and Pearce, 1983). Once saturated, photoassimilate may accumulate in leaves (Farrar and Gunn, 1996; Thomas and Stoddart, 1980), causing feedback inhibition of photosynthetic enzymes (Neales and Incoll, 1968) to reduce the supply of photoassimilate (Thomas and Stoddart, 1980). However, N assimilation is dependent on the rate of photoassimilate supply to roots (Pan et al., 1995). Thus, inhibited photosynthesis reduces N uptake (Hatrick and Bowling, 1973; Karlen et al., 1988; Wild and Breeze, 1981), and as a consequence, places more demand on vegetative organs to supply N (Figs. 3.14 and 5.2; Hageman, 1986; Reed et al., 1988). As the remobilisation of N from leaves impairs photosynthetic activity (Hageman, 1986; Muchow, 1988; Sinclair and deWit, 1976; Swank et al., 1982), photoassimilate supply to kernels and roots may be further restricted (Hageman, 1986). Hence, an inhibitory cycle (Fig. 7.1) may evolve from the limited sink strength of kernels.

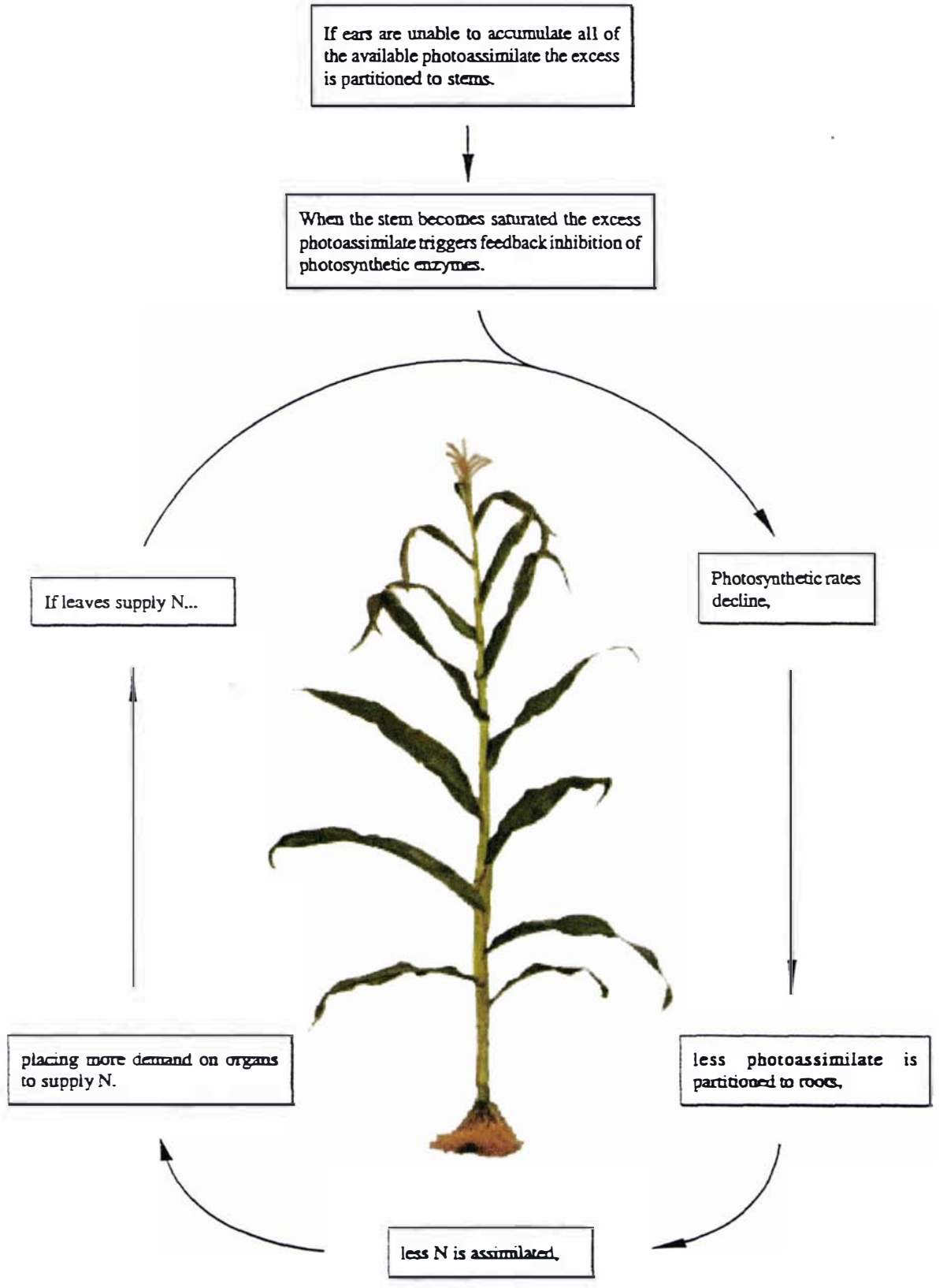

Fig. 7.1. Summary of the proposed inhibitory cycle.

