Growth and development of lucerne with different fall dormancy ratings

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Abstract of a thesis submitted in partial fulfilment of the requirements for the Degree of Doctor of Philosophy.

Growth and development of lucerne with different fall dormancy ratings

by

Hung T Ta

The main aim of this research was to understand differences in the growth and development of three lucerne genotypes with different fall dormancy (FD) ratings; FD2 (dormant), FD5 (semi-dormant) and FD10 (winter-active). To do this, one field experiment was undertaken over two years; a seedling establishment phase followed by multiple regrowth cycles (October 2014 to January 2017). By the end of the seedling phase, the FD10 genotype had produced 20% more shoot and 16% more root biomass than the other two genotypes. Lucerne physiology was examined to see if the yield advantage of FD10 was maintained during subsequent regrowth cycles. After the seedling phase, a second treatment of defoliation frequency regime (DF) at 28 (DF28), 42 (DF42) and 84 (DF84) days was used to create different levels of root reserves, to examine whether treatments affected the yield and quality potential of crops. Annual shoot yields ranged from 4.4 t DM/ha in DF28 crops to 17.5 t DM/ha in DF84 crops. Most of this difference was due to changes in the rates of shoot growth in response to temperature and photoperiod (Pp). When crops were growing into an increasing Pp, growth rate was 3.5 kg DM/ha/°Cd for DF28 crops compared with 7.5 kg DM/ha/°Cd for DF42 and 8.8 kg DM/ha/°Cd for DF84 crops. The leaf stem ratio (LSR) declined by 0.82 for each one ton increase in shoot DM. The CP and ME accumulation in whole shoots or in leaf, soft stem and hard stem followed an allometric relationship. As DM increased, CP and ME increased in a similar pattern for all treatments. By third year 2016/17, crops defoliated at 42 and 84 day intervals produced 1.3 t CP/ha and 55 GJ ME/ha greater than a 28 day regrowth crop. Thus, quality was unaffected by FD ratings and explained allometrically by the leaf and stem ratio, associated with shoot DM.

Physiologically, the differences in shoot yield among DF crops were explained mainly by differences in the amounts of radiation intercepted. More frequent defoliation caused lower radiation interception because short regrowth cycles reduced leaf area index (LAI). There was no difference in canopy architecture with an extinction coefficient of 0.83 for all treatments. The lower LAI in DF28 canopies was explained by a lower leaf area expansion rate (LAER). This was 50 and 62% slower during the main

spring-summer growth periods than for DF42 and DF84 crops, respectively. The lower LAER in DF28 crops was caused by slower development of individual leaf area and a longer phyllochron. However, other LAI components including branching, shoot population, leaf senescence and reproductive development (flowering) were relatively consistent for all crops. The shortest defoliation interval reduced the amounts and levels of root reserves (DM_{root}) by 40 and 60% in relation to the DF42 and DF84 regimes. The smaller root reserves in DF28 crops were caused by a decline in the fractional DM partitioning in roots (P_{root}). Therefore post defoliation, a lack of root reserves reduced RUE_{shoot} and consequently reduced biomass accumulation for DF28 crops.

There was no interaction between the effects of the FD and DF treatments. Irrespective of the DF regime, the FD10 genotype produced 23% higher shoot yield in autumn. During this period, stem expansion rate of FD10 was 0.99 mm/°Cd which was faster than FD5 (0.70) and FD2 (0.53). Autumn mean leaf area was 226, 369, and 489 mm^2 for FD2, FD5 and FD10, respectively. Therefore the higher autumn shoot yield of the FD10 genotype came from a faster stem elongation rate and larger leaves. However, individual leaf area was similar for all genotypes during the main spring-summer growth. In the 28 day defoliation treatment, FD10 had lower shoot growth rates during the spring-summer period 2016/17 and grew ～3 kg DM/ha/^{0}Cd lower than the FD2 and FD5 genotypes. The difference in P_{root} among genotypes was possibly due to different in base photoperiod response. The FD2 genotype showed the most response to Pp direction. This suggests this genotype had a lower base photoperiod response. Therefore this more dormant genotype recharged root reserves at all times of year. In contrast, the winter-active (FD10) genotype had a higher base photoperiod and therefore had less time to recharge root reserves than the FD2 genotype, FD5 was intermediate. This explains the faster decline in root reserves for FD10 growing in colder months in the DF28 regime. Consequently, the root reserves of FD10 declined over time to 1.5 t DM/ha by the end of the experiment in January 2017. It is likely that this progressive reduction in root reserves is the cause of reported decreases in persistence of FD10 genotypes over time. Ongoing monitoring of this experiment will be used to test this hypothesis. Thus this research showed growth differed among FD ratings. Phenological development (phyllochron, branching, canopy structure and leaf senescence) and reproductive development were conservative among FD ratings. In contrast, vegetative growth (leaf area expansion and stem elongation) was most closely correlated with fall dormancy ratings during atumn period.

Keywords: Alfalfa, *Medicago sativa*, fall dormancy, defoliation frequency, phyllochron, partitioning, persistence, root reserves, radiation use efficiency, photoperiod.

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Chapter 1 Introduction

1.1 General introduction

In New Zealand, lucerne cultivars with low to moderate fall dormancy ratings (FD) such as 'Wairau' (FD3) have been widely grown on dryland farms (Douglas, 1986; Moot *et al.*, 2003). These genotypes produce high yields of high quality feed in spring to summer, but dry matter (DM) production declines during autumn. This reduction in forage yield is due to lucerne becoming dormant in the early autumn season when daylength and temperature are decreasing (Barnes *et al.*, 1979). One way to increase forage yield might be through growing of non-dormant or winter-active (FD10) cultivars, as these are higher yielding in the cooler months and have faster shoot growth rates after defoliation (Leach, 1969).

For winter-active genotypes to be successfully introduced on farms, their potential advantage will depend on greater annual productivity. Quality is also a crucial factor and for adoption they will need to be equal or better than lower producing altenatives. The suitability of lucerne for dryland farms also depends on them persisting under winter conditions. In New Zealand more winter-active genotypes are starting to be promoted onto farms (Harvey *et al.*, 2014). However, it is unclear how the yield, quality and persistence of genotypes differs with FD rating. To select appropriate lucerne genotypes, it is necessary to understand the physiological drivers of FD that may influence growth and development.

Historically, it is well known that the level of endogenous reserves in crowns and taproots is an important component of lucerne crops that supports shoot regrowth (Graber *et al.*, 1927; Reynolds and Smith, 1962). Low levels of endogenous reserves have been shown to reduce yields because they are used to renew the canopy of stems at the beginning of each regrowth cycle (Avice *et al.*, 1997b). For a fall dormancy 5 (FD5) lucerne genotype, Teixeira *et al.* (2007c) reported a 42-day rotation produced twice the amount of dry matter of a crop harvested every 28 days. This yield reduction could be due to a decline in the amount of radiation intercepted by the canopy (Teixeira *et al.*, 2008). However, it remains unclear how these mechanisms change with different FD ratings and defoliation frequencies (DF). Non-dormant (FD10) lucerne exhibits higher shoot growth rates after defoliation when compared with dormant types (Leach, 1969), particularly in autumn. This results in large differences in canopy expansion and radiation use efficiency (RUE; Volenec, 1985). Dormancy related differences in shoot growth rate might influence the partitioning of dry matter (C and N) to crown and taproot. Post-defoliation, a lack of underground reserves can reduce canopy expansion rates of the earliest initiated leaves (Teixeira *et al.*, 2008). Ultimately, this may affect production and persistence of lucerne crops. The physiological mechanisms involved in these processes are unknown or insufficiently quantified to be predictive.

1.2 Hypothesis and objectives of this thesis

The hypothesis of this thesis is that the growth and development of different fall dormancy (FD) ratings is conservative in response to defoliation frequency (DF) regimes. To test this hypothesis, research was conducted in four main steps:

(i) Experimental data collection for seedling lucerne of three different fall dormancy to test physiological responses of FD ratings during taproot establisment.

(ii) Experimental data collection for established lucerne to determine agronomic performance of FD ratings respond to DF regimes.

(iii) Phenological data collection to explain how growth difference among FD ratings.

(iv) Relate yield differences to perenial reserves. This was to verify the linkage between the seasonal biomass partitiong and activity levels of genotypes.

The overall goal of this thesis is to understand differences in the growth and development of lucerne genotypes with FD ratings of FD2, FD5 and FD10. To do this one field experiment was used over two years; from seedling establishment followed by multiple regrowth cycles (October 2014 to January 2017). The DF regime at 28 (DF28), 42 (DF42) and 84 (DF84) days was used to create different levels of root reserves, to examine how this interacted with FD ratings for yield and quality potential of crops. A long 84 day interval was used to allow the response of crops to environmental factors to be assessed independently of defoliation pressure. It also created crops of overly mature lucerne to extend the range of yield and quality parameters that could be analysed.

This thesis is structured in eight chapters (Figure 1.1). Chapter 2 reviews the literature and focuses on lucerne physiology and management which determines crop productivity and persistence. Chapter 3 describes the experimental design, methods, analysis and physical environment, which are common to the results in Chapters 4 to 7.

The specific objectives of this thesis are related to each of the four experimental chapters:

1. The objective of Chapter 4 is to investigate the influence of FD on DM production and phenological development during the seedling phase.

2. The objective of Chapter 5 is to investigate the yield and quality responses of the FD genotypes when they were grown in changing environmental conditions and defoliation managements, created by different cutting regimes.

3. The objective of Chapter 6 is to explain any differences in agronomic performance reported in Chapter 5 by quantifying radiation interception, canopy expansion and development, and crop phenology in relation to thermal time and photoperiod.

4. The objective of Chapter 7 is to relate yield differences to perennial reserves and dormancy levels of genotypes. To do this DM shoot yield will be related to the amount of intercepted radiation to compare the efficiency with which radiation is converted to biomass. Biomass partitioning to above and below ground organs will then be assessed.

5. Overall, Chapter 8 discusses the knowledge gained through the intensive experiment which includes how the FD and DF– environment response relationships could be used to determine management strategies of different FD ratings grown in a temperate climate. This includes recommendations for farmers of how to select appropriate lucerne genotypes to increase production on farms. The potential to use the equations developed for crop modelling puposes is also discussed along with limitations of the current dataset that opens opportunities for further research.

1.3 Thesis structure

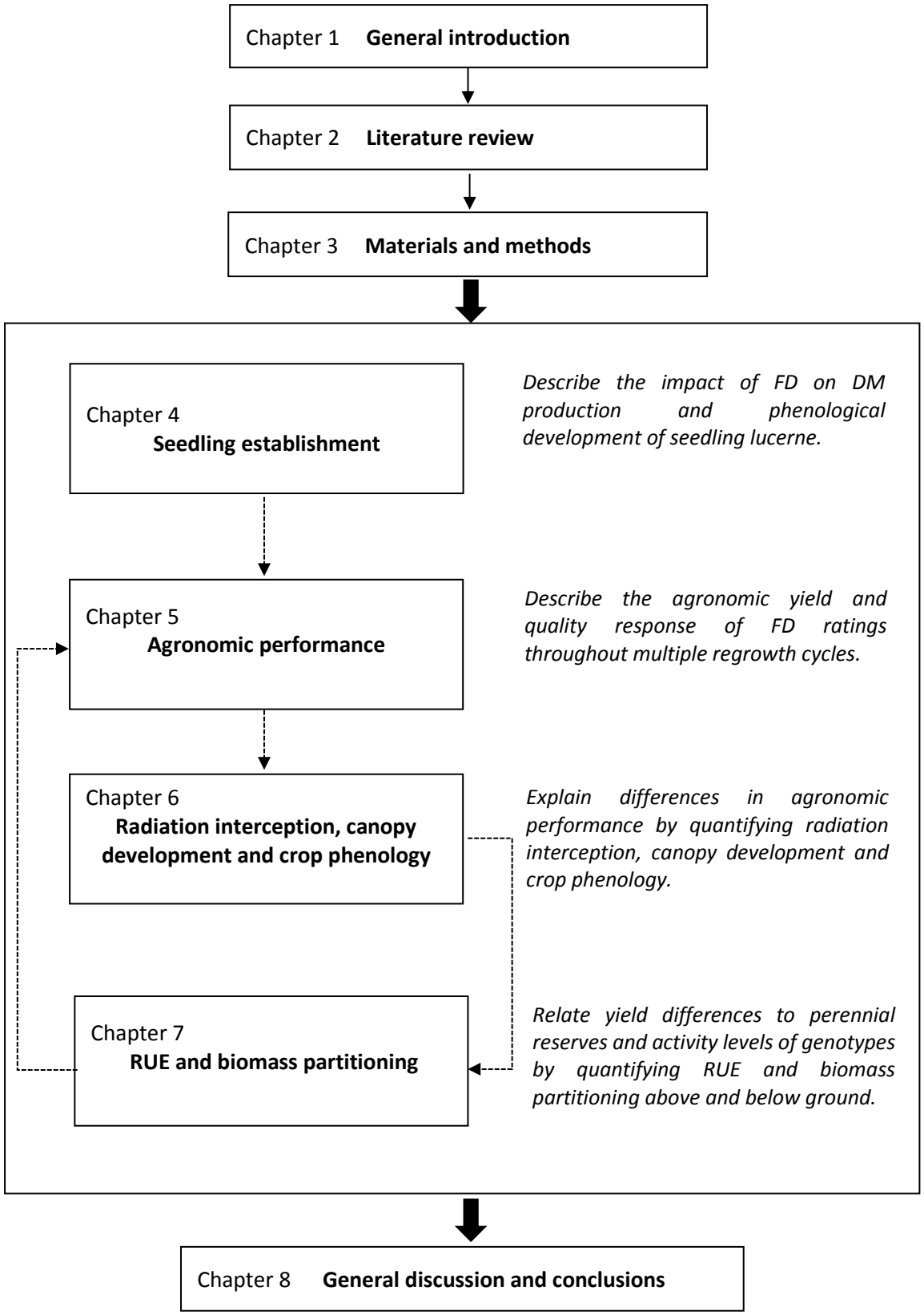


Figure 1.1 Schematic diagram of the thesis structure

Chapter 2 Literature review

Introduction

This chapter reviews the current literature on lucerne physiology and management as it relates to crop productivity and persistence. It quantifies the yield forming processes which result from both crop growth and development. Crop growth and development (Section 2.2.2) are driven by environmental factors mainly through radiation, temperature, photoperiod and also defoliation management. The influence of the level of fall dormancy as determined by genotype is integrated in this review and will highlight the knowledge gap of management strategies for different fall dormancy ratings grown in a temperate climate.

2.1 Lucerne in New Zealand pastoral systems

Lucerne (*Medicago sativa* L.) is the world's oldest (Michaud *et al.*, 1988) and most important forage legume due to its high energy and protein contents and suitability for grazing and hay making. It has the potential to grow in environments ranging from hot arid to cool temperate, and high productivity and persistence are essentially prerequisites for its production success (Michaud *et al.*, 1988; Frame *et al.*, 1998). In New Zealand, the potential of lucerne has been recognised as a most suitable forage species to benefit pastoral systems, particularly in dryland areas (Iversen, 1967). This is because, in these areas, the traditional ryegrass/white clover pastures fail to persist due to water stress conditions in summer months (Knowles *et al.*, 2003). Lucerne has a deep taproot that gives the plant access and ability to extract water and nutrients from deeper layers in the soil profile than other forage species (Langer, 1967). For this reason, lucerne has been shown to have superior drought tolerance and preference over grasses in lower rainfall (400-800 mm) areas (Moot, 2012). For example, under dryland conditions lucerne crops consistently produce 40% more dry matter (DM) than pasture with yields up to 21 t DM/ha/year (Iversen, 1967; Douglas, 1986). The yield advantage of dryland lucerne came from higher growth rates in September and during the periods of high soil water deficit in summer (Brown *et al.*, 2005a). This allows grazing to start in early spring to meet livestock feed demand, thereby shortening the time to sale of surplus stock and lessening the summer feed gap, because fewer animals are retained on farms (Avery *et al.*, 2008). However, lucerne cultivars grow in New Zealand declines their DM productivity during autumn (Lucas, 1984) which may cause autumn-winter feed shortages. This may require a change in farming system or the growing of winter feed crops or supplementation to meet feed demand or through growing the winter-active or non-dormant lucerne.

2.2 Fall dormancy (FD) and defoliation frequency regime (DF)

Fall dormancy (FD) is an important criterion used to classify lucerne genotypes. The FD rating for lucerne is based on stem height during autumn (Barnes *et al.*, 1979) with commecially available cultivars ranging from a low of FD2 to a highly active FD10 (Harvey *et al.*, 2014). To successfully integrate lucerne on farm requires matching the correct genotype to the environment where it will be grown. In temperate New Zealand, lucerne with low to moderate FD rating such as 'Wairau' (FD4) and 'Kaituna' (FD5) have been widely grown on dryland farms (Douglas, 1986; Moot *et al.*, 2003). These genotypes produce high yields and quality feed from spring to summer, but dry matter (DM) production declines during autumn (Lucas, 1984). This reduction in forage yield is due to lucerne becoming "dormant" in the early autumn or fall season when daylength and temperature are decreasing (Barnes *et al.*, 1979). In warmer environments non-dormant or winter-active (FD10) lucerne is recommended with an expectation of greater yields (Leach, 1969; Lowe, 1985).

In addition to high yields, an ideal forage crop must also support animal production and thus be of high quality. Lucerne is known to be palatable to livestock and typically has ME values of at least 11 KJ ME/kg DM, crude protein (CP) levels greater than 20%, and high digestibility (Burke *et al.*, 2002). The combination of total CP and ME in the palatable fraction (leaves and soft stems) of lucerne crops is also an important factor that determines potential livestock production. This high quality palatable fraction is the main part of the lucerne sward that sheep consume when grazing *in situ* (Brown and Moot, 2004). Therefore, the ratio of the amount of leaf to stem (LSR) is the primary factor which determines the nutritive value of lucerne (Woodman and Evans, 1935). Fletcher (1976) reported LSR decreased as regrowth duration increased due to lignification of stem. This suggests lucerne quality could be improved by shortening the regrowth duration. For example, Allison and Vartha (1973) reported lucerne leaf percentage increased 55 to 65% when regrowth duration was reduced from 5 to 4 weeks. However, increased defoliation frequency may reduce yield and persistence of lucerne (Keoghan, 1982). Teixeira *et al.* (2007c) showed that a 28-day rotation reduced annual shoot yield by 50% compared with a crop harvested every 42 days. To couple forage yield and forage quality, Lemaire *et al.* (1992) proposed an allometric relationship between LSR and shoot DM; as shoot DM yield increased the LSR decreased. However, it is unclear if or how forage yield and quality might change with genotypes of different FD ratings. Reportedly, the non-dormant or winter-active (FD10) lucerne may have faster shoot growth rates after defoliation (Lowe, 1985), so it might change the allometric ratio. This suggests winter-active genotypes may be harvested earlier without reduction in yield and therefore can be managed at higher defoliation frequency than the more dormant genotypes. However, Harvey *et al.* (2014) reported that genotypes with higher FD ratings are less persistent than those with a lower rating when working with different dormancy classes in New Zealand. Similar studies on lucerne in temperate (Lodge, 1986) and subtropical regions of Australia (Gramshaw *et al.*,

1993), and in South America (Ventroni *et al.*, 2010) have shown that the yield advantage for the winter active cultivars only appeared in the first year. It is also known that these winter-active genotypes (FD10) have taller shoots in autumn (Barnes *et al.*, 1979) which suggests more biomass has been allocated into shoot growth. This strategy of elongating shoot length may result in higher individual shoot mass (Volenec, 1985) but potentially lower shoot quality because of increased lignification to support the extra height (Christian *et al.*, 1970). The impact of FD ratings on lucerne yield and quality in response to DF regimes is unknown or insufficiently quantified to be predictive.

Another important aspect in crop growth is the quantification of phasic development from vegetative to reproductive. This is because changes in partitioning priority often occur as crops become reproductive. Lucerne has been recommended to cut at flowering stage for achieving a high yield and herbage quality (Smith, 1972). This cutting management implies the appearance of flowering is an indicator that biomass demand in the perennial organs (crown plus taproot) is complete. Post-defoliation, these perennial reserves are remobilised to support shoot growth mainly through increasing the rate of canopy expansion of the earliest initiated leaves (Volenec *et al.*, 1996; Teixeira *et al.*, 2008). In the field, the first sign of the reproductive phase is observed by visual appearance of floral buds on the meristems. However, the transition from vegetative phase to reproductive phase varies with temperature (Smith, 1972). For an FD5 regrowth lucerne "Kaituna" crop, Teixeira *et al.* (2011) reported the phasic transition was driven by temperature but also manipulated by photoperiod. It is unclear if, or how, phenological development might change with genotypes of different FD ratings. The non-dormant FD10 genotype exhibited faster regrowth in autumn, consequently it might reach the reproductive phase earlier than the winter-dormant (FD2) and semi-dormant (FD5) genotypes (Lowe, 1985). The impact of phenological development on partitioning and growth processes is unknown or insufficiently to be predictive.

Currently more winter-active lucerne genotypes are starting to be introduced onto New Zealand farms (Harvey *et al.*, 2014). However, it is unclear how yield production, quality and persistence changes with genotypes of different FD. To select appropriate lucerne genotypes, it is necessary to understand the physiological drivers of FD lucerne growth. This requires an understanding of crop growth and development in relation to enviromental factors and different defoliation management.

2.3 Environmental factor influences on growth and development

2.3.1 Temperature

Temperature is an important factor that influences crop growth and development (Monteith, 1972). Generally, the rates of growth and development increase with increasing temperature. However, within the linear phase, crops cannot distinguish between temperature and duration (*e.g.* 5°C for 20 h and 10°C for 10 h) (Hay and Porter, 2006). Therefore thermal time (Tt; °Cd or degree days) has been used widely to quantify the effect of temperature on development and growth of lucerne crops (Moot *et al.*, 2001) and many other agricultural crops (Hodges, 1991). The calculation of Tt is often based on three cardinal temperatures. Development rate increases linearly above a constant crop-specific base temperature (T_b) or temperature threshold to an optimum temperature (T_0) and declines linearly to a maximum temperature (T_{max}) above which development also ceases. Thermal time is calculated on a daily basis the mean daily temperature (T_{mean}) minus T_b, as described in Equation 2.1.

Equation 2.1 Thermal time (Tt; °Cd) = $\sum (T_{mean} - T_b)$

Where $T_{mean} = (T_{max} – T_{min})/2$

Generally, interpretation of development responses to thermal time for lucerne has identified a constant T_b of 5 °C, T_0 of 30 °C and T_{max} of 40 °C (Fick *et al.*, 1988). However for lucerne growing in temperate environment Moot *et al.* (2001) reported that this T_b was too high and suggested a broken-stick threshold model to account for different development rate responses at lower temperatures. Their model defined a T_b of 1.0 °C for temperate pasture species (Moot *et al.*, 2000). At temperatures less than 15^{o}C, development rate responded linearly at a rate of 0.7 ^{o}Cd/°C and then at a rate of 1.0 ^{o}Cd/°C until the optimum temperature (T_o) of 30 ^{o}C is reached. The upper threshold (T_{max}=40 ^{0}C) is not usually required in New Zealand temperate environment because T_{mean} does not exceed T_o. This method to calculate Tt will be used in the current research.

2.3.2 Crop growth, development and yield formation

Lucerne growth and development are strongly influenced by environmental signals across seasons (Moot *et al.*, 2003), which consequently determines yield (Hay and Porter, 2006). Development is the change in organ structures through which a crop progresses its life cycle from germination to maturity. Thus, development rate is measured by morphology. The rates of development processes, such as expansion of vegetative nodes and appearance of floral buds, are determined by temperature (Fick *et al.*, 1988) and modified by photoperiod (Pp). For example, Brown *et al.* (2005b) reported the rate of leaf appearance (phyllochron) on the main stem was consistent at 37°Cd for a regrowth lucerne crop but declined from 60 to 37°Cd as photoperiod decreased from 15.7 to 11.4 h. Growth refers to the

increase in crop DM as the result of radiation interception and partitioning of the products of photosynthesis. Growth rate is measured by yield which is strongly depend on environmental factors (Fick *et al.*, 1988). For example, Gosse *et al.* (1988) observed a decrease in growth rate for a lucerne crop "du Puits" from 150 kg DM/ha/day in summer to 90 kg DM/ha/day in autumn. This decrease in growth rate during autumn was partially explained by the reduction in mean air temperature and the available amount of solar radiation intercepted during this period. However, Moot *et al.* (2003) indentified lower growth rates in autumn than spring for irrigated lucerne at the same mean air temperature. This difference was used as the basis to develop a set of management rules to increase lucerne use on-farm (Avery *et al.*, 2008; Anderson *et al.*, 2014). However, these decisions were based on a FD5 variety. It is known that genotypes with higher FD ratings produce more herbage in autumn but are less persistent than those with lower ratings (Harvey *et al.*, 2014). To elucidate the physiological mechanisms responsible for these different responses, a systematic investigation of crop growth and development of lucerne with different FD is required. It is also known that the physiological responses of seedling lucerne during taproot establishment differs from established crops, so they must be considered separately (Teixeira *et al.*, 2011). This will be investigated in the current experiment. For lucerne, yield forming processes are mainly driven by temperature and solar radiation (Fick *et al.*, 1988) and can be described in Equation 2.2;

Equation 2.2 $DM_{shoot} = R_0 * R/R_0 * RUE * H$

Where the shoot dry matter (DM_{shoot}) is the product of the incident solar radiation above canopy (R_0), and the fractional radiation intercepted by the whole canopy (R/R_0). RUE is the radiation use efficiency which represents the conversion of intercepted radiation into DM. H represents the rate of partitioning of DM between harvested parts and the rest of the crop (Monteith, 1977; Robertson *et al.*, 2002). In annual crops H is the harvest index from grain. In perennial lucerne it represents the proportion consumed as forage.

In order to explain the differences of agronomic performance among genotypes or between defoliation treatments, it is necessary to understand how temperature and solar radiation affect these yield forming processes. The following sections will discuss each component in Equation 2.2 in relation to environmental factors.

2.4 Radiation intercepted by the canopy

Radiation interceptance (R/R_0) is modulated by changes in canopy structure and size. The size of canopy is quantified by the leaf area index (LAI; m^2 leaf/m^2 ground) throughout the growth period. Technically, all green material is photosynthetically active so some authors refer to the green area index (GAI) but in this thesis the term LAI is used to represent the photosynthetically active plant

material. The canopy structure is characterized by factors such as leaf angle, leaf surface properties, leaf shape and arrangement (Hay and Porter, 2006) which determines leaf optical properties (reflection and transmission). The relation between R/R_0 and LAI can be described by an exponential reduction of radiation through the canopy using the Beer-Lambert law (Equation 2.3, Monsi and Saeki (2005).

Equation 2.3 $R/R_0 = 1-\exp(-k*LAI)$

Where, k is the extinction coefficient that describes interception per unit of leaf area. The lucerne literature shows that k does not vary among genotypes (Gosse *et al.*, 1988; Teixeira *et al.*, 2011; Thiébeau *et al.*, 2011) or defoliation treatments (Teixeira *et al.*, 2007b). Many authors have reported a high and stable k for lucerne crops of 0.83 to 0.93. Therefore, a single value of k is used to describe canopy structure when estimating radiation interception (Thornley and Johnson, 2000). The implication of a single and stable k value is that differences in the pattern of radiation interceptance among genotypes or defoliation frequencies (DF) are mainly explained by LAI.

2.4.1 Developmental processes of LAI formation

The LAI has components of stem population, leaf number on the main-stem, and branching with each of these components driven by temperature (Robertson *et al.*, 2002) but potentially also modified by photoperiod (Pp) (Brown *et al.*, 2005b).

For lucerne, the rate of primary leaf appearance on the main stem is the main driver of leaf appearance (Robertson *et al.*, 2002). It also determines the potential of axillary leaves from the axial buds (Hay and Porter, 2006). The interval between the appearance of successive primary leaves is defined as the phyllochron and is quantified by Tt (°Cd/primary leaf). Phyllochron has been considered constant at 34°Cd/primary leaf for lucerne crops (Robertson *et al.*, 2002). However, Teixeira *et al.* (2007b) reported that the phyllochron changed between 34 – 60°Cd throughout seasons. This means using a constant phyllochron is inappropriate for lucerne growing in a temperate climate such as New Zealand. The seasonal changes in phyllochron could be described by Pp at the start of each regrowth cycle. This is because, the Pp response for lucerne phyllochron was induced near the beginning of the crop cycle with the time of first leaves appearance (Brown *et al.*, 2005b). Therefore, the direction of Pp changes (increasing or decreasing Pp) may influence phyllochron. For example, the phyllochron of a regrowth lucerne crop was 37°Cd but declined from 60 to 37^0Cd as Pp decreased from 17.5 to 11.4 (Brown *et al.*, 2005b). They reported longer phyllochron in autumn-winter (Pp decreased). This longer phyllochron in autumn (Pp decreased) possibly relates to the seasonal assimilate supply when dry matter is preferentially partitioned into perennial reserves rather than shoots during this period (Teixeira *et al.*, 2007c). This causes a limited availability of assimilate to support cell division and

expansion (Hay and Porter, 2006) and therefore reduces the rate of phyllochron expression. It is unknown how these mechanisms change with different FD ratings and defoliation frequencies (DF). This will be investigated in the current research (Chapter 6).

Branching is the initiation of secondary leaves at each node. It allows crops to expand their potential leaf area and increase radiation interception (Hay and Porter, 2006). The extent of branching, defined as branching rate can be described by thermal time. Alternatively, branching can be quantified as the total number of leaves in relation to the number of primary leaves. For example, Teixeira *et al.* (2007b) showed that in a regrowth lucerne "Kaituna" crop, the first axillary leaf initiated when the 4th primary leaf was fully expanded and then progressed bi-linearly at a rate that was consistent with primary leaf appearance. The appearance of axillary leaves was 3.1/primary leaf until the expansion of the 9th primary leaf. Then branching rate increased to 6.8/primary leaf until the 11th primary leaf. Environmental factors like radiation quality and quantity are also known to influence branch development (Thompson, 1993). This is because both quality and intensity (*e.g.* the red/far red ratio) could modulate assimilate supply (Stoskopt, 1981) and stimulate cell division and expansion (Hay and Porter, 2006) and consequently determine the rate of branching.

Stem population is determined by plants/m^2 and shoots/plant which are the components of lucerne yield (Volenec *et al.*, 1987). The number of plants is strongly dependent on sowing rate (kg seed/ha), conditions during the seedling phase, and declines throughout the growing years after establishment (Fick *et al.*, 1988). For example, Teixeira *et al.* (2007a) working in irrigated lucerne grown at Lincoln reported 130 plants/m^2 in the first year but this decreased to 60 plants/m^2 in the second year, a more than 50% drop in plant population for their two year experiment. The decline in plant population was probably because of adaptation to stresses like diseases, pest, winter hardness (Cowett and Sprague, 1962; Nelson and Smith, 1968) or severe frequent defoliation (Lodge, 1986; Teixeira *et al.*, 2007a). However, the decrease in plant population is often compensated for by an increase in the number of shoots/plant (Gosse *et al.*, 1988). This plasticity of response ensures an optimum stem population at which yield component compensation maintains the productive potential of the lucerne crop (Teixeira *et al.*, 2007a). Competition among adjacent plants for radiation has been suggested as a main factor that influences the stem dynamics (Gosse *et al.*, 1988).

2.4.2 Individual leaf size

The size of leaves is an important factor that contributes to LAI, because the ultimate size of a leaf depends on the other components of LAI formation. Leaf growth is determined by the rate of cell division and expansion at the stem apex (Hay and Walker, 1989) which is driven by assimilate supply. Gastal and Nelson (1994) found that, in the early stages of leaf growth, cell division is highly sensitive to nitrogen (N) supply. Brown and Tanner (1983) also found a limited availability of carbohydrate from

small leaf area gives the small leaf size. It is known that endogenous N in perennial reserves was reduced by frequent defoliations (Avice *et al.*, 1997a). Post defoliation, a lack of underground reserves can reduce expansion rates of the earliest initiated leaves (Teixeira *et al.*, 2008). However, it is unclear if these mechanisms change with different FD ratings. This will be investigated in the current research.

2.4.3 Leaf senescence

Senescence refers to the yellowing of a dying leaf and has been describes as a linear function of Tt for a number of crops (Carberry and Muchow, 1992; Chapman *et al.*, 1993). For lucerne, senescence progresses from the bottom to the top of the canopy probably due to the recycling of the resources from lower old leaves to form new leaves during the expansion of the canopy. This strategy ensures that the later leaves are the main source of assimilate and tend to live longer (Hay and Porter, 2006). Senescence is also progressively enhanced by increased mutual shading by an overlying canopy. Teixeira *et al.* (2007b) showed senescence in a regrowth lucerne crop "Kaituna" (FD5) commenced at the time of appearance of the 4th primary leaf at a rate of 0.2 leaves/primary leaf. This was maintained until the 6th primary leaf when senescence increased to 0.48 leaves for each primary leaf appearance. Whether senescence is consistent across genotypes of different FD is unknown and will be examined in this thesis.

2.5 Radiation use efficiency (RUE)

2.5.1 Biomass accumulation and RUE

Biomass accumulation can be estimated as the product of the amount of radiation intercepted by the canopy and radiation use efficiency (Equation 2.2). Radiation interception is modulated by canopy development and expansion (Section 2.3). Radiation use efficiency (RUE) refers to the net efficiency of conversion of radiation energy into crop dry matter and is usually calculated as shoot biomass in relation to the amount of radiation intercepted (Monteith, 1977; Sinclair and Muchow, 1999). Considerable and precision caution is needed when defining RUE, because this terminology can be expressed in different forms. These include; (i) photosynthetically active radiation (PAR ; 400 to 700 nm) or total solar radiation; (ii) intercepted or absorbed radiation; (iii) the fraction of biomass production expressed on above-ground DM or on a total DM basis including below-ground DM. In this current research, RUE will be defined by intercepted total solar radiation and expressed as shoot RUE (RUE_{shoot}) or total (shoots plus crowns and roots) RUE (RUE_{total}).

The relationship between accumulated crop DM and the amount of intercepted solar radiation was described experimentally and theoretically by Monteith (1977) who concluded that under optimum conditions, a constant RUE of 1.4 g DM/MJ is assumed for most C_3 species. This classical analysis has been determined for many annual crops (Gallagher and Biscoe, 1978; Kiniry *et al.*, 1989) and extended

to perennial crops (Robertson *et al.*, 2002) such as lucerne. However, this approach does not accurately reflect the whole crop physiology, because the partitioning of biomass to below-ground (taproot and crown) changes within regrowth cycles (Reynolds and Smith, 1962) and between seasons (Khaiti and Lemaire, 1992) and, therefore, RUE_{shoot} varies with seasons. Because of this Teixeira *et al.* (2008) defined RUE_{shoot} as the easily measured above-ground component of biomass in relation to radiation interception, analogous to RUE in annual crops. RUE_{total} was defined on the basic of shoot biomass, plus biomass in crowns and roots to 30 cm. To cope with this seasonal dynamic of lucerne, Teixeira *et al.* (2009) proposed a framework to explicitly account for partitioning of biomass to below-ground, as represented in Equation 2.4.

Equation 2.4 $DM_{shoot} = R_0 \times R/R_0 \times RUE_{total} \times (1-p_{per})$

Where DM_{shoot} is the above-ground yield, R_0 is the amount of incident solar radiation at the top of the canopy, R is the amount of transmitted radiation at the bottom of the canopy, R/R_0 is the fractional radiation intercepted by the whole canopy, RUE_{total} is the conversion factor of R/R_0 to "total dry matter" (g DM/MJ), and $1-p_{per}$ is the fractional difference of the partitioning to perennial organs.

This method has been used successfully to explain yield production of a fall dormancy 5 (FD5) lucerne cultivar 'Kaituna' but it remains unclear how these mechanisms change with different FD and defoliation frequency (DF). Non-dormant (FD10) lucerne exhibits higher shoot growth rates after defoliation when compared with dormant types (Leach, 1969), particularly in autumn. This results in large differences in canopy expansion and RUE (Volenec, 1985). This is a consequence of accumulation and depletion of C and N reserves in taproots for shoot regrowth (Volenec *et al.*, 1991; Volenec *et al.*, 1996) possibly in response to activity level of the cultivar and environmental signals such as temperature and photoperiod (Smith, 1972; Fick *et al.*, 1988). Dormancy related differences in shoot growth rate might influence the partitioning of dry matter (C and N) to crown and taproot. Post defoliation, a lack of reserves can affect the photosynthetic capacity and canopy extension rates of the earliest initiated leaves post-defoliation (Teixeira *et al.*, 2008) and ultimately may affect production and persistence of lucerne crops. The physiological mechanisms involved in these processes are unknown or insufficiently quantified to be predictive. This hypothesis will serve as the basis for the approach used to quantify RUE and partitioning to perennial organs in this thesis. The following sections discuss in detail the three main factors (leaf nitrogen, light environment and temperature) that influence photosynthesis and therefore RUE.

2.5.2 Leaf nitrogen content effects on RUE

Leaf nitrogen content has shown a high correlation with leaf photosynthesis capacity, because the largest fraction of leaf nitrogen is associated with photosynthetic apparatus such as Calvin-cycle,

Rubisco, or radiation harvest compounds (Lawlor *et al.*, 2001). For example in C_3 and C_4 species, Sinclair and Horie (1989) found a great sensitivity of RUE to leaf nitrogen content per unit area of leaf (SLN; specific leaf nitrogen g/m^2) at low levels of SLN until a maximal asymptote is reached. Therefore, a decrease in SLN below the saturated SLN could reduce the potential of crop biomass accumulation, whereas an increase of very high SLN level had no advantage in RUE. For lucerne, frequent defoliation has been recognised to diminish the endogenous N in taproots (Graber *et al.*, 1927; Reynolds and Smith, 1962). Post defoliation, a lack of endogenous N in perennial reserves can limit the supply of N to shoots in the early stages of leaf initiation and therefore reduce RUE_{shoot} (Avice *et al.*, 1997a). Considering the importance of leaf photosynthetic rates on RUE, variation in photosynthetic capacity throughout the growing seasons might influence RUE. Khaiti and Lemaire (1992) reported that RUE_{shoot} changes seasonally but was not different among genotypes within a regrowth period. The change in the seasonal pattern of RUE_{shoot} was explained by Teixeira *et al.* (2008). They suggested that environmental signals exerted a stronger control than the availability of N, created by DF. However, it is also known that RUE differs following phasic development. Specifically, maximum RUE is attained in the vegetative phase and declines during the reproductive phase, due to N mobilisation from leaf into reproductive organs and roots (Sinclair and Muchow, 1999). It is expected that frequent defoliation at a 42 day interval in New Zealand which would be insufficient for lucerne crop to complete its full growing cycle (*e.g.* fully flowering), would therefore limit the potential physiological performance. This will be investigated in the current research by creating crops with different stages of development at the same time of year, to examine how physiological responses differ with FD ratings and defoliation treatment.

2.5.3 Temperature effects on RUE

Temperature also affects photosynthesis activity of leaves. Therefore it can also be expected to alter RUE of species including lucerne (Sinclair and Muchow, 1999; Justes *et al.*, 2002). Gosse *et al.* (1982) found that lucerne photosynthesis rates reached a maximal asymptote at T_{mean} between 20 – 30°C and declined to 60% at T_{mean} of 13°C. Field RUE measurement for irrigated lucerne grown at Lincoln confirmed a strong linear relationship between temperature and RUE_{total} (Brown *et al.*, 2006). Following this approach, these authors proposed a framework to account for the effect of temperature on the seasonal pattern of RUE_{total}. Then, this was validated for "Kaituna" lucerne grown in the same environmental conditions by Teixeira *et al.* (2008) who showed RUE_{total} increased at 0.10 g DM/MJ/°C from 8 to 18°C. It is unclear whether these physiological mechanisms alter with different FD ratings. It is known that the winter dormant (FD2) lucerne accumulates higher perennial reserves in cooler months than non-dormant lucerne (FD10) (Volenec *et al.*, 1991). This suggests differences in the seasonal pattern of RUE_{total} may appear among genotypes. This will be investigated in the current research.

2.6 Summary

The main conclusions from this literature review;

- Potential shoot yield is the product of the amount of incident solar radiation intercepted by a canopy and the efficiency of conversion of intercepted radiation.

- The amount of intercepted radiation is mainly determined by the canopy expansion and development processes. These processes are driven by temperature, expressed cummulatively as thermal time but potentially also modified by photoperiod.

- RUE is defined as the amount of shoot biomass produced in relation to accumulated radiation interception. The partitioning of DM between the shoot and root alters the apparent RUE of the shoot. However, the partitioning of DM changes seasonally, caused by temperature, photoperiod and potentially by DF regimes and FD ratings.

- Leaf N and temperature affect photosynthesis activity of leaves. Therefore they might also alter RUE. The lower RUE_{shoot} is associated with lower amounts of perennial reserves, possibly due to reduced N reserves. This is because frequent defoliation diminishes the endogenous N in taproots. Post defoliation, a lack of endogenous N in perennial reserves can limit the supply of N to shoots in the early stages of leaf initiation and therefore reduces RUE_{shoot}.

For lucerne to be successful on-farms, the potential advantage of genotypes with different FD ratings will be greatest on productivity and quality year round. To select appropriate lucerne genotypes, it is necessary to understand how FD determines the physiological drivers of growth. This requires an understanding of crop growth and development in relation to enviromental factors and defoliation management. Therefore, one field experiment involving three different FD ratings (genotype; FD2, FD5 and FD10) and three defoliation regimes (DF; 28-, 42-, and 84 day interval) was conducted over two years from the seedling phase in October 2014 to January 2017. The defoliation regimes were used to create different levels of root reserves, to examine how this affected the yield potential of the crops with different FD ratings. Differences in the agronomic performance were then explained by physiological features. This was done through analyses of quantified radiation interception, radiation use efficiency, canopy expansion and development, biomass partitioning and C/N dynamics in relation to environmental factors and defoliation management. Full details of the materials and methods are given in Chapter 3. This is followed by a comparision of the seedling crop growth and development in Chapter 4 prior to the introduction of different defoliation regimes. In Chapter 5, the yield and quality of the regrowth lucerne crops is presented followed by a physiological explanation of radiation interception in Chapter 6 and partitioning in Chapter 7 with a general discussion of the implication of the research results in Chapter 8.