Evidence supporting this inhibitory cycle is provided by several observations in Chapters 2, 3, and 5. For example, stems and husks were partitioned 72% of the available DM between R1 and R2/R3, consistent with kernels and rachis of Furio (wild type) having a combined sink strength of only 15% (Fig. 5.1). In contrast, the significantly higher sink strength of both kernels and rachis of Jubilee resulted in 42% of the available DM being partitioned to these organs. Jubilee had a significantly higher kernel sink strength than SS42 and partitioned significantly more DM to roots (cf. Figs. 5.1a-c). Furio also partitioned DM to roots during this period despite having a significantly lower kernel sink strength than Jubilee. Such partitioning was probably a consequence of having a larger stem, thereby enabling more photoassimilate to be stored and avoiding feedback inhibition of photosynthetic enzymes (Neales and Incoll, 1968). The higher partitioning of DM to roots by both Jubilee and Furio compared to SS42 was associated with these cultivars assimilating significantly more N than SS42 between R1 and R2/R3 (Table 5.6). As Furio continued to partition DM to roots between R2/R3 and R4 (cf. Figs. 5.2a-c), it assimilated significantly more N during this period than SS42 (Table 5.7). A lower N assimilation rate by SS42 combined with a significantly higher kernel sink strength for N resulted in SS42 remobilising significantly more N from stems and leaves than kernels of Furio between R1 and R2/R3 (cf. Figs. 5.1d and 5.1f). Although Jubilee partitioned DM to roots for N uptake between R1 and R2/R3, this cultivar also remobilised N during this period, sourcing N from leaves and roots (Fig. 5.1e). Collectively, these observations suggest that the lower sink strength of SS42 kernels resulted in this cultivar being more influenced by the inhibitory cycle (i.e., possible greater feedback inhibition of photosynthesis) than Jubilee.

The observation in Chapter 2 that a short silk delay for the secondary ear at low densities (i.e., 40,000 plants per hectare) was associated with greater kernel recovery from the primary ear is also consistent with the inhibitory cycle theory. It is consistent as the production of a secondary ear would help establish a large sink sooner and therefore minimise any effects of the inhibitory cycle.

Further evidence for the existence of an inhibitory cycle is derived from the remarkable similarity between the sequence of events proposed in Fig. 7.1 and the pattern of senescence in barren plants. Barrenness, whether arising naturally or by physical ear removal, is associated with

accelerated leaf senescence (Allison and Weinmann, 1970; Christensen et al., 1981; Kiniry et al., 1992; Prioul and Schwebel-Dugué, 1992; Uhart and Andrade, 1995a) as shown by a loss of chlorophyll and leaf N (Crafts-Brandner et al., 1984b; Feller et al., 1977; Fujita et al., 1994; Reed et al., 1988), a loss of photosynthetic enzymes (Christensen et al., 1981; Jeannette, 1993; Millard, 1988; Prioul, 1996; Tsai et al., 1986), and a significant decline in the net assimilation rate (Barnett and Pearce, 1983; Fujita et al., 1994; Moss, 1962; Thiagarajah et al., 1981). However, the onset of enzyme degradation is preceded by soluble sugar accumulation in leaves and stems (Allison and Watson, 1966; Allison and Weinmann, 1970; Setter and Flannigan, 1986; Verduin and Loomis, 1944).

The proposed inhibitory cycle is, however, inconsistent with observations that some corn plants rapidly senesce in the absence of developing grain (Allison and Weinmann, 1970; Christensen et al., 1981; Kiniry et al., 1992; Prioul and Schwebel-Dugué, 1992; Uhart and Andrade, 1995a) whereas senescence in others is either delayed or does not occur (Crafts-Brandner et al., 1984a; Crafts-Brandner and Poneleit, 1987b; Genter et al., 1970; Moss, 1962). According to the inhibitory cycle theory, barren plants should senesce rapidly. However, such differences may be explained by differences in the capacity to store photoassimilate, differences in net assimilation rates, or both (Crosbie and Pearce, 1982; Earl and Tollenaar, 1998; Vietor and Musgrave, 1979). While a high net assimilation rate would quickly saturate storage organs, the time at which this occurs will depend on the capacity of the storage organs to accumulate photoassimilate.