Chapter 3 Materials and methods

3.1 Site description

3.1.1 Site location and history

The experiment was at the Field Research Center (FRC), Lincoln University, Canterbury, New Zealand (43^0 38' S, 172^0 28' E) within a 0.61 ha (135 x 45 m) area of flat land in Iversen Field paddock 12 (I12).

Historically Paddock I12 had grown annual ryegrass (*Lolium multiflorum*) and kale (*Brassica oleracea spp. acephala*) in the 2010/2011 growth season. Oil seed rape (*Brassica napus*) was sown and grown from September 2011 until April 2012 when oil seed rape and ryecorn (*Secale cereale*) were re-sown on the paddock. Following this, 'ARI' ryegrass was sown and grown on March 2013 until the site was prepared for the experiment. Ryegrass was grazed and then the area was sprayed with Roundup 360 (glyphosate; 720 g a.i/ha) on 25 August 2014, followed by harrowed, ploughed, roto-crumbled and rolled on 2, 9, 10 September and 5 October.

3.1.2 Soil characteristics

The soil at the I12 is a Wakanui silt loam (Aquic Haplustept, USDA Soil Taxonomy) which is classified as "Younger Pallic soil" in the New Zealand Soil Classification (Hewitt, 2010). These soils cover 12% of New Zealand and usually are dry in summer but wet in winter with rainfall ranging from 500 mm to 1000 mm (Hewitt, 2013). Wakanui soils typically have 0.3 m of topsoil and subsoil horizons consisting of silt to loamy sand to a depth of 2 to 3 m. These soils have imperfect drainage due to their high density but a high mineral nutrient content, especially sulphur. The available water content (WAC) of the Wakanui ranges from 120-180 mm/m (Webb *et al.*, 2000). Sim *et al.* (2015) has previously shown that WAC for lucerne extraction at the I12 is about 360 mm to a depth of 2.3 m.

3.2 Meteorological conditions

3.2.1 Long-term meteorological conditions

The long-term mean data (LTM) from 1960 to 2016 for the experimental site is displayed in Table 3.1. The annual mean temperature in Canterbury is 11.6 ^{0}C and ranges from 16.7 ^{0}C in January to 6.1 ^{0}C in July. Annual rainfall is 628 mm and Penman potential evapotranspiration (PET) is 1082 mm, which gives a long-term maximum potential soil moisture deficit ($PSMD_{max}$) of 520 mm (Figure 3.4).

Table 3.1 Monthly long term means from 1960 to 2016 for total solar radiation (R_o), maximum (T_{max}), minimum (T_{min}) and mean (T_{mean}) air temperatures, Penman potential evapotranspiration (PET), and wind run measured at the Broadfields Meteorological Station, Lincoln, Canterbury, New Zealand.

Month	R_o MJ/m^2/day	T_{max} (^{0}C)	T_{min} (^{0}C)	T_{mean} (^{0}C)	Rainfall (mm)	PET (mm)	Windrun (km/day)
Jan	22.1	22.1	11.3	16.7	49	157	372
Feb	19.1	21.9	11.3	16.6	42	126	347
Mar	14.1	20.0	9.8	14.9	53	103	337
Apr	9.5	17.2	6.9	12.1	55	64	290
May	5.9	14.3	4.3	9.2	58	45	281
Jun	4.5	11.4	1.7	6.6	61	33	251
Jul	5.1	10.8	1.4	6.1	60	36	256
Aug	7.8	12.1	2.6	7.3	61	51	296
Sep	12.1	14.5	4.3	9.4	40	74	332
Oct	17.3	16.8	6.1	11.5	47	109	355
Nov	21.4	18.7	7.8	13.3	50	133	365
Dec	22.7	20.6	10.0	15.2	53	151	365
Annual	13.5	16.7	6.5	11.6	628	1082	321

3.2.2 Solar radiation and temperature during the experiment

Mean daily total solar radiation and daily air temperature during the experiment followed the long-term patterns (Figure 3.1). Total solar radiation increased from a minimum of 5 to 6 MJ/m^2/day in winter to a peak of about 23 MJ/m^2/day in summer. On a daily basis, mean total solar radiation ranged from >1.0 MJ/m^2/day in July to <34.0 MJ/m^2/day in December. Mean daily air temperature ranged from 6 to 7 ^{0}C in July to 17 to 19 ^{0}C in January and February. Air temperature extremes over the experiment were -4.7 ^{0}C on 12 July 2015 and 33.1 ^{0}C on 21 December 2015.

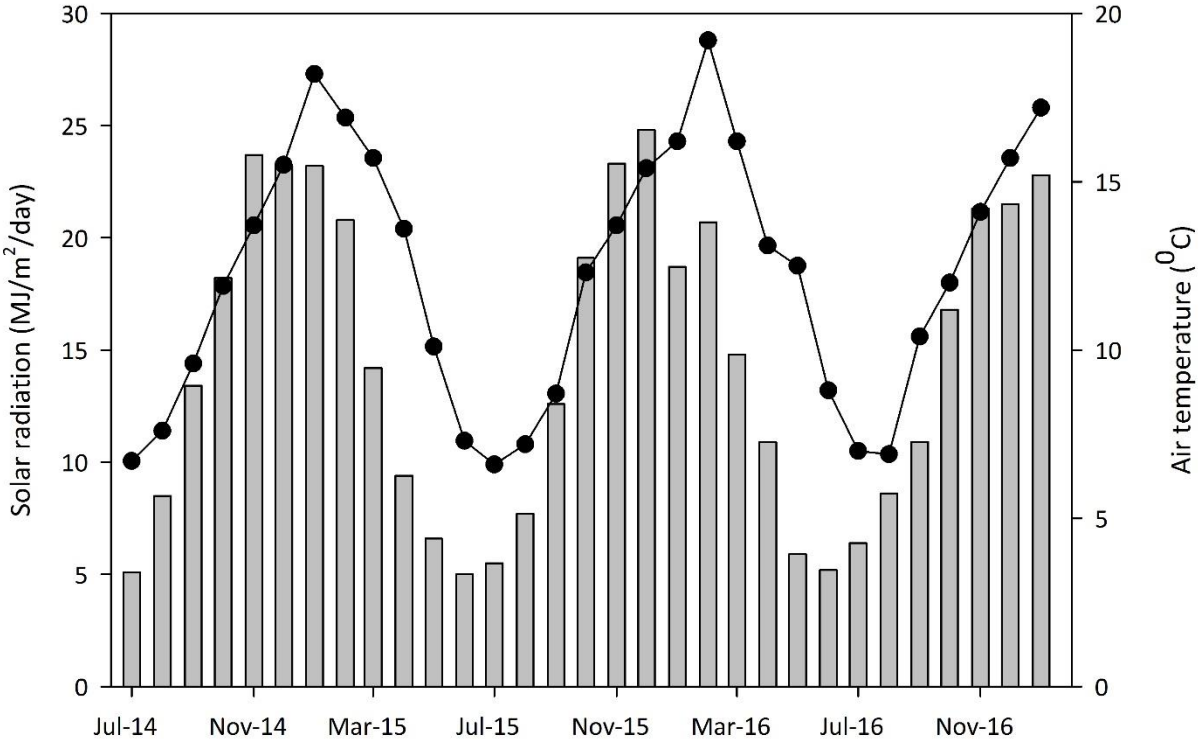


Figure 3.1 Mean daily solar radiation (bars) and mean daily air temperature (–●–) for monthly periods from 1 July 2014 to 31 January 2017 at Lincoln University, Canterbury, New Zealand. Note: Data were collected at the Broadfields Meteorological Station.

3.2.3 Rainfall, PET and PSMD during the experiment

The experiment occurred through two dry years (2014/15 and 2015/16). In the 2014/15 year, rainfall was only 403 mm, or 36% below the LTM (Table 3.2). PET was 1028 mm, which was similar to the LTM. In the 2015/16 year, the site continued to be exposed to dry conditions with 488 mm rain (22% below the LTM) and PET of 969 mm (10% below the LTM).

Table 3.2 Total season rainfall, Penman potential evapotranspiration (PET) and maximum potential soil moisture deficit (PSMDmax) for two growing seasons from 1 July 2014 to 30 June 2016 and sub-growing season from 1 July 2016 to January 2017 at Iversen 12 Lincoln University, Canterbury, New Zealand.

Year	Rainfall (mm)	PET (mm)	$PSMD_{max}$ (mm)
2014/15	403	1028	714
2015/16	488	969	597
2016/Jan 2017	249	638	392

Monthly rainfall was variable and followed the long-term distribution pattern (Figure 3.2). From 1 July 2014 to 31 January 2017, daily rainfall only exceeded 36 mm on 31 May 2016. Total monthly PET followed a similar pattern to the LTM in each season which increased from a low of 21 mm in June to reach a maximum between 168-154 mm in January or December, before decreasing to a minimum again in June.

In general, long-term mean PET exceeds rainfall from September to April. This meant the PSMD began to increase in September through to a maximum in April. However, in the 2014/15 year, PET exceeded rainfall from August. The PSMD began to increase in August through to the $PSMD_{max}$ of 714 mm in April, which was 27% higher than the LTM of 520 mm (Figure 3.4). In the 2015/16 year, PET exceeded rainfall in October resulting in the $PSMD_{max}$ of 597 mm in May, 13% higher than the LTM. Availability of water is the main factor determining yield for lucerne crops. Yield is be expected to decrease when 50% of available water content is extracted to the 2.3 m soil depth which occurs after about 250 mm for Iversen 12. During this experiment, irrigation was applied to alleviate drought stress (Section 3.3.5) but this was not always adequate to prevent water stress in each year. Water stress occured in mid-November 2014 for seedling crops and mid-December 2015 and 2016 for established crops.

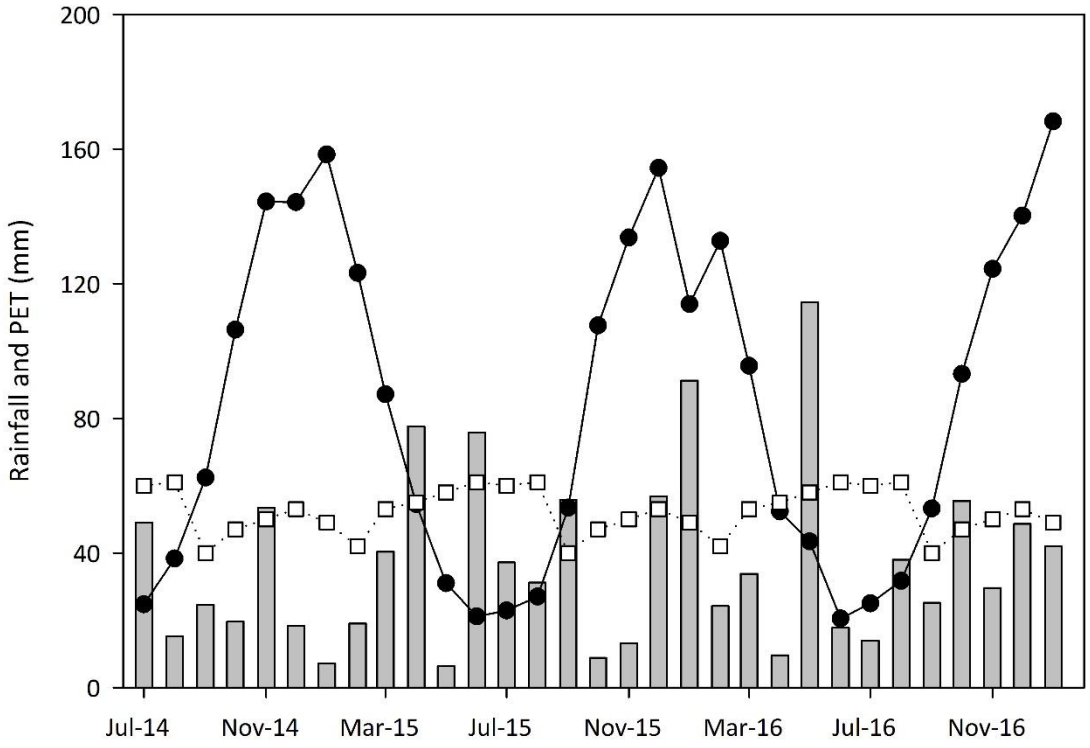


Figure 3.2 Monthly rainfall (bars) and Penman potential evapotranspiration (PET, –●–) from 1 July 2014 to 31 January 2017 at Lincoln University, Canterbury, New Zealand. Note: Monthly LTM rainfall (····□····) for reference. Data were collected at the Broadfields Meteorological Station.

3.3 Agronomic management

3.3.1 Experimental treatments and design

The experimental treatments were a factorial combination of three genotypes with contrasting fall dormancy FD: a dormant genotype (FD2), a semi-dormant genotype (FD5), a non-dormant genotype (FD10) and three defoliation frequency regimes DF: 28-, 42-, 84 days. They were established as a split-plot randomised complete block design with 4 replicates. The nine treatments were designated into 36 plots (Appendix A1). The main-plots were the three DF treatments and the sub-plots (20 x 4.2 m) were the three FD ratings. The experiment was sown on 8 October 2014. Seeds were inoculated with NoduleN® and seed of FD2, FD5 and FD10 were sown at 15.1, 11.8 and 11.1 kg/ha, respectively. Rates differed to account for differences in final germination test results with the aim of sowing 10 kg/ha of bare seed equivalent. All crops were first harvested at the end of the seedling phase on 25 January 2015 and then defoliated at the three DF regimes as follows:

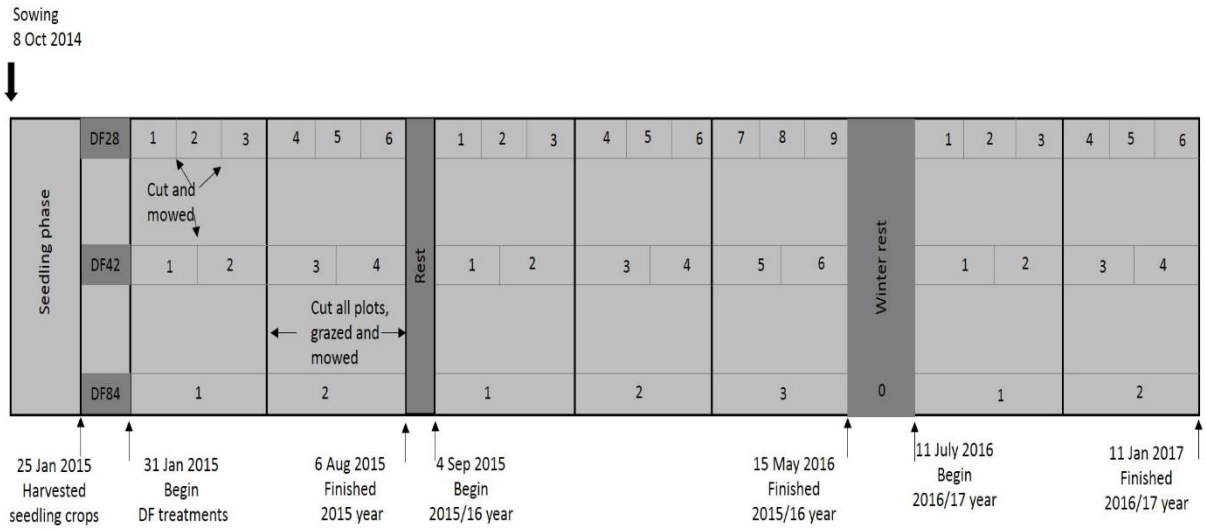


Figure 3.3 Schematic layout of defoliation frequency (DF) treatments of DF28-, DF42- and DF84 day and dates of the begin/finish regrowth years for lucerne with different fall dormancy ratings from 8 October 2014 to January 2017 at Lincoln University, New Zealand.

Note: Cycle numbers (0-9) are included for reference (e.g. duration for cycle 1 from the DF84 = cycles 1+2 from the DF4 = cycles 1+2+3 from the DF28). Cycle 0 represents for winter growth for two months for all crops before DF treatments were started again to examine spring-summer growth.

Seedling crops were defoliated when 80% of marked stems had an open flower. For regrowth lucerne crops, defoliation occurred at the end of each regrowth cycle according to the defoliation treatments.

After each regrowth cycle from the DF28 and DF42 treatments, plots were cut to 50 mm above ground using a stickle bar mower. This prevented damage to the crowns but also ensured that no residual

stems were transferred to the next regrowth cycles and only new lucerne growth was measured. At the end of each regrowth cycle from the DF84 treatment, all plots were first grazed for 3 or 7 days by sheep and/or lambs and then remaining stems were trimmed and carried by using a Fieldmaster forage harvester multi-cut chopper with a tow behind forage trailer.

3.3.2 Experimental period

The experimental period was over two years from October 2014 to January 2017. This period included the seedling phase and three regrowth periods in which the DF regimes were applied (Table 3.3).

Table 3.3 Experimental period for seedling phase and defoliation management for lucerne genotypes with contrasting fall dormancy in the Iversen 12 at Lincoln University, Canterbury, New Zealand.

Experimental season	Growing year	Experimental duration
Seedling	2014	From 8 October 2014 to January 2015 (110 days)
1st regrowth	2015	From 31 January 2015 to August 2015 (188 days)
2nd regrowth	2015/16	From 4 September 2015 to 15 May 2016 (255 days)
3rd regrowth	2016/17	From 11 July 2016 to January 2017 (185 days)

3.3.3 Soil fertility

The soil test results for Iversen 12 are displayed in the Table 3.4. At the initial experiment setup on 3 October 2014, soil fertility was analysed from a bulk sample of 20 soil cores of the topsoil (0-150 mm) collected randomly from each half (North to South) of the trial site. Based on these results no fertiliser was added at the establishment.

In early August 2016, another soil consisted 20 cores per each DF regime was taken randomly across the trial site and bulked (5 per main-plot). The soil test results indicated Olsen phosphorous (P) and sulphate sulphur [S(SO4)] were below optimum levels. Therefore, 350 kg/ha superphosphate (0% N. 9% P. 0% K. 11% S) was applied to the trial site on 18 August 2016.

Table 3.4 Soil test results for the trial site in the Iversen 12 at Lincoln University, Canterbury, New Zealand from 2014 to 2016. Note: Soil tests were evaluated using the Ministry of Agriculture and Fisheries Quick Test (MAF QT) procedures. Lower optima for plant growth according to (Morton and Roberts, 1999).

Site	K	Ca	Mg	Na	P	S(SO4)	pH
	……m.e./100 g ……				mg/L	mg/kg	in water
October 2014							
North	0.28	7.2	0.86	0.13	13	3	5.9
South	0.39	7.0	0.76	0.12	16	3	5.8
August 2016							
DF28	0.25	6.4	0.8	0.2	10	5	5.9
DF42	0.29	7.2	0.9	0.22	9	6	5.8
DF84	0.3	7.1	0.86	0.2	9	8	5.9
Lower optima	**0.26**	**-**	**0.34**	**-**	**15 - 20**	**11**	**5.3**

3.3.4 Weed control

Before ploughing, the experimental site was sprayed with Roundup 360 (glyphosate; 720 g a.i/ha) on 25 August 2014 to control annual grasses. In the seedling phase, plots were hand-weeded as needed for about 2 months after seedling emergence. On 2 December 2014, all plots were sprayed with Spinnaker (Imazethapyr; 96 g a.i/ha) to control fathen (*Polygonum aviculare*) and other broadleaf weeds. In spring October 2015, white clover (*Trifolium repens*) invaded the trial site, mainly in the DF28 crops. Therefore, after these crops were sampled and mowed, Classic® (Chlorimuron-ethyl; 30 g a.i/ha) was sprayed over these 28 cut plots on 8 October 2015, to control white clover and avoid affecting the lucerne crops. In the winter 4 July 2016, Nu-Trazine 900DF (Atrazine; 720 g a.i/ha) was sprayed over the entire trial site to control an infestation of perennial ryegrass (*Lolium perenne*, L.), annual Poa (*Poa annua*, L) and annual ryegrass (*Lolium multiflorum*).

3.3.5 Irrigation

During the seedling phase, irrigation was not applied because a reasonable plant population had emerged. For regrowth crops, the irrigation requirement was calculated from a water balance. A target of maximum 250 mm actual soil profile moisture deficit was set to avoid water stress. Irrigation was applied by using a hand shift pipe irrigation system with a water application rate of 6-8 mm/h. The amount of water applied was measured with two rain gauges. Details of irrigation are shown in Table 3.5.

Table 3.5 Irrigation water applied to the paddock I12 in the Field Research Centre, Lincoln University. Canterbury, New Zealand from 2015 to 2017.

Start date	Finish date	Amount (mm)
First regrowth 2015		
13 January 2015	14 January 2015	52
31 March 2015	1 April 2015	42
Total		**94**
Second regrowth 2015/16		
3 November 2015	4 November 2015	38
26 November 2015	27 November 2015	40
30 December 2015	2 January 2016	40
19 January 2016	20 January 2016	42
9 February 2016	10 February 2016	42
13 May 2016	14 May 2016	50
Total		**252**
Third regrowth 2016/Jan 17		
9/1/2017	10/1/2017	42

The soil moisture deficit (SMD) to 2.3 m depth is shown in Figure 3.4. The experimental site had a SMD of 181 mm when measurements began on 26 December 2015. After that a total of 94 mm of irrigation was applied, but this was not enough to bring the SMD up and it exceeded 250 mm from March to April 2015, due to the exceptionally dry 2014/15 year (Section 3.2.4). During the following winter to spring, SMD decreased to 84 mm by 24 September 2015. From then, SMD increased to a maximum of 340 mm by 16 May 2016. A total amount of 252 mm was applied during this period but this still was not sufficient to maintain the SMD above 250 mm from February to May 2016. In the winter 2016, SMD decreased to 94 mm and it was then maintained < 100 mm throughout spring before it increased to a maximum of 159 mm by 7 January 2017.

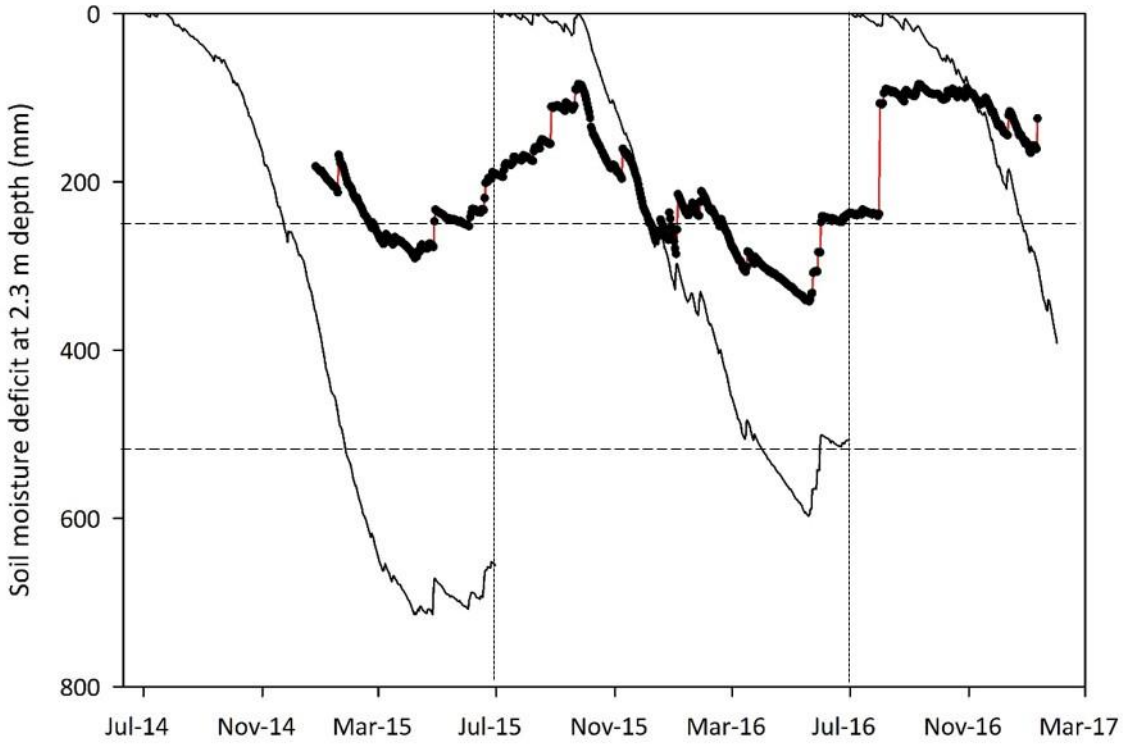


Figure 3.4 Seasonal patterns of potential soil moisture deficit (PSMD) (solid line) and actual soil moisture deficit (SMD) (black circles) to 2.3 m depth from 1 July 2014 to 31 January 2017 at Lincoln University, Canterbury, New Zealand. Note: (- - - -) dashed lines represent long-term mean $PSMD_{max}$ of 520 mm, and SMD of 250 mm for references.

3.4 Measurements

3.4.1 Meteorological measurements

Soil and air temperature data were collected on-site. A soil temperature (T_{soil}) probe was placed at seed depth about 20 mm below the soil surface, and was monitored from sowing until 50% emergence of the first trifoliate leaf. The air temperature (T_{air}) was measured by a thermistor installed at 1.5 m above ground. T_{soil} and T_{air} were measured at hourly intervals by a Hobo 4 channel logger (Onset Computer Corporation, Bourne, Maryland, USA) and used for thermal time calculations. Other data were collected at the Broadfields Meteorological Station, 2 km north of Lincoln University, which monitors rainfall (mm), Penman potential evapotranspiration (mm), solar radiation ($MJ/m^2/day$), and wind run (m/s). Measurements were recorded hourly and caculated to daily means.

3.4.2 Soil water measurements

Soil water content was measured in the topsoil (0-0.2 m depth) using a Time Domain Reflectometer (TDR; Trace system, Soil Moisture Equipment, Santa Barbara, California, USA). From 0.2 m to 2.3 m soil depth, soil water content was measured with a neutron probe (Troxler Electronic Industries Inc, Research Triangle Park, North Carolina, USA). Measurements were taken at four points on the experimental site which were located in plots 5, 12, 26 and 36. Soil water content measurements were taken at around 1 month intervals throughout the experimental period.

Additional measurements related to specific procedures are reported in the relevant chapters.

3.5 Calculations

3.5.1 Photoperiod

Photoperiod (Pp) for each day was determined from longitude and latitude coordinates using the method presented by Goodspeed (1975). At this latitude Pp increases from 10 h on 21 June to 16.6 h on 21 December.

3.5.2 Thermal time calculation

Daily thermal time (Tt, ^{o}Cd) was calculated using a broken-stick threshold model (Jones and Kiniry, 1986) where Tt was assumed zero for air and soil temperatures (T_{air}, soil) below the base temperature (T_b) of 1.0 ^{o}C (Moot *et al.*, 2001). For temperatures less than 15^{o}C, Tt was accumulated linearly at 0.7 ^{o}Cd/°C and then at 1.0 ^{o}Cd/°C until the optimum temperature (T_{opt}) of 30 ^{o}C was reached (Moot *et al.*, 2001; Teixeira *et al.*, 2011). Tt was calculated hourly intervals and then integrated over each day. Thermal time accumulation was calculated as the sum of daily Tt using soil temperatures for emergence and air temperatures for leaf appearance.

Additional calculations related to specific procedures are reported in the relevant chapters.

3.6 Statistical analysis

Statistical analysis was conducted in GENSTAT (version 16) (Lawes Agricultural Trust, IACR, Rothamsted, U.K.). When comparing FD rating with DF regime, results for all variables were analysed as a split-plot design with DF regime (28-, 42-, and 84 days) as main plots and FD rating (FD2, FD5 and FD10) as sub-plots. When necessary, FD ratings within a DF regime were analysed and compared as a one-way ANOVA in randomised blocks. Means were seperated by Fishers protected l.s.d ($P \leq 0.05$) when significant. Linear and non-linear regressions were calculated using the least-squares regression method. Unless otherwise stated, there were no significant interactions between FD and DF frequency of the measured variables.

Chapter 4 Seedling establishment of lucerne with different fall dormancy ratings

4.1 Introduction

This chapter describes the initial lucerne growth and development during the seedling phase to test physiological responses of FD ratings during taproot establisment. This is because the physiological responses of seedling lucerne during taproot establishment differs from established crops, so they must be considered separately (Teixeira *et al.*, 2011). Thus, the objective was to investigate the influence of FD on DM production and phenological development during the seedling phase, defined as sowing to first harvest.

4.2 Material and methods

A detailed description of the experimental design and treatments was given in Section 3.3. In this chapter, only measurements related to results in this chapter are reported.

4.2.1 Seedling phenology

Lucerne emergence was considered complete when both cotyledons were visible and had unfolded (Moot *et al.*, 2000). The number of emerged seedlings was counted in 2 x 1 m drill rows in each plot. Counts were made every 1-3 days until seedling number became constant for three consecutive dates. Appearance of primary leaves was measured on five tagged stems per plot. Starting from seedling emergence, these tagged stems were assessed every 1-3 days for (i) the number of fully expanded primary leaves, (ii) stem height (from ground to apical bud) and (iii) the number of axillary leaves (branching) at each main-stem node.

4.2.2 Seedling shoot and root biomass

Seedling shoot and root biomass were assessed when 50% of the tagged seedlings had reached the three and six trifoliate main-stem leaves. A single 20 cm long section of drill row in each plot was excavated intact. In the laboratory, shoot and root fractions in each section were separated. The root fraction included the entire root system. Shoot dry matter (DM) measurements were also taken every 14 days, starting when more than 50% of the tagged seedling plants had initiated buds (visible buds) until open-flower. At the end of the seedling period (when 80% of the stems had an open flower), crown and taproot DM were sampled. Shoot samples were initially harvested from a single 0.2 m^2 quadrat per plot using hand shears to cut all shoots just above crown height (50 mm from ground to crown). A root sample (crowns + taproots) was then obtained from the same quadrat by digging a

trench to a depth of 300 mm. Materials were washed clean of soil and all shoot and root samples were dried in a forced-air oven set to 60°C until a constant weight was achieved.

4.2.3 Canopy expansion and radiation interception

Leaf area was measured from a subsample of 20 stems. Leaves were removed from stems and the area of green lamina was quantified with a leaf area meter (LICOR 3100; Licor Inc. Lincoln, USA). These measurements were done on three occasions when the shoot DM was measured.

The amounts of incident radiation above (R_0) and transmitted radiation below (R) the canopy were measured directly, non-destructively using a Sunscan plant canopy analyser (Delta-T Devices Ltd, Burwell, Cambridge, England). R_0 and R measurements were taken every 7 days, starting 45 days from sowing, when canopy height was above the sensor height (30 mm). Seven above and below canopy readings were taken per plot.

4.2.4 Phyllochron

The phyllochron (°Cd/ primary leaf) was calculated as the slope of the linear relationship between the number of primary leaves on tagged stems and accumulated thermal time (Section 3.5.2) for each genotype.

4.3 Results

4.3.1 Final population

Final emergence of FD2, FD5 and FD10 was 303, 319 and 255 plants/m^2, respectively (Figure 4.1). Based on their respective sowing rates of 577, 490 and 450 seeds/m^2 these represented 52%, 65% and 56% emergence. All genotypes showed two phases in emergence with an initial 150-200 plants/m^2 emerging up to 27 October 2014. During November, rainfall of 50 mm (Figure 3.2) induced a second phase of emergence which resulted in a final population of more than 250 plants/m^2. This is considered sufficient for high yielding crops in this environment (Moot *et al.*, 2012). Neither the number of days from sowing to 50% emergence (P=0.19) nor the accumulated thermal time to 50% emergence (P=0.20), which averaged 263°Cd, differed among the three genotypes.

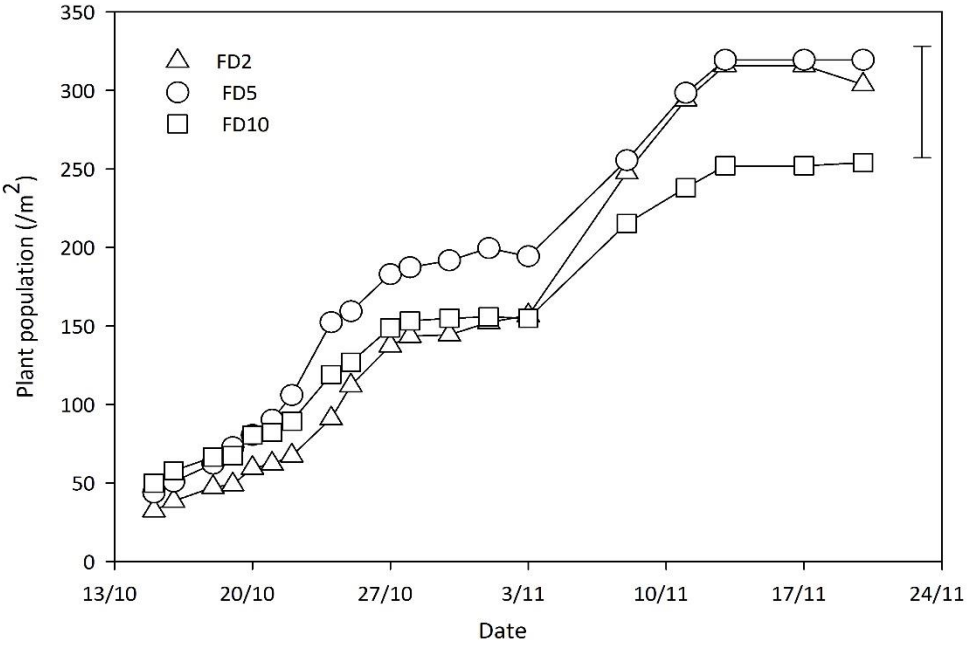


Figure 4.1 Field emergence over time of lucerne seedlings with different fall dormancy (FD) ratings sown on 8 October 2014. Note: Error bar represents the LSD (α=0.05) for the final emergence population.

4.3.2 Seedling shoot and root biomass

Table 4.1 shows the seedling shoot and root biomass of all three crops was not different at the third (P=0.90) or sixth (P=0.22) trifoliate stages. The exception was for the initial fraction of biomass partitioned to root (P_{root}) which was lowest (P<0.01) for FD10 at 0.17 at the third trifoliate stage.

Table 4.1 Shoot and root plant dry weight (mg/plant) and the proportion of partitioning of biomass to roots (P_{root}) for seedling lucerne genotypes with different fall dormancy (FD) ratings at the 3rd and 6th trifoliate leaf stage from sowing on 8 October 2014.

Lucerne genotypes	Date	18/11			11/12	
		3rd trifoliate leaf			6th trifoliate leaf	
	Shoot	Root	P_{root}	Shoot	Root	P_{root}
FD10	29.8	6.02	0.17a	482	154	0.25
FD5	28.0	7.22	0.21b	427	163	0.27
FD2	29.3	8.49	0.22b	386	142	0.26
P	0.90	0.08	<0.01	0.22	0.60	0.21
SE	3.94	1.07	0.01	53.9	20.81	0.02

The shoot yields calculated from these seedling measurements and subsequent quadrat cuts show that the FD10 genotype had the highest (P=0.03) shoot yield at the end of the seedling phase at 3.2 t DM/ha. The separation of yield was visually apparent in the field by early December (6th trifoliate stage) but only significant at later December to the final harvest (Figure 4.2).

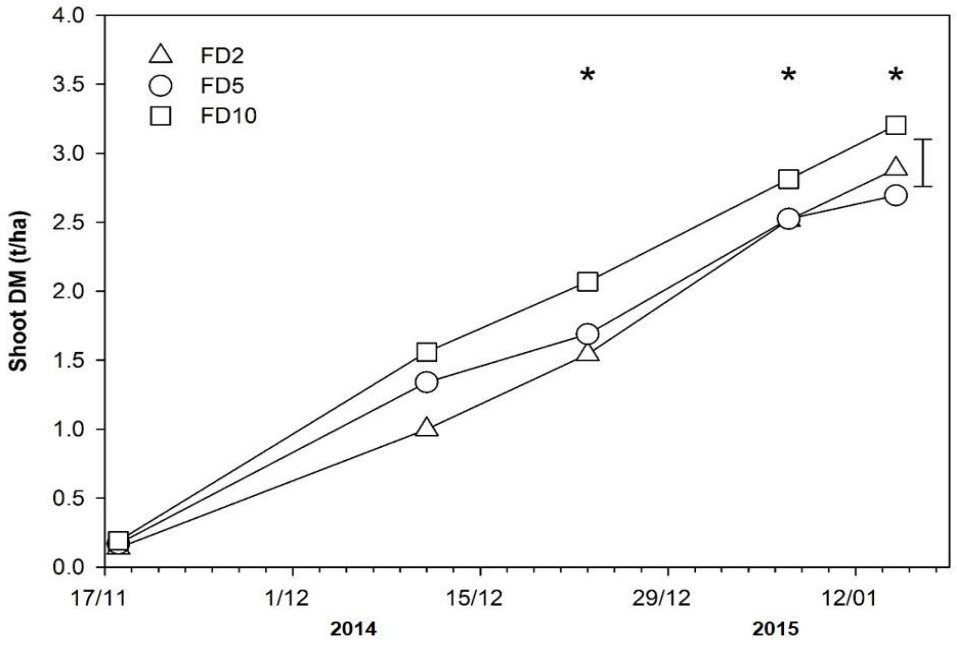


Figure 4.2 Shoot dry matter (DM) yield of lucerne genotypes with different fall dormancy (FD) ratings sown on 8 October 2014. Note: Error bar represents the LSD (α=0.05) for the final harvest. *= P<0.05.

The root biomass of the FD10 (3.3 t DM/ha) genotype was also higher (P=0.02) than the others at the final harvest (Figure 4.3), but P_{root} (0.50) was not different. Root and shoot yields at the end of the seedling phase were 6.55 t DM/ha for FD10 compared with 5.57 t DM/ha for FD2 and FD5.

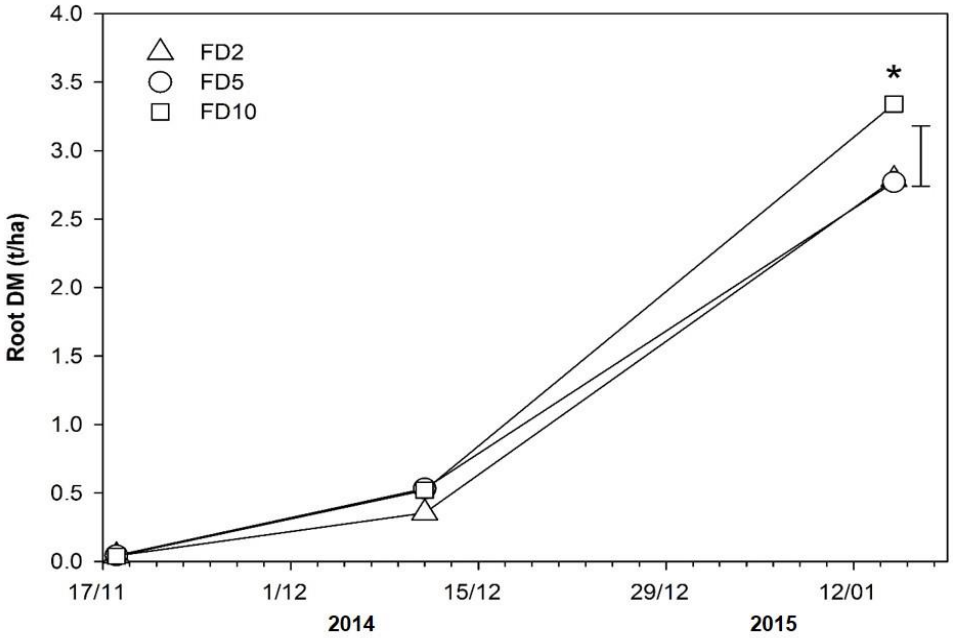


Figure 4.3 Root dry matter (DM) yield of three lucerne genotypes with different fall dormancy (FD) ratings sown on 08 October 2014. Note: Error bar represents the LSD (α=0.05) for the final harvest. *=P<0.05.

4.3.3 Leaf area and light interception

In the early seedling growth period the FD2 crop intercepted the lowest fraction of incident radiation (0.35) but there were no differences at the end of the seedling phase (Figure 4.4).

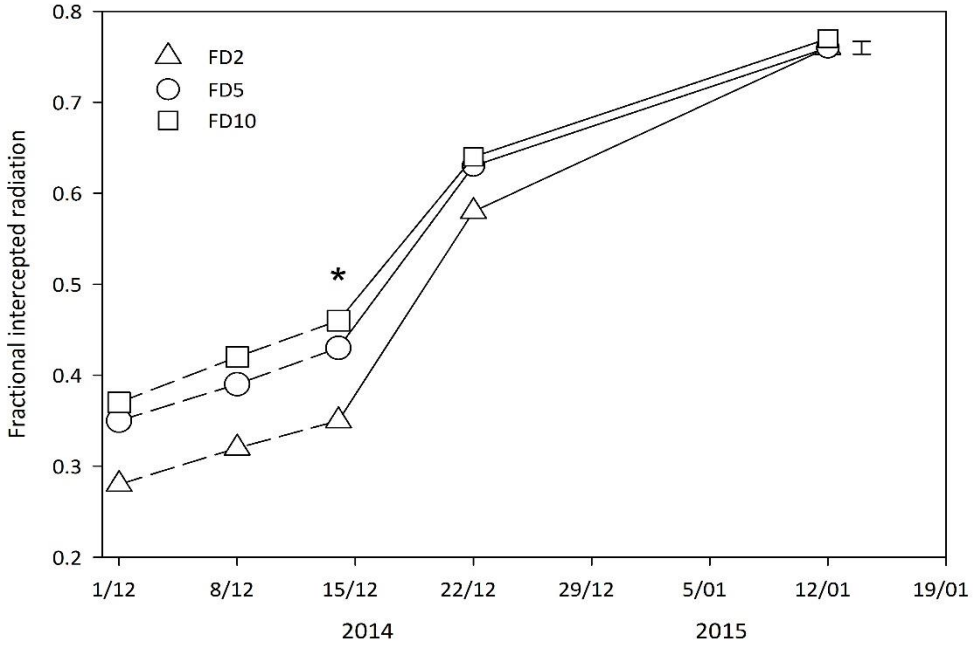


Figure 4.4 Fractional interception of incident radiation of three genotypes of seedling lucerne with different fall dormancy (FD) ratings sown on 08 October 2014. Note: Dashed line shows radiation interception prior to bud visible. Error bar represents the LSD (α=0.05) for the final measurement. *= P <0.05.