As grain filling proceeds, effects of the inhibitory cycle apparently become less important as plants bearing ears generally do not senesce until late in their ontogeny (Pan et al., 1995). This may occur because as kernel sink strength for DM increases (cf. Figs. 3.13, 3.14, 5.1, and 5.2), the concentration of photoassimilate in the stem declines (Daynard et al., 1969; Hanway, 1962a; Jones and Simmons, 1983; Jordan et al., 1950; Kiesselbach, 1950), and the inhibition of photosynthetic enzymes is alleviated (Barnett and Pearce, 1983; Neales and Incoll, 1968). However, effects of the cycle may still be evident. Continued remobilisation of N from stems for both SS42 and Jubilee and leaves for SS42 between R2/R3 and R4 (Fig. 5.2; Table 5.5) provides such evidence. Moreover, the observation that SS42 also remobilised DM from stems between R2/R3 and R4 (Fig. 5.2a) indicates that less photoassimilate was available for N

acquisition by roots (Pan et al., 1984), and therefore a greater influence from the inhibitory cycle as compared to Jubilee.

Eventually plants of maize and sweet corn senesce. As the DM content of kernels approaches physiologically maximum levels and kernel sink strength for DM declines (Hanft et al., 1986; Johnson and Tanner, 1972), photoassimilate begins to accumulate in the stem (Hume and Campbell, 1972), N assimilation declines (Friedrich et al., 1979), and plants begin to senesce. Such a striking similarity between this sequence of events and the premature senescence in barren plants suggests that ultimately, the inhibitory cycle may be part of the senescence process.

The inhibitory cycle offers plausible explanations for many physiological responses observed in sweet corn and maize. However, confirming the existence of an inhibitory cycle requires further research. In particular, research on ontogenetic changes in photoassimilate concentrations and photosynthetic rates using genotypes differing in kernel sink strength but with similar prolificacy characteristics is required. Further, if confounding influences (e.g., moisture stress, photosynthetic photon flux density (PPFD), lodging) are to be avoided, controlled environments would be essential. Confounding influences among cultivars for quantifying kernel sink strength may also be eliminated by using heterozygotes pollinated with *sh2* and *su1* pollen to obtain equal segregation of normal, *sh2*, and *su1* kernels on the same ear (Tsai et al., 1983). Such techniques would avoid the confounding effects of interplant variability, interacting pleiotropic effects (e.g., reduced photosynthetic rates; Morot-Gaudry et al., 1978) caused by the mutations, and environmental interactions (Tsai et al., 1980).

Confounding influences of different incident radiation levels between cultivars should also be avoided. While different levels were identified for the cultivars in Chapters 3 and 5, data adjustment to account for this variable showed only minor influences. Hence, although effects were identified, general trends (as discussed in relation to the inhibitory cycle) were unchanged.

7.2 Breeding and crop management to increase yield

Confirmation that an inhibitory cycle exists would have profound effects on both the management and breeding of sweet corn and maize crops for increased grain yield. Strategies which aim to increase sink strength during early grain filling or better coincide photoassimilate production with kernel sink strength would be paramount. As such, this may involve increasing kernel sink strength during early grain filling to accumulate more photoassimilate. Immediately, one might conclude that to increase yield, kernel sink strength should be increased by increasing the concentration of zein in the kernel; assuming there is a functional relationship between zein and kernel sink strength. However, zein concentration is commonly negatively associated with grain yield (Dudley et al., 1977; Frey, 1951; Motto et al., 1989; Murphy, 1980; Sander et al., 1987) due to the movement of amino acids into kernels (presumably for zein synthesis) decreasing sugar concentrations, thereby limiting starch synthesis (Doehlert and Kuo, 1990; Nelson and Pan, 1995; Preiss, 1982; Preiss et al., 1991). Under conditions of zein saturation (Tsai et al., 1992) kernel DM may not further increase (Tsai et al., 1983, 1991). The Illinois High Protein cultivar which contains zein as the major protein (Dudley et al., 1974) is a good example where the synthesis of a large quantity of protein occurs at the expense of starch accumulation leading to reduced yield (Tsai et al., 1983). Hence, high yielding hybrids are associated with a low protein concentration or a high carbon/nitrogen (C/N) ratio in kernels (Tsai et al., 1990, 1992). Low-yielding hybrids, on the other hand, have a high percentage of protein (or low C/N ratio) in the kernel so that their N sink is saturated rapidly with only a small amount of N fertiliser (Tsai et al., 1990, 1992). This may explain why some hybrids exhibit only a limited response to N fertilizer (Tsai et al., 1984). Tsai et al. (1983, 1984) suggest that hybrids with a low percentage of protein in the kernel, but where zein synthesis can be induced with increasing levels of N fertilizer, should maximise grain yield. Such hybrids avoid early zein saturation and are therefore likely to have a long grain filling period, an important characteristic of high yielding hybrids (Daynard and Kannenberg, 1976; Hanway and Russell, 1969; Poneleit et al., 1980). Such a selection programme would need to be further investigated for sweet corn as kernels are harvested before reaching maximum levels of zein (Fig. 6.2).