At the final harvest the radiation interceptance was still less than 0.78. This means the leaf area index was always below the critical level (LAI_{crit}) of 3.2 (Teixeira *et al.*, 2011) required to intercept 95% of incident radiation (Figure 4.5). The LAI increased rapidly between the samplings on 15 and 23 December 2014. This may reflect water stressed crops (Section 3.2.3) with wilted canopies until 3.1 mm of rain restored turgor pressure on 21 December 2014.

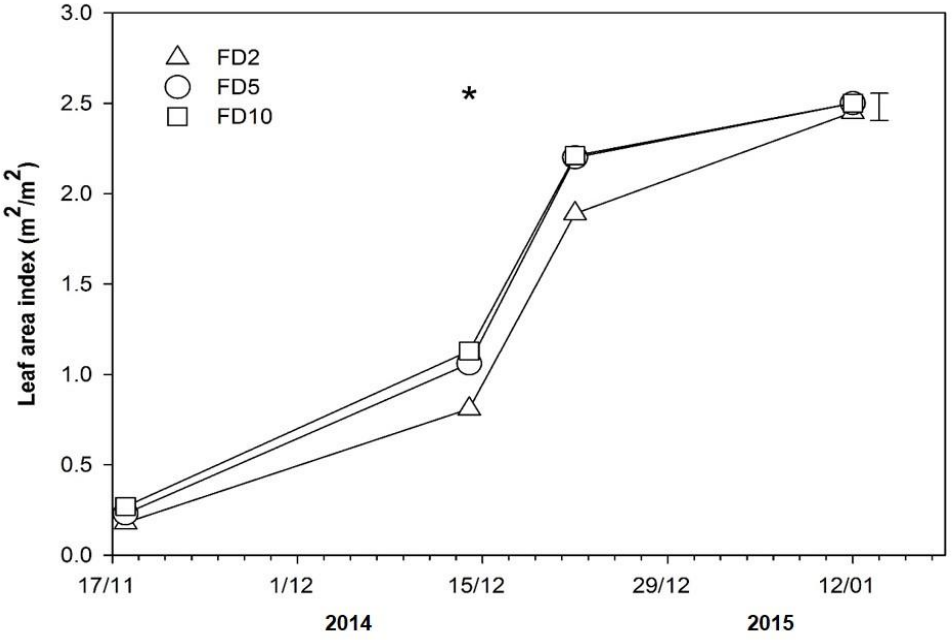


Figure 4.5 Leaf area index of three lucerne genotypes with different fall dormancy (FD) ratings sown on 8 October 2014. Note: Error bar represents the LSD (α=0.05) for the final measurement. *= P<0.05.

4.3.4 Phyllochron and plant height

The number of leaves on the main stem was also consistent among genotypes. Each genotype expanded up to 17 leaves by the time of harvest (Figure 4.6).

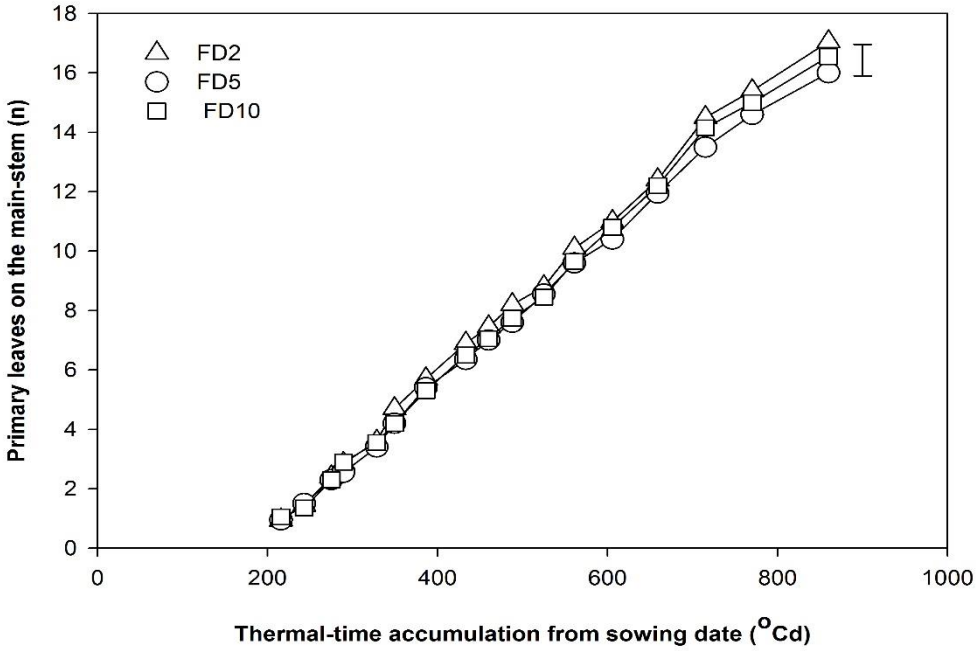


Figure 4.6 Number of primary leaves on the main-stem of three lucerne genotypes with different fall dormancy (FD) ratings sown on 8 October 2014. Note: Error bar represent LSD (α=0.05) for the final number of primary leaves.

The phyllochron for all genotypes across the seedling phase was 52 ± 1.4 °Cd per primary leaf (P = 0.06). Branching was not different (P=0.21) among the genotypes (Figure 4.7).

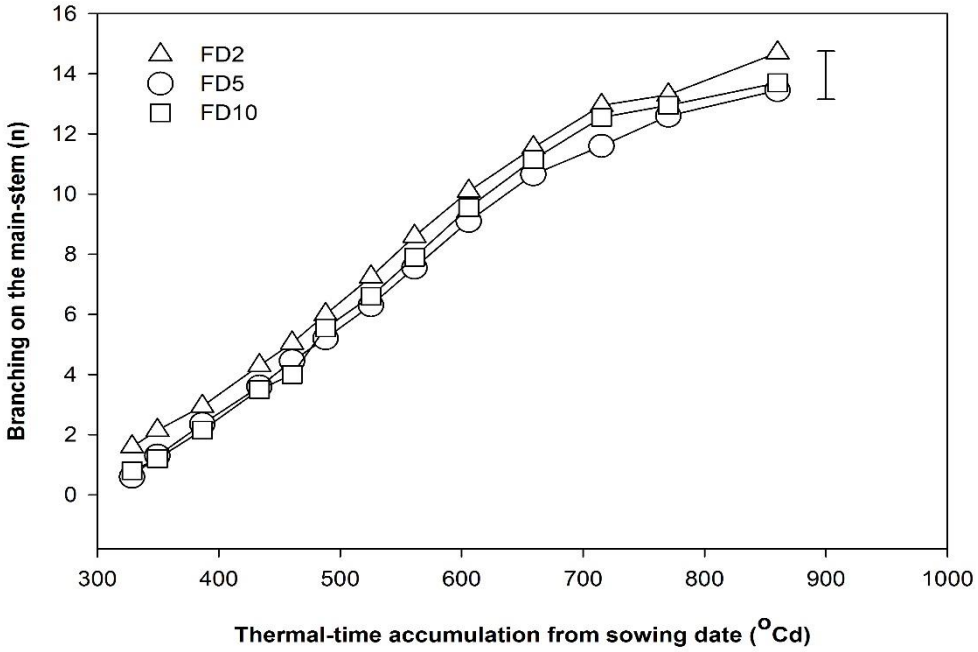


Figure 4.7 Number of branches on the main-stem of three lucerne genotypes with different fall dormancy (FD) ratings sown on 8 October 2014. Note: Error bar represents the LSD (α=0.05) for the final total number of branches.

In contrast, leaf area differed (P<0.05) among genotypes. It was 142, 119 and 111 cm^2/stem for FD10, FD5 and FD2, respectively by 23 December 2014 (Figure 4.8).

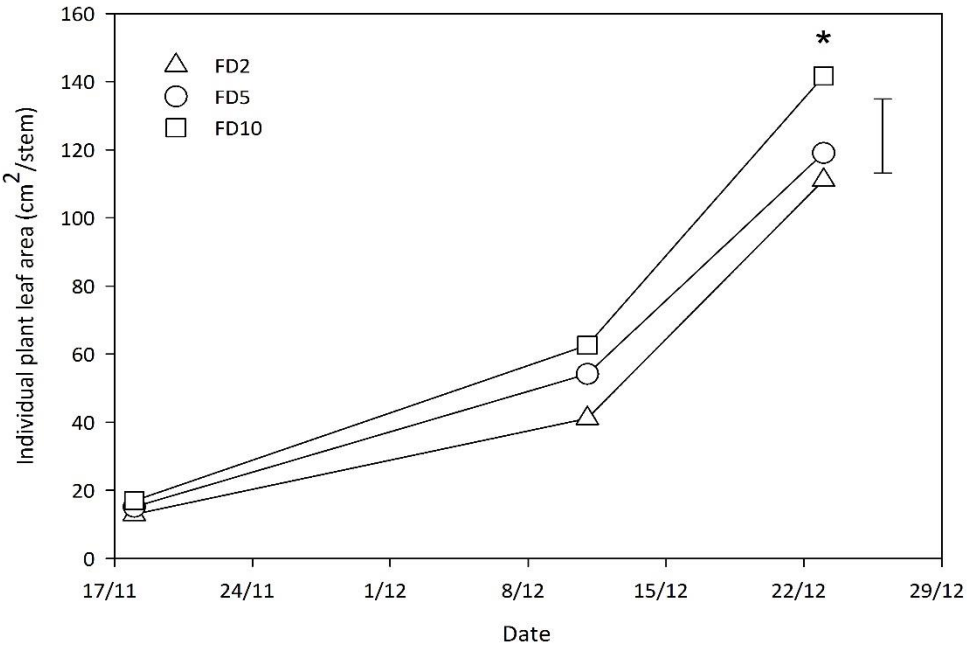


Figure 4.8 Leaf area per stem of three lucerne genotypes with different fall dormancy (FD) ratings sown on 8 October 2014. Note: Error bar represents the LSD (α=0.05) for the final measurement. *=P<0.05.

Furthermore, plant height at the open-flower stage was greater (P<0.05) at 39.5 cm for FD10 which was taller than the 34.5 cm for FD5 and 33.5 cm for FD2 (Figure 4.9).

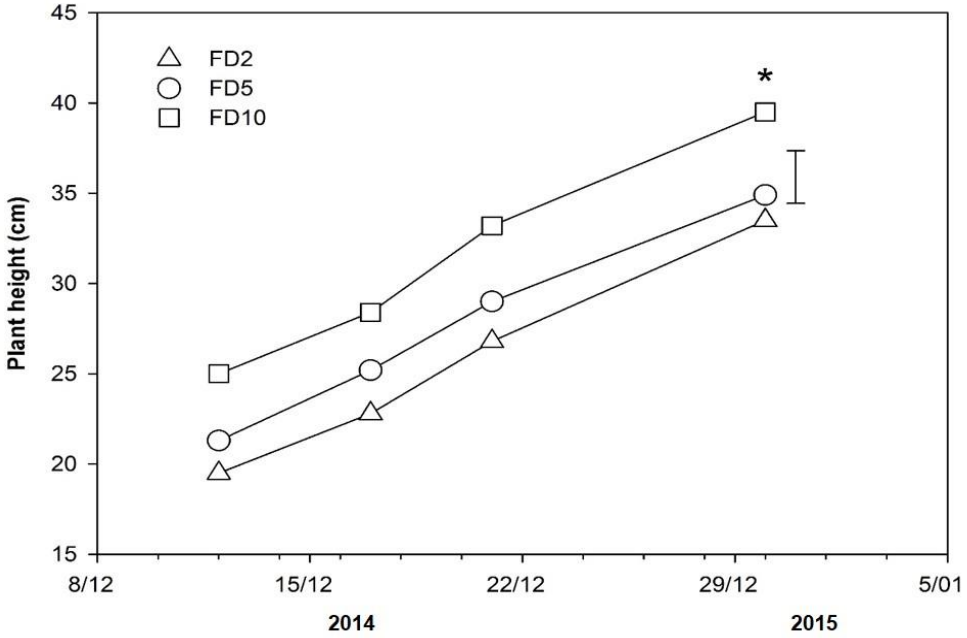


Figure 4.9 Plant height of three lucerne genotypes with different fall dormancy (FD) ratings sown on 8 October 2014. Note: Error bar represents the LSD (α=0.05) for the final measurement. *=P <0.05.

4.4 Discussion

These results indicate that two growth components of genotype (leaf area expansion and stem elongation) were most closely correlated with autumn or fall dormancy ratings during spring seedling growth. In contrast, the development (emergence and phyllochron) was consistent among genotypes.

4.4.1 Seedling establisment

The collective results of seedling growth and development suggest some similarities but also important differences among these lucerne genotypes with different FD ratings. Thermal times to emergence were not different and consistent with previous reports (Sim *et al.*, 2015). A second flush of emergence (Figure 4.1) with rain has previously been reported (Wigley *et al.*, 2012) for lucerne and may indicate an effect of seed coating or an innate population response to different soil temperature and moisture conditions (Sharifiamina *et al.*, 2016). Despite differences in the temporal pattern of emergence all crops established at sufficiently high plant populations (Teixeira *et al.*, 2011; Moot *et al.*, 2012) to maximise yields.

4.4.2 Shoot and root bimass production and phenology development

The early shoot and root growth, between the third and sixth trifoliate leaf stages, also showed no differences amongst the genotypes (Table 4.1). The implication was that ontogeny was consistent across genotypes and independent of any environmental signals or FD rating. However, FD10 had

partitioned a lower proportion of biomass to the roots by the third trifoliate stage. This suggests the priority for this genotype was shoot over root production at this early stage. By the end of the seedling phase (15 January) priority of shoot growth for FD10 had resulted in a higher fraction of intercepted radiation (Figure 4.4), particularly compared with FD2. As a consequence of more radiation intercepted, it had 20% higher shoot and 16% more root biomass than FD2.

The cause of the yield difference appears related to the development of individual leaf area per plant (Figure 4.8) and plant height (Figure 4.9). This implies that the leaf arrangement on these taller plants allowed greater radiation interception, particularly as the canopy was below the critical leaf area index for the whole establishment phase (Figure 4.5). Given the highest proportion of radiation interception was only 0.7, the crops were all below critical leaf area index for all of the seedling growth period. For FD10 greater height and leaf area have resulted in the higher shoot (Figure 4.2) and root (Figure 4.3) biomass at the end of the seedling phase. Ability to intercept radiation is often the key limitation to crop and pasture establishment because water and nutrients are provided to ensure the maximum opportunity for success (Fick *et al.*, 1988). This means the early advantage in leaf area and light interception for FD10 was cumulative throughout this establishment phase. This has been the most successful strategy to maximise seedling yield (Figures 4.8 and 4.9). The results also suggest the advantage in leaf area was not associated with leaf appearance. The phyllochron was not different among genotypes and consistent with previously reported values (Teixeira *et al.*, 2011).

A difficulty in non-destructive measurement of radiation interception with seedling crops is that the instruments require some canopy height and leaf area before accurate measurements can be taken. This prevented radiation interception measurement until mid December which was 67 days after sowing (Figure 4.4). Despite this, the individual plant leaf area data coupled with these non-destructive measurements consistently highlighted the advantage in radiation interception to the FD10 crop. Similarly the separation in height measurements from mid-December (Figure 4.9) indicates the expression of taller plants from higher FD ranking, occurred throughout the seedling phase. This provides an independent validation of the breeders FD rankings for these genotypes.

Species differences allocation of biomass to shoot and root are often used to define their success at establishment (Thomas, 2003). Specifically, the lack of competitive ability of Caucasian clover has been linked to its disproportionate allocation to roots at the expense of shoots (Black *et al.*, 2002). Differences among genotypes are less well documented. The FD rating for lucerne is based on height with an emphasis on fall or autumn growth. However, these results suggest the height and leaf area advantage for FD10 were expressed after spring sowing. This resulted in greater seedling growth. It remains to be seen if this yield advantage is apparent during future regrowth crop cycles. This will be investigated in the following chapters.

Rainfall during October was half that normally expected (Figure 3.2). However, the cultivated seedbed had provided sufficient soil moisture for initial emergence to commence. The decision not to irrigate during this phase was made because a reasonable plant population had emerged. These early emerged plants formed the basis of the samples taken for the third trifoliate measurement. The subsequent second flush of emergence after November rainfall meant there were plants of different sizes and ages in the seedling samples taken at the sixth trifoliate stage. The tagged plants all came from the initial phase of emergence so time of sampling was presented accurately. The different aged plants were not recorded separately and may have affected the result at the sixth trifoliate stage and resulted in no significant difference in shoot yield until the end of the cycle. Agronomically, it seems likely that these later emerged plants were smaller and potentially will be the first ones to die in the intense self-thinning process that occurs in establishing lucerne stands (Teixeira *et al.*, 2007a; Moot *et al.*, 2012). It follows that management decisions should be made on the basis of the growth and development of the oldest and therefore largest plants in the crop, as occurred in this study.

4.5 Conclusions

Based on the results from this chapter the following conclusions can be made;

- All lucerne genotypes established succesfully with a final population of more than 250 plants/m^2.
- Shoot and root DM production of the least dormant genotype (FD10) were higher than the other two genotypes (FD2 and FD5). Higher DM production of FD10 was associated with greater radiation interception at the early stages of crop establishment caused by a higher LAI expansion rate.
- The FD10 genotype also showed a distinct morphology with taller stems and increased radiation interception.
- Thermal time to emergence, fractional partitioning of biomass to roots, leaf appearance and branching rates were similar among the three genotypes.

The following chapter aims to investigate if the shoot yield advantage of the FD10 genotype was maintained during future regrowth cycles.

Chapter 5

Shoot DM production of established lucerne with different fall dormancy ratings

5.1 Introduction

After establishment, the capacity of lucerne shoots to grow following defoliation depends on the level of reserves (C and N) in the crown and taproot. This is because, these endogenous reserves are remobilised to facilitate restoration of physiological process that subsequently drive biomass accumulation (Kim *et al.*, 1993; Ourry *et al.*, 1994; Teixeira *et al.*, 2007c). It is known that frequent defoliation reduces shoot growth and yield, and limits accumulation of C and N reserves in perennial organs (Moot *et al.*, 2003). Consequently, low levels of reserves influence shoot DM production in the following regrowth cycle (Teixeira *et al.*, 2008). However, it is unclear how this yield production might differ among genotypes with different FD. For the seedling lucerne during taproot establishment, growth of shoots and roots of the non-dormant genotype (FD10) was higher than the FD2 and FD5 genotypes (Chapter 4). It remains to be seen if this yield advantage is maintained during following regrowth cycles of the established crops. Thus, the objective of this chapter was to investigate the dry matter and quality responses of crops with different FD ratings when they were grown in the field with different DF regimes.

The null hypothesis of this investigate is shoot DM and forage quality will be the same regardless of FD rating. The defoliation regimes were used to create different levels of root reserves, to examine how this affected the growth of the crops with different FD ratings. To do this, all treatments were first harvested at the end of the seedling phase on 25 January 2015 and then defoliated at 28-, 42- or 84 day intervals (Section 3.3). In this chapter the assessment of the annual and seasonal DM yield was undertaken with emphasis on agronomic aspects of the FD ratings. Additionally, any differences in forage quality and ultilisation were assessed within regrowth cycles and among FD ratings. In subsequent chapters the physiological basis of any differences in crop growth and development are examined.

5.2 Material and methods

A detailed description of the experimental design and treatments was given in Section 3.3. This chapter reports the agronomic performance of the regrowth lucerne crops with different FD ratings.

5.2.1 Regrowth shoot biomass

Shoot samples were taken at the end of each regrowth cycle by using a 0.2 m^2 quadrat placed randomly in each plot. During year 1 and year 2, intermediate measurements were also taken at 28-day or 14 day intervals before the 42-day regrowth crops were harvested. Similarly, for 84-day regrowth cycles, intermediate measurements were taken at the mid-point after 42-days. Shoots were harvested by using the same method described for seedling crops (Section 4.2.2). Following shoot harvest, a sub-sample of 10 representative shoots was taken from the harvested quadrat. From each sub-sample, shoots were separated into leaf (plus petioles), soft stem and hard stem. Hard and soft stem parts were differentiated for the individual stems by using the tip of thumb and a finger squeezing from top of each stem down the stem until it felt harder. The section of soft stems plus all leaves were considered the palatable fraction and the harder stems unpalatable (Brown and Moot, 2004). The unpalatable proportion represents the lignified stems that would be left in the paddock as residual after grazing. Main shoot samples and sub-samples were dried in a forced-air oven set to 60˚C until constant weight.

5.2.2 Nutritive analysis

Nutritive values of forage were determined for the palatable and unpalatable proportion from each regrowth cycle throughout the regrowth years. Dried samples were ground to pass through a 1 mm mesh sieve (Cyclotec Mill, USA) and sub-sampled for measurements of nutritive values at the Lincoln University, Forage assessment laboratory, Riddolls Building. Total N content was analysed from 500 mg dried samples using near infrared spectroscopy (NIR; Foss NIR Systems 5000 Rapid Content Analyser).

5.2.3 Calculations

4.2.5.2 Seasonal growth rates

Growth rates (kg DM/ha/°Cd) were calculated by linear regression between accumulated shoot DM and accumulated Tt (Section 3.5.2) for each FD and DF within each individual regrowth cycle. The term “season(s)” refers to the recognised seasons of the year (e.g. spring, summer, autumn and winter). Seasonal growth rates were considered as growth rates changed throughout the regrowth seasons. This is a common way to express shoot growth affected by seasonal temperatures and identify environmental effects.

4.2.5.3 Leaf/stem ratio (LSR) and un-palatable proportion

Leaf/stem ratio (LSR) was calculated by dividing leaf DM by stem DM (soft plus hard stems). The un-palatable proportion represented the hard stem DM per unit of shoot DM (t hard stem DM/ha).

4.2.5.4 Crude protein (CP) and metabolisable enery (ME) contents

CP and ME were determined as the following equations

CP (%) = N%*6.25

ME (MJ/kg DM) = DOMD*0.16 where DOMD is digestible organic matter in dry matter

5.3 Results

5.3.1 Annual and seasonal shoot DM production

5.3.1.1 Total annual shoot DM production

The accumulated shoot dry matter yields of all treatment and season combinations are displayed in Figure 5.1. Analysis of the temporal pattern of accumulated yield allowed the overall annual growth of each genotype and each DF regime to be compared (Table 5.1). In the 2015 regrowth year, the total annual yield of the FD10 genotype was about 31% and 16% greater ($P<0.001$) than that of the FD2 and FD5, respectively, regardless of DF regime. In contrast, there was no effect of FD on yield in the following 2015/16 (Figure 5.1 a, b, c) and 2016/17 regrowth years (Figure 5.1 a, b). A separation of yield among FD ratings was apparent in the third regrowth (2016/17). Especially, in the DF28 regime, the FD10 genotype produced lower ($P<0.001$) yield (Figure 5.1 c). The FD10 genotype yielded 5.2 t DM/ha, compared with 6.8 t DM/ha for FD5, and 8.4 t DM/ha for FD2. When the full 24 month period was analysed all genotypes ($P<0.22$) produced ～ 27 t DM/ha (Table 5.1).

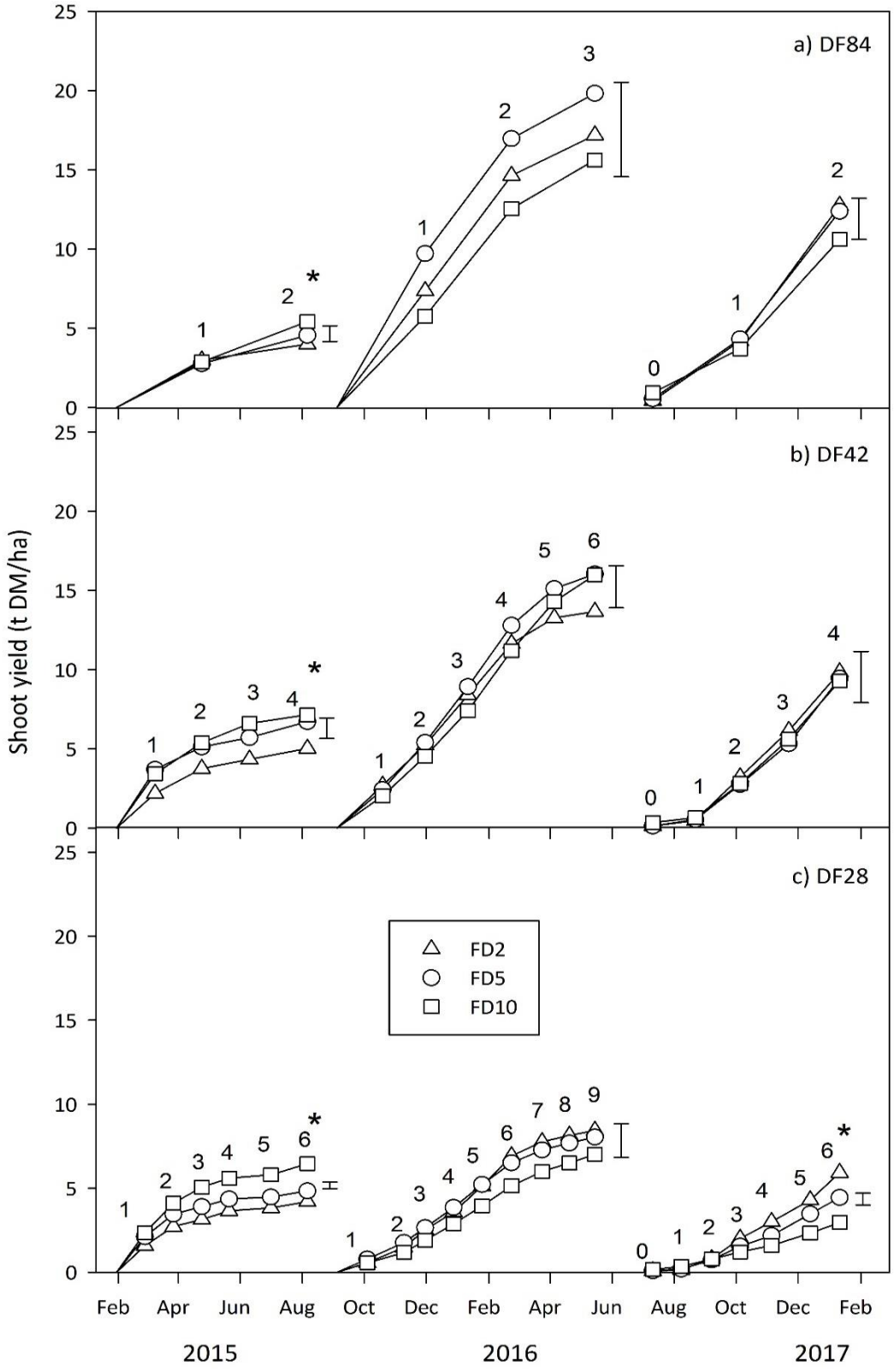


Figure 5.1 Accumulated shoot dry matter (DM) of three lucerne genotypes with fall dormancy (FD) of 2 (Δ), 5 (O) and 10 (□) ratings subjected to 28- (c), 42- (b) and 84 day (a) defoliation frequencies (DF) in the 2015; 2015/16 and 2016/17 regrowth years.

Note: Error bar represent LSD (α=0.05) at the end of each regrowth year. * represents significant differences at α=0.05. Number (0-9) indicates the regrowth cycle.

The interaction between FD and DF was not significant (P<0.13) for annual shoot yield (Table 5.1). As expected in 2015 and over the three years, DF regimes had a stronger influence (P<0.001) on annual shoot yield than FD genotypes (Table 5.1). In 2015, DF42 crops yielded ~1 t DM/ha higher than DF84 and DF28 crops. However, in the 2015/16 regrowth year, DF84 crops produced the highest (P<0.001) annual yield. The effect of defoliation regimes on yield was carried forward into the following regrowth year, in 2016/17. Both DF42 and DF28 crops had lower (P<0.001) yields than DF84 crops.

Table 5.1 Yield of lucerne genotypes with different fall dormancy (FD) ratings over a three regrowth periods under three defoliation (DF) regimes.

	Total shoot yield (t DM/ha)			
	2015	2015/16	2016/17	Overall regrowth period
FD2	4.4_a	13.1	9.5_b	26.9
FD5	5.4_b	14.6	8.7_{ab}	28.6
FD10	6.4_c	12.9	7.5_a	26.8
P <	0.001	0.15	0.01	0.22
SEM	0.23	0.93	0.58	2.45
DF28	5.2_a	7.84_a	4.4_a	17.4_a
DF42	6.3_b	15.2_b	9.4_b	30.7_b
DF84	4.7_a	17.5_c	11.9_c	34.1_c
P <	0.05	0.001	0.001	0.001
SEM	0.40	0.75	0.80	1.18
FD x DF				
P <	0.13	0.22	0.69	0.15
SEM	0.52	1.50	1.15	2.10

Note: Means in a column followed by the same letter are not different at α=0.05.

5.3.1.2 Seasonal shoot DM production

Figure 5.2 shows the seasonal pattern of shoot DM of each genotype (FD) and defoliation (DF) regime throughout the three growth years.

The effect of FD rating on shoot DM yield was carried on to the 2015 regrowth year following the seedling phase, which differed (P<0.001) in annual yield among genotypes. Irrespective of DF regimes, during the first year, final yields achieved for individual regrowth cycles of the FD10 genotype averaged 0.82 and 0.44 t DM/ha higher (p<0.05) than FD2 and FD5 genotypes, respectively.

In the following regrowth year (2015/16), FD rating had no effect (p< 0.53) on shoot DM production in the spring and summer cycles (Figure 5.2 a, b, c). From these periods, 81% of the annual shoot DM was produced in all genotypes. The FD effect was expressed (P<0.01) in the autumn cycles, for crops

defoliated at 42-day intervals (Figure 5.2 b, DF42-Cycle 5 and 6). Specifically, there was an interaction ($P<0.001$) between FD and regrowth season. The higher FD rating genotype produced higher herbage yield in the autumn regrowth, with 3.2 t DM/ha for the FD10 genotype compared with 2.5 t DM/ha for FD5 and 2.0 t DM/ha for FD2. The advantage in shoot DM production of the FD10 genotype during these months contributed around 8% of the total annual shoot DM yield. However, accumulated shoot DM overall seasons showed no difference ($P<0.15$) among FD ratings (Table 5.1).

In the third regrowth year (2016/17), there was also no effect of FD rating on shoot DM yield in the 84-day and 42-day cutting intervals (Figure 5.2 a, b). In contrast, the FD effect was different ($P<0.05$) among genotypes where crops were defoliated at 28-day intervals. In spring-summer, shoot DM yield from FD10 was 0.8 t DM/ha lower than the FD2 genotype in each regrowth cycle in October, November and January (Figure 5.2 c). There was no interaction ($P<0.65$) between FD and season (spring and summer) although, the summer regrowth had 13.5% higher ($P<0.001$) shoot DM yield than in the spring regrowth for all genotypes.

Overall, DF regimes produced yields in excess of 2 t DM/ha for all 42 day regrowth cycles and 4 t DM/ha for all 84 day regrowth cycles (Figure 5.2 a, b). In contrast, the yields of all genotypes on the 28-day regrowth cycle were below 2 t DM/ha, with the exception of the first DF28-Cycle 1 in February 2015 (Figure 5.2 c).

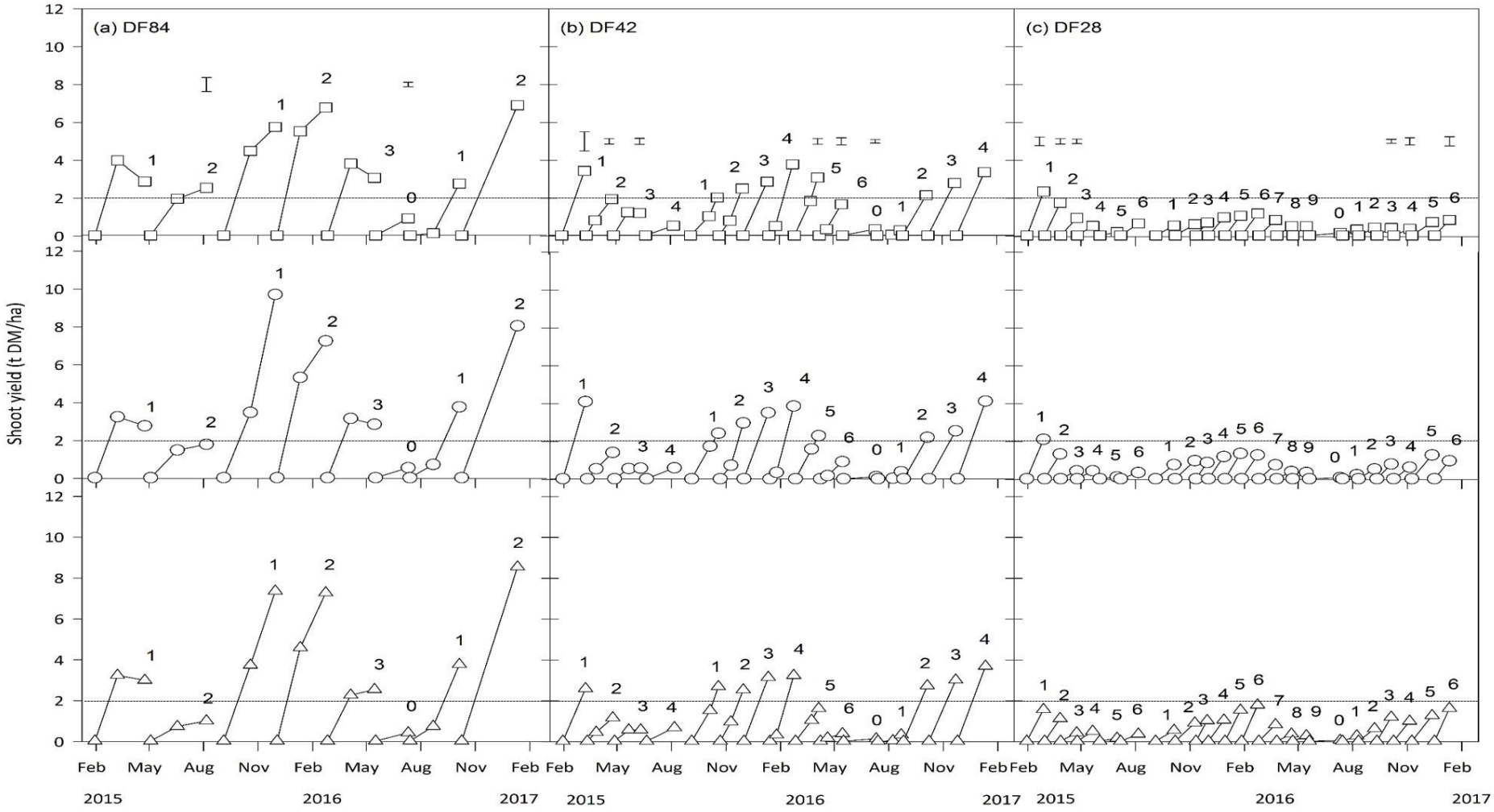


Figure 5.2 Shoot dry matter (DM) yield within regrowth cycles of three lucerne genotypes with fall dormancy (FD) ratings of 2 (Δ), 5 (○), and 10 (□), subjected to 28- (c), 42- (b) and 84 day (a) defoliation frequencies (DF) in the 2015, 2015/16, and 2016/17 regrowth seasons.

Note: Error bars represent LSD (α=0.05) for differences among genotypes within each regrowth cycle. Dotted line represents yield of 2 t DM/ha for reference. Number (0-9) indicates the regrowth cycle as described in Section 3.3.1.

5.3.1.3 Seasonal shoot growth rate

The shoot growth rates of the three FD ratings is shown in Figure 5.3 for each regrowth cycle throughout the three regrowth years.

Over the three regrowth years, DF84 crops always had higher ($P<0.001$) shoot growth rates than DF42 and DF28 crops during spring-summer. Maximum growth rate in the DF84 crops during spring-summer was 10.7 kg DM/ha/^{0}Cd compared with 7.4 kg DM/ha/^{0}Cd for DF42 and 3.9 kg DM/ha/^{0}Cd for DF28 crops (Figure 5.3 a, b, c).

Irrespective of DF regimes, throughout the two regrowth years (2015/16 and 2016/17), all genotypes showed an increase in growth rates from winter reaching maximum rates in early summer (December 2015 or November 2016). In both years, 2015 and 2015/16, the growth rates decreased during the autumn defoliation (March to May) and reached minimum rates in winter (July).

Also of note, the FD10 genotype (winter-active) defoliated with a 42-day interval during colder months grew 1.2-2.5 kg DM/ha/^{0}Cd faster ($P<0.01$) than FD5 and FD2, during both 2015 and 2015/16 (Figure 5.3 b). However, the advantage in shoot growth rate of the winter-active genotype during these colder months was not consistent for crops defoliated at 28 or 84-day intervals (Figure 5.3 a, c). Furthermore, the FD10 genotype in DF28 crops had lower shoot growth rates during spring-summer period 2016/17, and grew ～3 kg DM/ha/^{0}Cd, lower ($P<0.01$) than the FD2 and FD5 genotype (Figure 5.3 c). This may be due to the impacts of photoperiod change and biomass partitioning on shoot DM production (Teixeira *et al.*, 2008) and will be discussed in Section 5.3.1.4 and in Chapter 7.

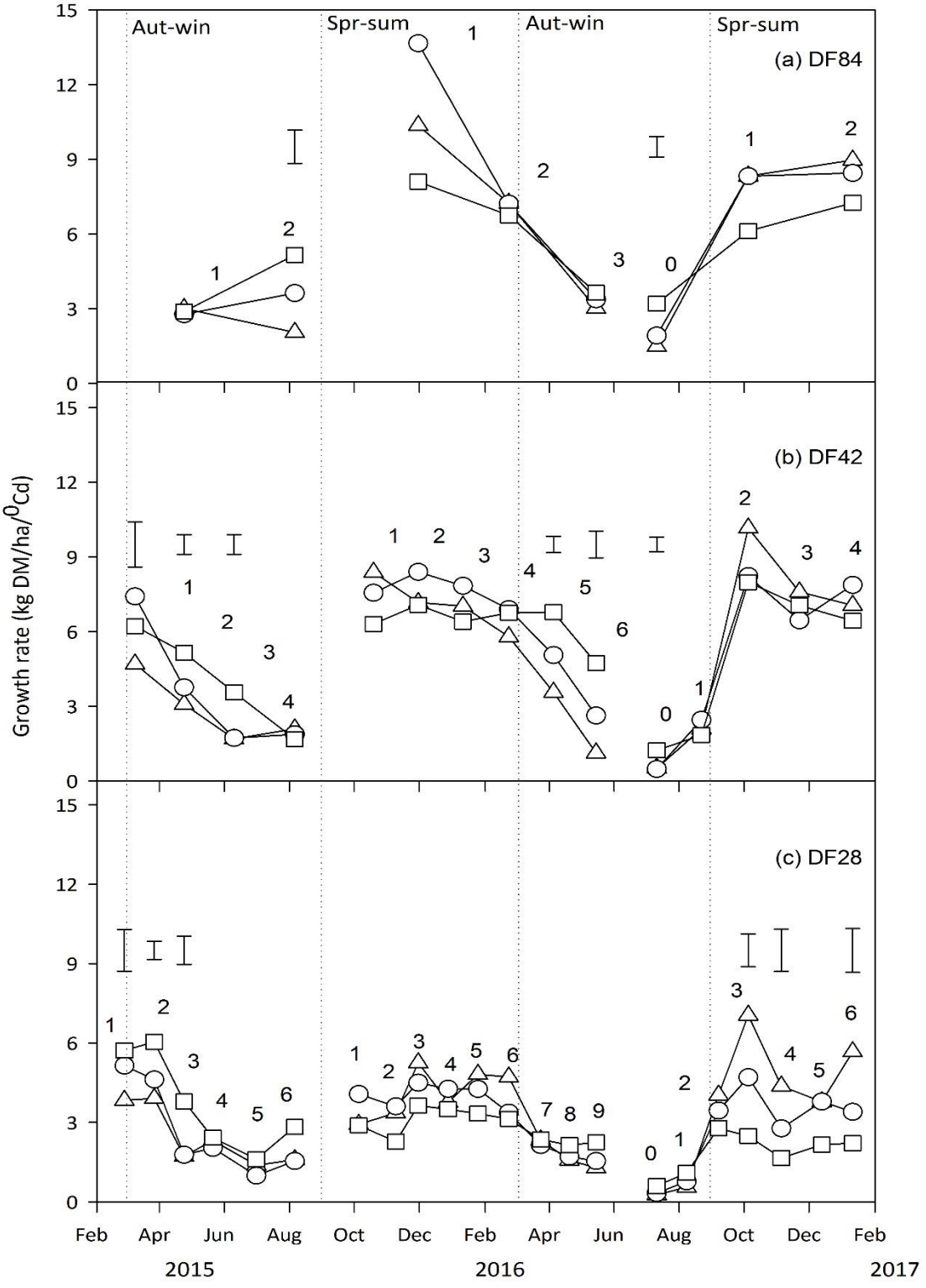


Figure 5.3 Shoot growth rates of three lucerne genotypes with fall dormancy (FD) ratings of 2 (Δ), 5 (○), and 10 (□) subjected to 28- (c), 42- (b) and 84 day (a) defoliation frequencies (DF) in the 2015, 2015/16, and 2016/17 regrowth seasons.

Note: Error bars represent LSD (α=0.05) for differences among genotypes within each regrowth cycle. Thermal time accumulated using air temperature (Tb = 1°C). Number (0-9) indicates the regrowth cycle.

5.3.1.4 Growth rate in response to photoperiod

Figure 5.4 shows the shoot growth rates for the three genotypes in response to increasing and decreasing photoperiod (Pp) at start of each regrowth period.