Breeding to minimise the adverse effects of the inhibitory cycle may involve increasing the storage capacity for excess photoassimilate, presumably through larger stems. Ironically, Lafitte and Edmeades (1994a) observed in their study that the taller plants yielded highest. However, tall plants may shade lower leaves (Tetio-Kagho and Gardner, 1988a), thereby reducing the photoassimilate supply to roots (Criswell et al., 1974; Eastin, 1969, 1970; Fairey and Daynard, 1978a, 1978b). Ottman and Welch (1988) highlighted the importance of solar radiation on lower leaves by demonstrating that supplementing the PPFD of lower leaves not only increased endogenous N levels and yield, but delayed their senescence. Thus, increased stem storage capacity should involve selecting for increased stalk diameter rather than height. Johnson et al. (1986) reported that selection for reduced height of the maize hybrid 'Tuxpeño Crema I' reduced plant stature by 37% and increased grain yield and harvest index 50-70%. Lodging incidences were also substantially reduced. Modarres et al. (1998) also reported increased grain yield from reduced stature plants. While it was not reported whether the selection program employed by Johnson et al. (1986) increased stalk diameter, decreased leaf area per plant, or both, leaf area above the primary ear was significantly lower than normal stature plants in Modarres et al.'s (1998) study.

Management of N inputs may also offer ways to minimise effects of an inhibitory cycle. As suggested by Early et al. (1967), enhanced vegetative growth on soils with high N fertility, while pleasing in appearance, merely leads to an earlier complete leaf canopy and enhanced mutual shading that is detrimental to grain yield. Thus, future management of both N inputs and breeding should aim to better coincide photoassimilate production with kernel sink strength. This may be achieved through better managing N inputs, e.g., later applications of N. Delaying N fertiliser applications until the crop is well established or splitting the quantity of N to be applied into several applications during ontogeny (Rhoads and Manning, 1985; Rhoads et al., 1978) improves NUSE (Bigeriego et al., 1979; Stanley and Rhoads, 1977; Russelle et al., 1981, 1983; Welch et al., 1971) as later applied N is preferentially translocated to reproductive organs (Below et al., 1981; Weiland, 1989b; Weiland and Ta, 1992). However, current commercial methods of application do not allow N fertiliser application later than 6-8 weeks after emergence without causing an unacceptable level of plant damage (Thom and Watkin, 1978).

Better coinciding photoassimilate supplies with sink demand may also improve yield by preserving the photosynthetic system and deferring the remobilisation of carbon and N until late grain filling (Prioul et al., 1990; Ta and Weiland, 1992). Such deferral extends the leaf area duration (Crafts-Brandner and Poneleit, 1987a), an important characteristic of higher yields in many species (Adelana and Milbourn, 1972b; Eddowes, 1969; Evans et al., 1975; Gifford and Jenkins, 1982). Genetic variation for remobilisation of N from leaves and stems to grain is known (Beauchamp et al., 1976; Chevalier and Schrader, 1977; Eghball and Maranville, 1991; Tsai et al., 1991) so there is potential to develop cultivars which accumulate large amounts of N in stems for remobilisation to the grain (Beauchamp et al., 1976).

There is no doubt that the potential for producing higher yields is related to N accumulation and the capacity of plants to continue N uptake into grain filling. Achieving higher yields therefore requires accumulation of newly assimilated N to remain at a relatively high rate throughout the grain filling period, preservation of photosynthetic activity throughout the grain filling period, and accumulation of N and DM by kernels to occur at relatively high rates (Muruli and Paulsen, 1981; Pan et al., 1984; Singer and Cox, 1998; Swank et al., 1982; Tsai et al., 1991). In all instances, the physiological basis for maintaining these processes centres around minimizing the adverse effects of the inhibitory cycle. Therefore, crop management which prolongs both N and DM accumulation will be translated into kernel DM, and hence yield.

Chapter 8

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