In the DF84 and DF42 regimes, all genotypes followed a similar pattern of response to photoperiod (Figure 5.4 a-i). For example, genotypes under DF84 (Figure 5.4 a, b, c) grown in an increasing photoperiod grown 9.5 kg DM/ha/^{0}Cd for all genotypes ($P<0.45$). In contrast, when they grew into a decreasing photoperiod, growth rate decreased ($P<0.001$) at a rate of 1.0 kg DM/ha/^{0}Cd per hour from 11.4 kg DM/ha/^{0}Cd at 16.5 h to 2.2 kg DM/ha/^{0}Cd at 10.4 h. Growth rate of genotypes in the DF42 (Figure 5.4 d, e, f) displayed a similar temporal pattern. The regressions showed growth rate decreased ($P<0.001$) at a rate of 0.86 kg DM/ha/^{0}Cd per hour from 6.5 kg DM/ha/^{0}Cd at 16.5 h to 0.7 kg DM/ha/^{0}Cd at 10.4 h. All genotypes grown in the DF28 regime produced growth rates below 6.0 kg DM/ha/^{0}Cd in increasing or decreasing photoperiods (Figure 5.4 g, h, i). DF28 crops had the flattest photoperiod response but the FD2 genotype did show an impact of photoperiod direction (Figure 5.4i). In contrast, for the FD10 genotype, growth rate averaged ~2.7 kg DM/ha/^{0}Cd, and was independent of photoperiod (Figure 4g).

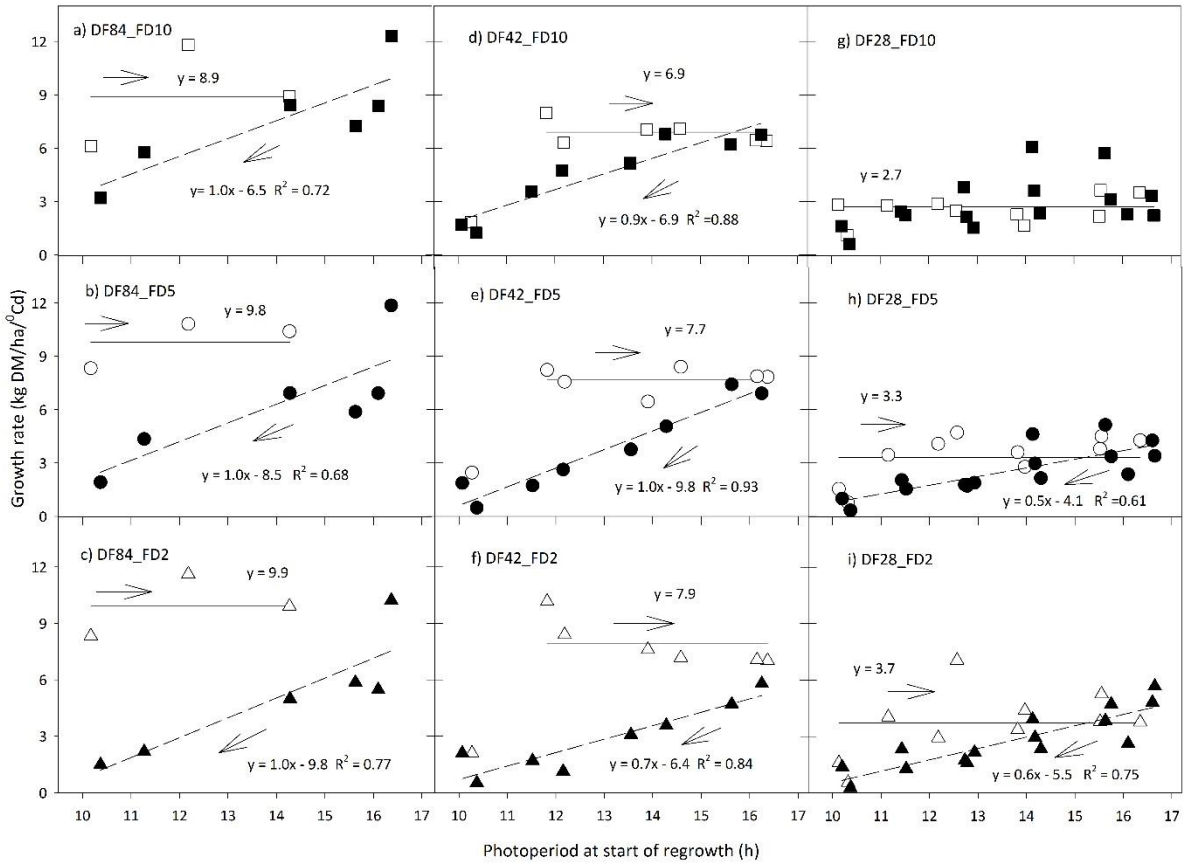


Figure 5.4 Growth rates of three lucerne genotypes with fall dormancy (FD) ratings of 2 (Δ), 5 (○), and 10 (□) subjected to 28 (g, h, i), 42 (d, e, f) and 84 day (a, b, c) defoliation frequencies (DF) in response to increasing (white symbols) or decreasing (black symbols) photoperiod (Pp) at the start of each regrowth period.

Note: Regression solid lines (—) represent for increasing Pp, dashed lines (– – –) represent for decreasing Pp. Arrow indicates Pp direction.

5.3.2 Nutritive value

5.3.2.1 Leaf/stem ratio (LSR) and un-palatable proportion

Figure 5.5 shows the LSR of each regrowth cycle over the three year growth period. LSR was negligible during the winter growth cycles for DF28 crops (Cycle 5 in year 2015 and Cycle 1 and 2 in year 2016/17) and DF42 crops (Cycle 1 in year 2016/17).

There was no systematic difference in LSR among genotypes. The LSR was different only in autumn or winter. The FD2 genotype had the highest ($P<0.05$) LSR in most regrowth cycles, compared with the FD5, and FD10 genotypes. In contrast, the spring-summer regrowth seasons had no effect on LSR among genotypes (Figure 5.5 a, b). The exception was 2015/16 year in the DF28 crops (Figure 5.5 c), when the early spring regrowth resulted in a higher LSR for the FD10 genotype (Cycle 1) and FD2 genotype (Cycle 2 and 3).

Overall, the LSR was lower in periods of higher growth (spring-summer) and in treatments (long regrowth cycle) that accumulated more shoot DM. For example, at the same time and environmental conditions, LSR in $DF84_{2015/16}$-Cycle (1+2) was 0.37, lower ($P<0.001$) than the comparable $DF42_{2015/16}$-Cycle (1+2+3+4) which averaged 0.79 for all genotypes. In contrast, LSR in $DF28_{2015/16}$-Cycle (1+2+3+4+5+6) was highest ($P<0.001$) among the DF regimes, an averaged of 1.48 for all genotypes (Figure 5.5 a, b, c).

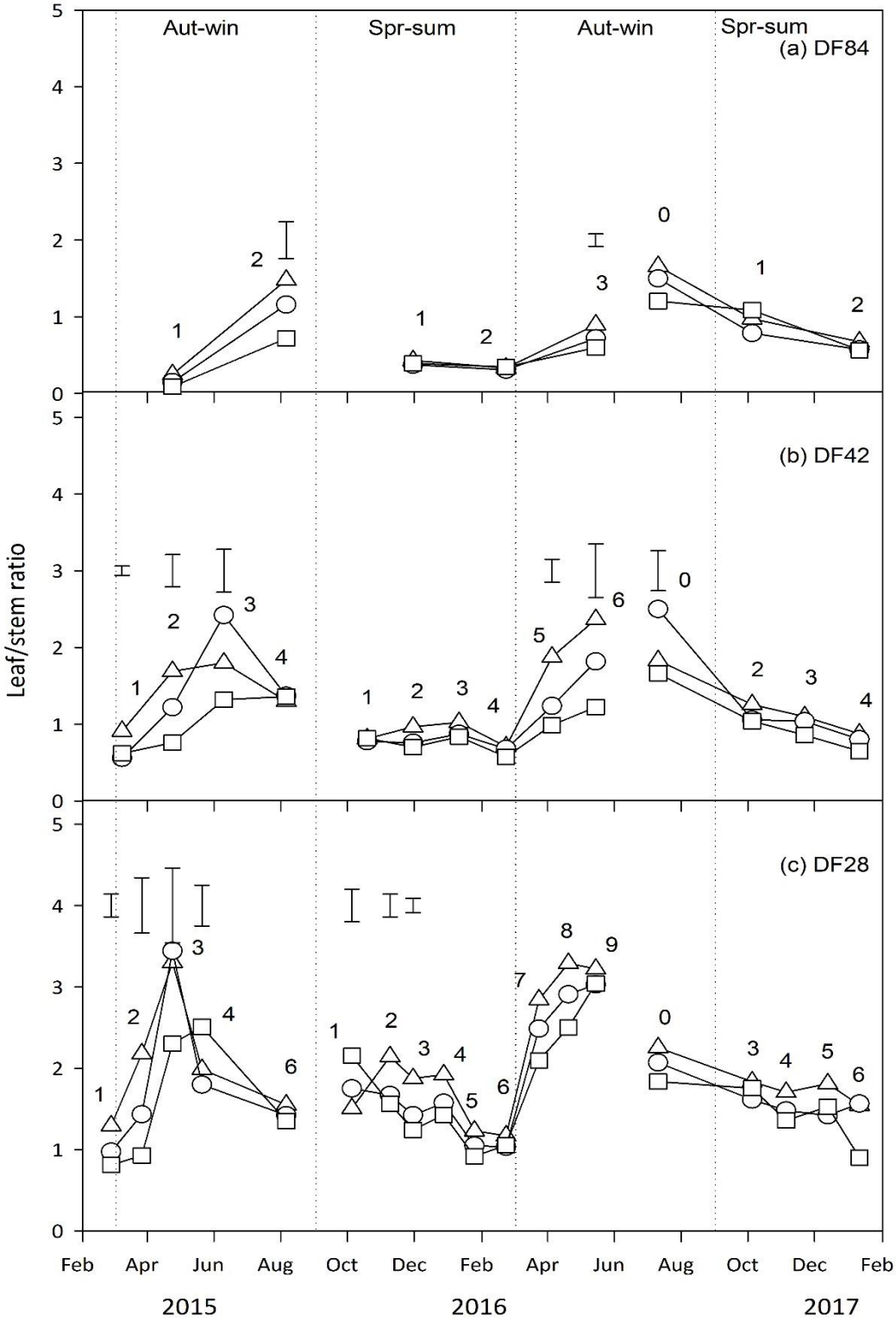


Figure 5.5 Leaf/stem ratio at the end of each regrowth cycle of three lucerne genotypes with fall dormancy (FD) ratings of 2 (Δ), 5 (○), and 10 (□) subjected to 28 (c), 42 (b) and 84 day (a) defoliation frequencies (DF) in the 2015, 2015/16, and 2016/17 growth periods.

Note: Error bars represent LSD (α=0.05) for differences among genotypes within each regrowth cycle. Number (0-9) indicates the regrowth cycle.

The change in LSR among DF regimes was attached to the un-palatable proportion. Figure 5.6 shows the change in palatable and un-palatable proportions of each genotype through each regrowth cycle over seasons. Irrespective of DF regimes, the un-palatable proportion was higher ($P<0.05$) in spring-summer than in the autumn-winter period for all genotypes. During spring-summer regrowth, all genotypes produced about 25% un-palatable proportion. In contrast, during the autumn-winter period, the FD2 genotype produced only 8% un-palatable proportion, lower ($P<0.05$) than the FD5 (16%) and FD10 (22%) genotypes. In all regrowth cycles, the un-palatable proportion of DF84 crops was higher ($P<0.05$) than for DF42 and DF28 crops (Figure 5.6 a, b, c, d, e, f, g, h, i). Averaged over all seasons and regrowth cycles, the 36% un-palatable proportion of DF84 crops was higher ($P<0.05$) than DF42 (21%) and DF28 crops (13%). Conversely, the utilisable proportion was 64% for DF84 crops followed by 79% for DF42 crops and 87% for DF28 crops.

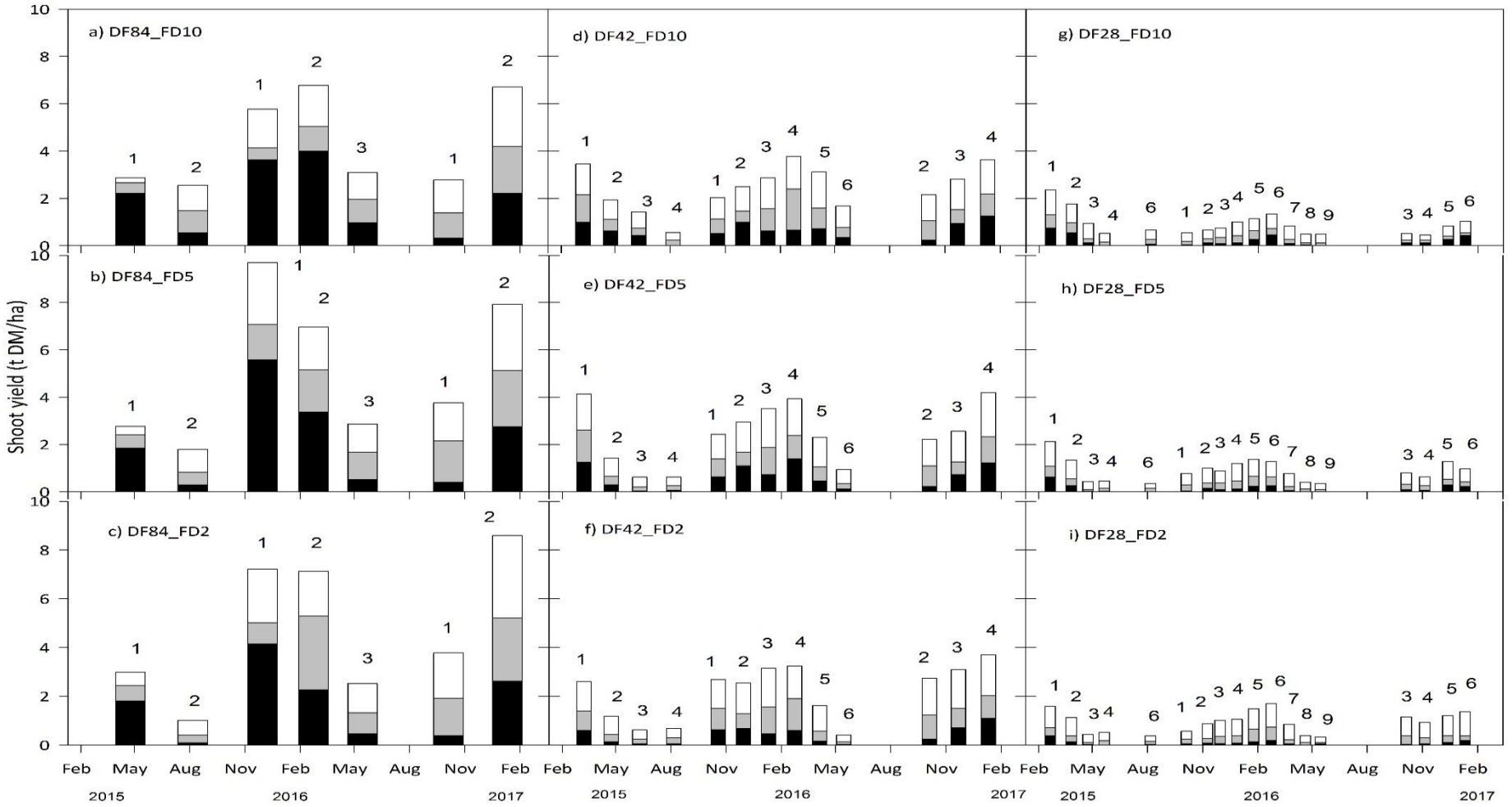


Figure 5.6 Dry matter (DM) yield of hard stem (black bars), soft stem (gray bars) and leaves (white bars) within regrowth cycles of three lucerne genotypes with fall dormancy (FD) ratings of FD2, FD5, and FD10 subjected to 28- (g, h, i), 42- (d, e, f) and 84 day (a, b, c) defoliation frequencies (DF) in the 2015, 2015/16, and 2016/17 regrowth seasons.

Note: Refers Figure 5.2 for statistical analysis for total DM yield for each regrowth cycle.

The relationship between yield and LSR or un-palatable proportion of all treatments over the three year regrowth periods is shown in Figure 5.7. Shoot DM yield explained 88% of variation in the un-palatable proportion, regardless of treatments or seasons. For all regrowth cycle, each unit increase in shoot DM yield resulted in an increase of approximately 20% of the un-palatable proportion. Similarly, shoot DM explained approximately 73% of the change in LSR. The LSR decreased ($P<0.01$) exponentially from an estimate of 2.6 when shoot DM of each regrowth cycle was <0.5 t DM/ha to a minimum of 0.6 when shoot DM was greater than 8 t DM/ha.

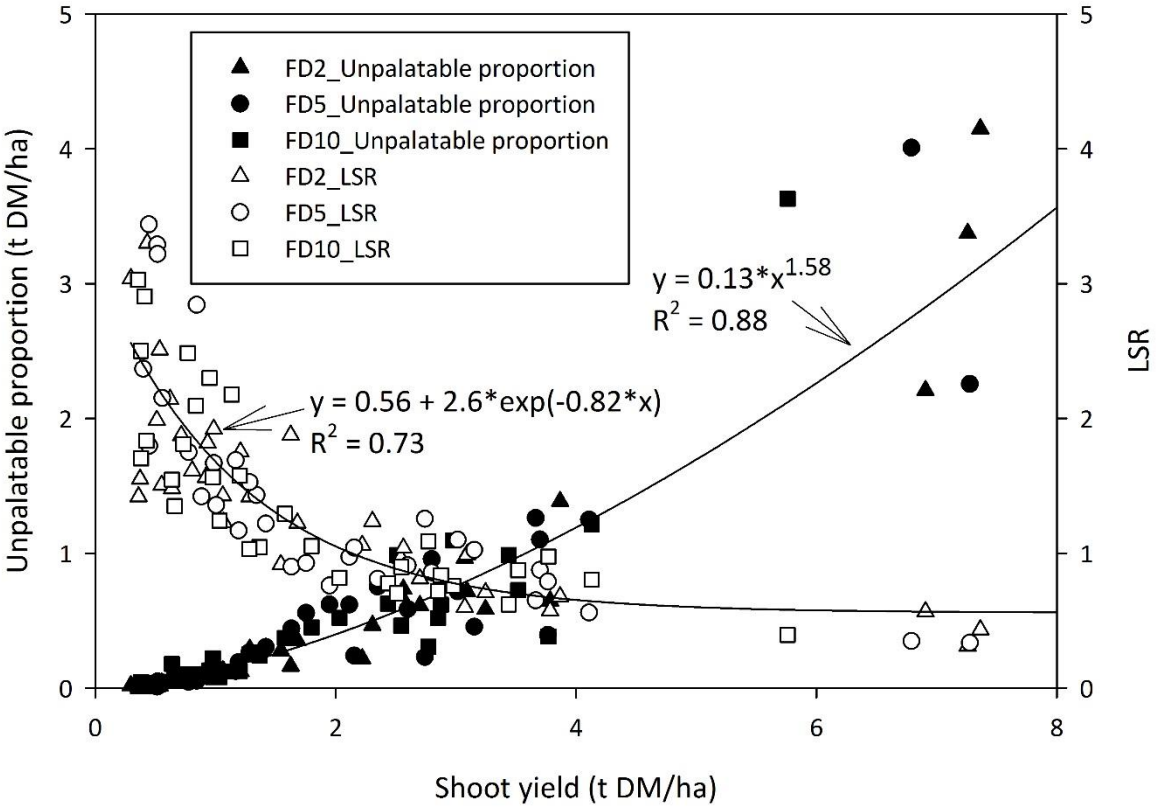


Figure 5.7 Relationship between un-palatable proportion and leaf/stem ratio with shoot DM yield of three lucerne genotypes subjected to three contrasting defoliation regimes in the 2015, 2015/16, and 2016/17 growth periods.

5.3.2.2 Total crude protein (CP) and metabolisable energy (ME) production

Figure 5.8 shows the total herbage CP yields of all treatment and season combinations. There was no difference (P<0.65) among all the genotypes for DF84 and DF42 crops (Figure 5.8 a, b). In contrast, herbage CP production differed (P<0.05) among genotypes for DF28 crops. In year 2015, the FD10 genotype produced 22% more (P<0.01) CP than FD5 and FD2 genotypes. In the following 2015/16 and 2016/17 regrowth years, the FD10 genotype had the smallest (P<0.05) CP yields (Figure 5.8 c).

Total CP production was influenced (P<0.05) by genotype and DF regime, separately. Over the three years, FD2 and FD5 genotypes produced total yields of 0.5 t CP/ha higher (P<0.02) than the FD10 genotype. This indicates the winter-active genotype had reduced shoot protein after three regrowth periods. For DF regimes, CP production was greatest (P<0.02) for DF84 and DF42 crops. They were ~2.0 t CP/ha greater than DF28 crops.

Table 5.2 Effect of defoliation frequency (DF) on total herbage crude protein (CP) of lucerne genotypes with different fall dormancy (FD) ratings over a three regrowth period

	Total crude protein (t CP/ha)			
	2015	2015/16	2016/17	Overall regrowth period
FD2	0.9_{a}	2.6_{ab}	1.9_{c}	5.5_{b}
FD5	1.1_{b}	2.8_{b}	1.6_{b}	5.5_{b}
FD10	1.3_{c}	2.4_{a}	1.4_{a}	5.0_{a}
P <	0.001	0.02	0.001	0.02
SEM	0.05	0.13	0.1	0.18
DF28	1.3_{b}	2.0_{a}	0.9_{a}	4.1_{a}
DF42	1.3_{b}	3.0_{b}	1.8_{b}	6.1_{b}
DF84	0.7_{a}	2.8_{b}	2.2_{b}	5.8_{b}
P <	0.01	0.04	0.001	0.02
SEM	0.13	0.35	0.17	0.18
FD x DF				
P <	0.25	0.14	0.48	0.10
SEM	0.15	0.4	0.23	0.63

Note: Means in a column followed by the same letter are not different at α=0.05.

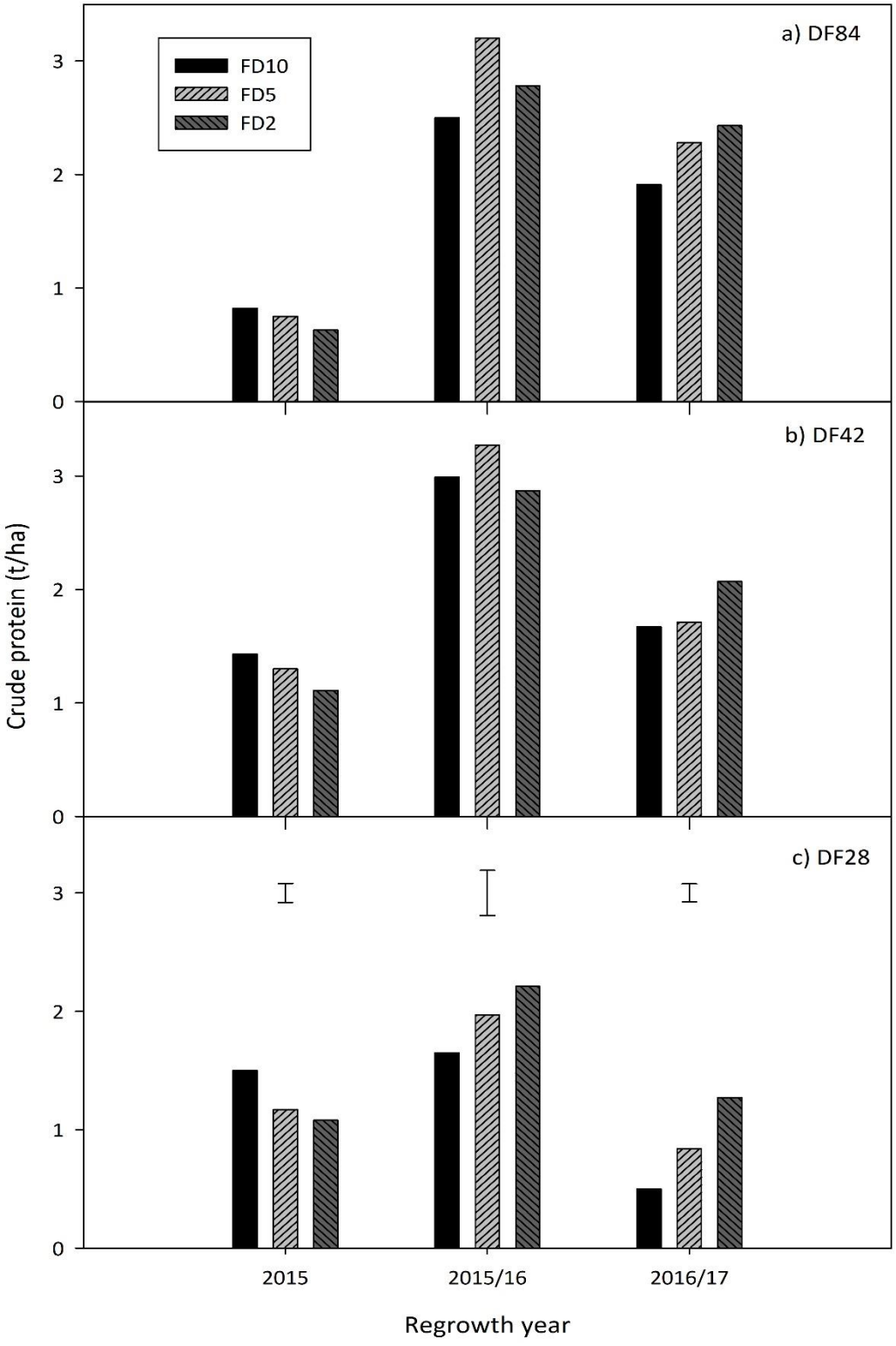


Figure 5.8 Total crude protein yields (CP) of three lucerne genotypes with different fall dormancy ratings subjected to 28- (c), 42- (b) and 84 day (a) defoliation frequencies (DF) in the 2015; 2015/16 and 2016/17 regrowth years.

Note: Error bars represent LSD (α=0.05) for differences among genotypes.

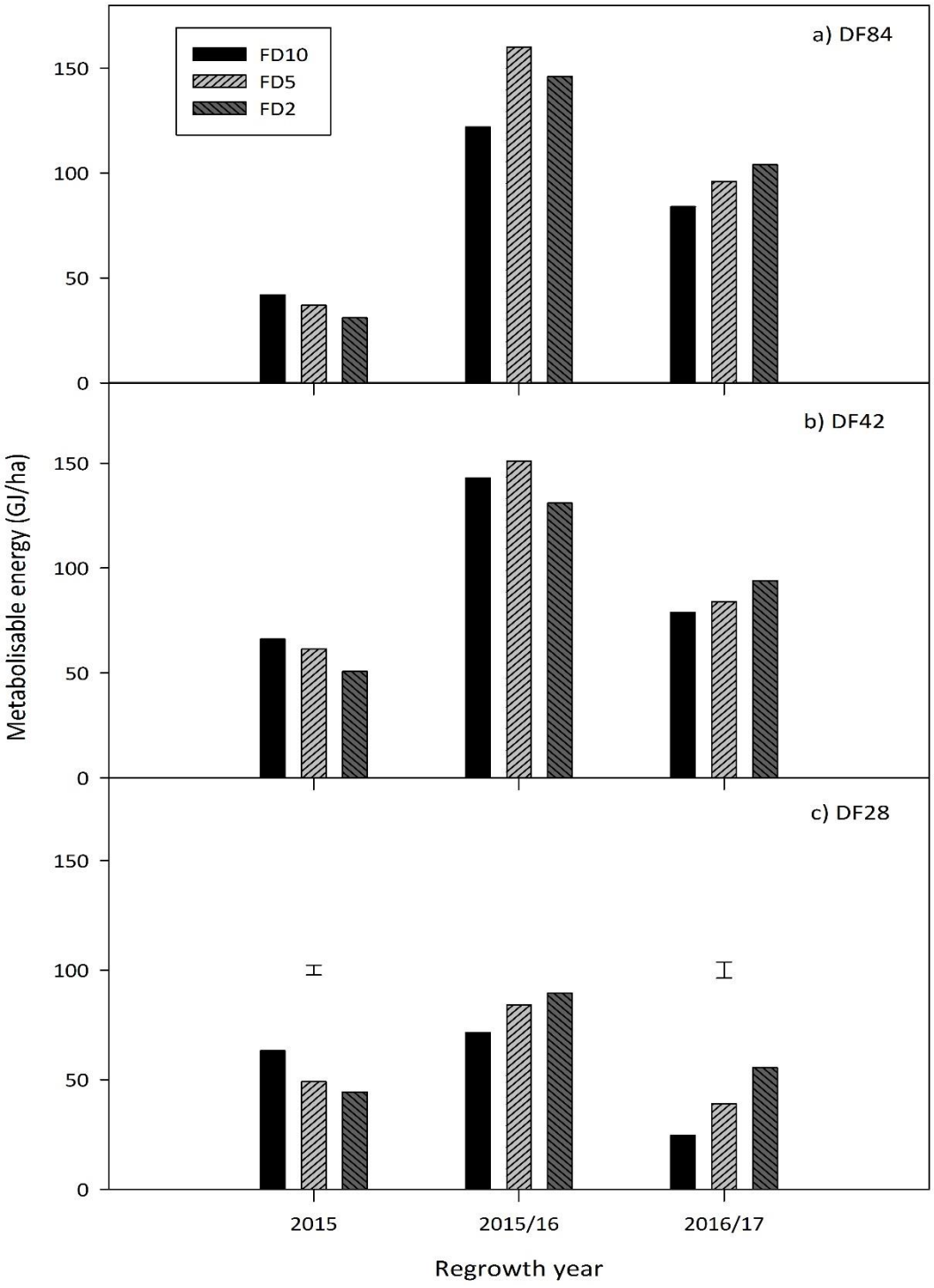


Figure 5.9 Total metabolisable energy (ME) yields of three lucerne genotypes with different fall dormancy (FD) ratings subjected to 28- (c), 42- (b) and 84 day (a) defoliation frequencies (DF) in the 2015; 2015/16 and 2016/17 regrowth years.

Note: Error bars represent LSD (α=0.05) for differences among genotypes.

Total metabolisable energy yield (Figure 5.9) followed a similar pattern to CP where ME did not differ (P<0.60) among genotypes for DF84 and DF42 crops (Figure 5.9 a, b). For DF28 crops, the FD10 genotype had the highest ME yield (P<0.001) at the beginning of the experiment (2015) but was lower (P<0.001) than the FD2 and FD5 genotypes by the end of the experiment (2016/17). In 2015 and over the three years, DF regimes had a stronger influence (P<0.001) on total ME than genotype (Table 5.3). Over all regrowth periods, DF28 crops had a smaller (P<0.001) ME than DF84 and DF42 crops.

Table 5.3 Effect of defoliation frequency (DF) on total herbage metabolisable energy (ME) of lucerne genotypes with different fall dormancy (FD) ratings over a three regrowth period

	Total metabolisable energy (GJ ME/ha)			
	2015	2015/16	2016/17	Overall regrowth period
FD2	42_a	122	84_b	249
FD5	49_b	132	73_c	254
FD10	57_c	112	63_a	232
P <	0.001	0.06	0.001	0.09
SEM	2.28	7.7	4.63	9.87
DF28	52_b	82_a	40_a	174_a
DF42	59_b	142_b	86_b	274_b
DF84	37_a	143_b	95_b	287_b
P <	0.01	0.001	0.001	0.001
SEM	3.87	7.28	6.26	10.8
FD x DF				
P <	0.33	0.25	0.67	0.20
SEM	5.03	13.1	9.06	17.64

Note: Means in a column followed by similar letters are not different at α=0.05.

5.3.2.3 Seasonal CP and ME

Figure 5.10 shows the seasonal CP yield for each shoot fraction of each genotype within each regrowth cycle throughout the three regrowth years. Irrespective of DF regimes, ～80% CP was produced in the spring-summer period. During this period, each genotype from each 42- and 84 day regrowth cycle produced CP in excess 0.5 t CP/ha (Figure 5.10 a, b, c, d, e, f). In contrast, each genotype from the 28 day regrowth cycles rarely exceeded 0.5 t CP/ha (Figure 5.10 g, h, i). In addition, the FD10 produced higher (P<0.001) CP yield during the autumn-winter period, but lower (P<0.05) CP yield than the FD2 and FD5 genotypes during the spring-summer period, regardless of DF regimes. This explains the FD10 having higher total CP production in the first year regrowth (2015; autumn-winter period) but lower total CP in the following regrowth years in 2015/16 and 2016/17 regrowth years (Table 5.2).

Also of note, the un-palatable fraction had lower (P<0.001) CP yield compared with the palatable proportion in each regrowth cycle throughout the seasons (Figure 5.10 a, b, c, d, e, f, g, h, i). The un-palatable proportion contributed 17% of total CP for each 84 day regrowth cycle compared with 9% and 6 % for each 42 and 28 day regrowth cycle.

The seasonal ME yield followed the same pattern as CP (Figure 5.11). The FD10 genotype had an advantage (P<0.001) in autumn-winter with an ME of 26 and 14% higher than FD2 and FD5 genotype, respectively. ME yield increased in the spring-summer period for all genotypes. During this period, each genotype produced ME in excess 20 GJ ME/ha for the 84 and 42 day regrowth cycles (Figure 5.11 a, b, c, d, e, f). In comparison, all genotypes from the 28 day regrowth cycle produced <20 GJ ME/ha (Figure 5.11 g, h, i). Similarly to CP, the un-palatable fraction had lower (P<0.001) ME than the palatable proportion in each regrowth cycle throughout seasons.

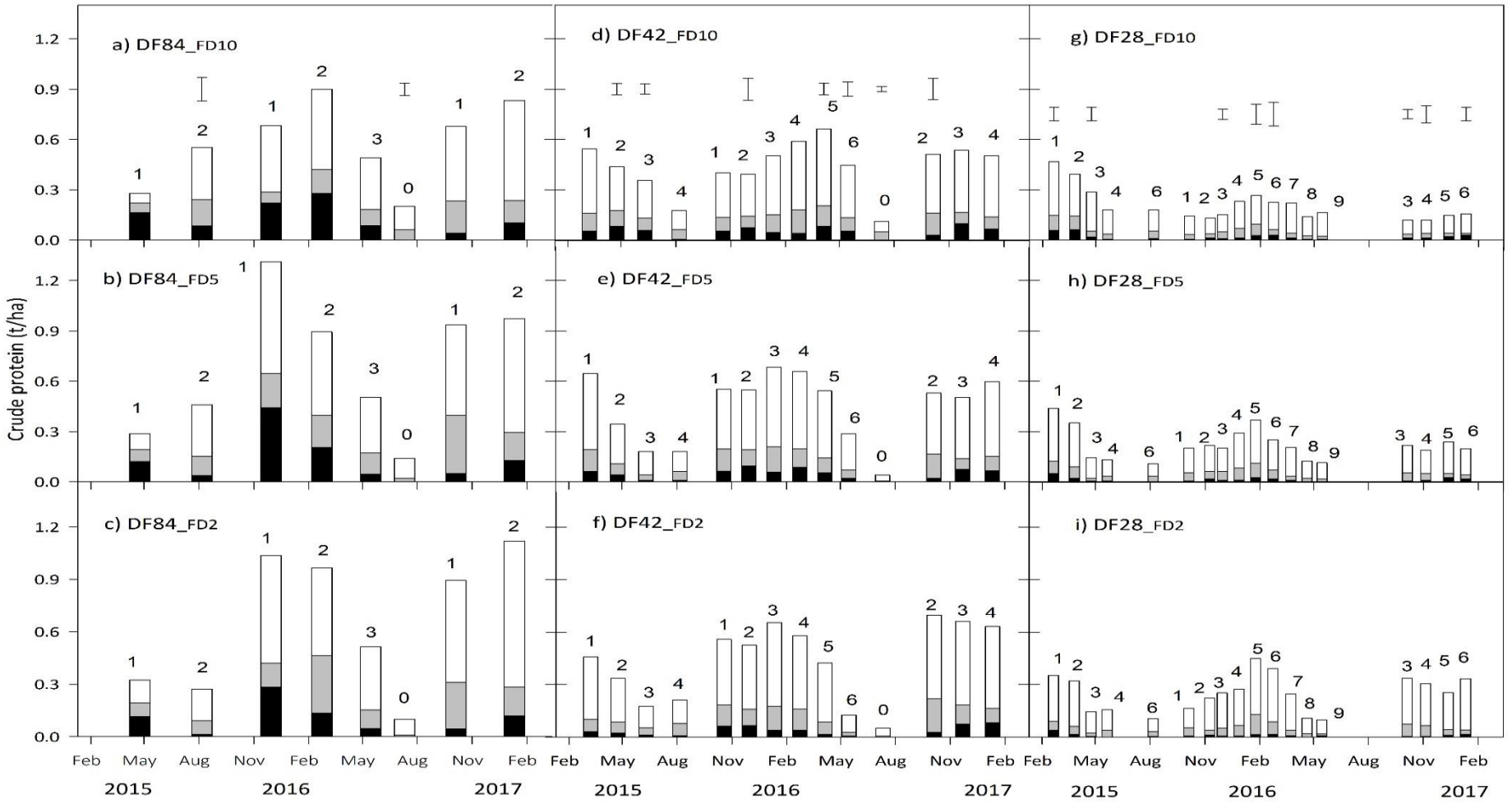


Figure 5.10 Crude protein (CP) of hard stem (black bars), soft stem (gray bars) and leaves (white bars) within regrowth cycles of three lucerne genotypes with fall dormancy (FD) ratings of FD10, FD5, and FD2 subjected to 28- (g, h, i), 42- (d, e, f) and 84 day (a, b, c) defoliation frequencies (DF) in the 2015, 2015/16, and 2016/17 regrowth seasons.

Note: Error bars represent LSD (α=0.05) for differences among genotypes. Number (0-9) indicates the regrowth cycles.

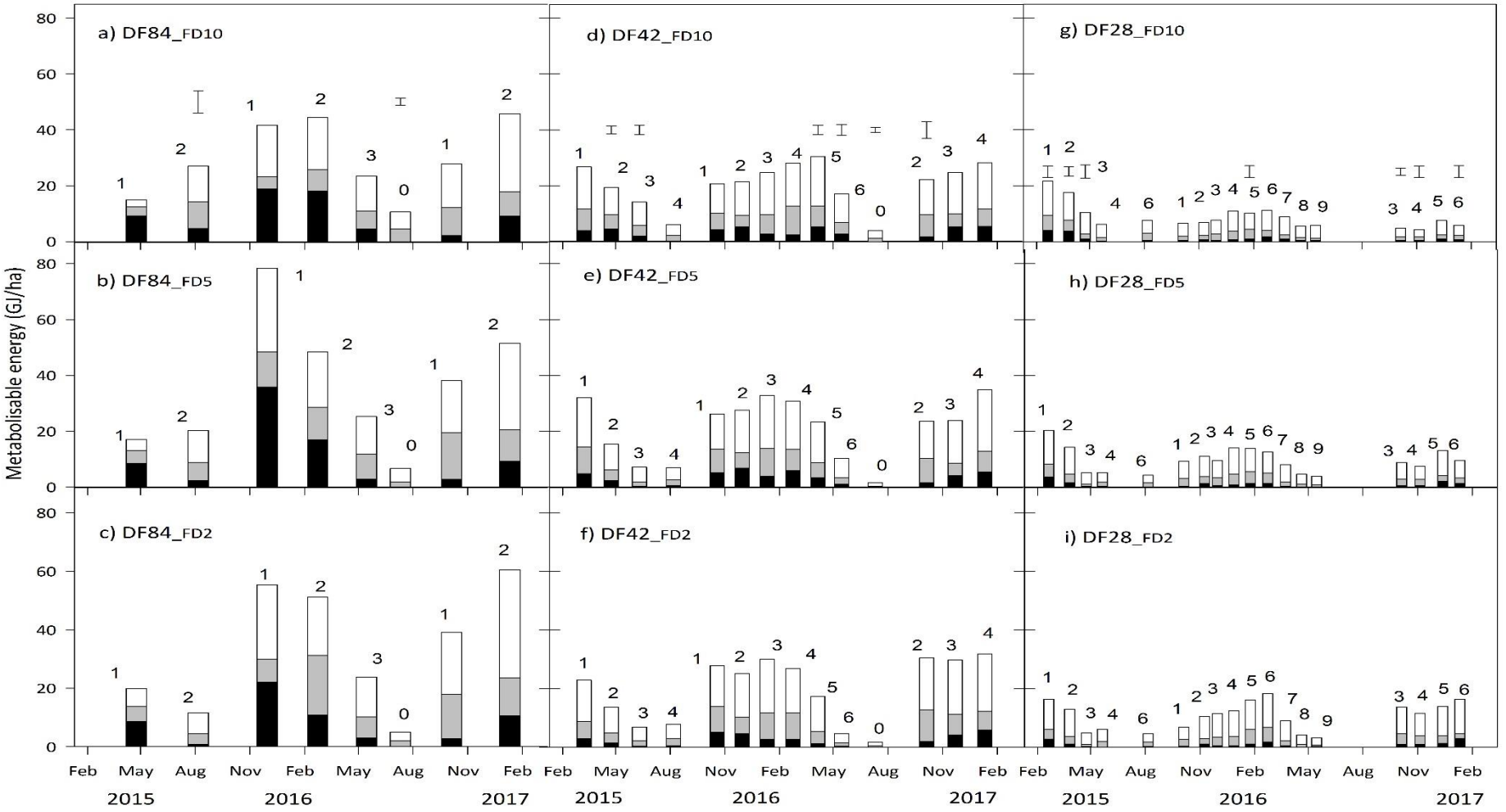


Figure 5.11 Metabolisable energy (ME) of hard stem (black bars), soft stem (gray bars) and leaves (white bars) within regrowth cycles of three lucerne genotypes with fall dormancy (FD) ratings of FD10, FD5, and FD2 subjected to 28- (g, h, i), 42- (d, e, f) and 84 day (a, b, c) defoliation frequencies (DF) in the 2015, 2015/16, and 2016/17 regrowth seasons.

Note: Error bars represent LSD (α=0.05) for differences among genotypes. Number (0-9) indicates the regrowth cycles.

5.3.2.4 Yield production and forage quality correlation

The relationships between CP or ME yield and dry matter production of the whole shoots or shoot components of all treatments over the three year regrowth periods are shown in Figures 5.12 and 5.13. The CP yield in whole shoots remained constant at 0.27 t CP for each one t DM shoot accumulation (Figure 5.12 a). Leaf CP accumulation was constant at 0.30 t CP/ t DM followed by soft stem at 0.12 t CP and hard stem at 0.07 t CP/ t DM (Figure 5.12 b, c, d). The ME accumulation in whole shoots (10.8 GJ/ha), leaf (11.7 GJ/ha), soft stem (8.5 GJ/ha) and hard stem (5.3 GJ/ha) also remained constant (Figure 5.13 a, b, c, d).

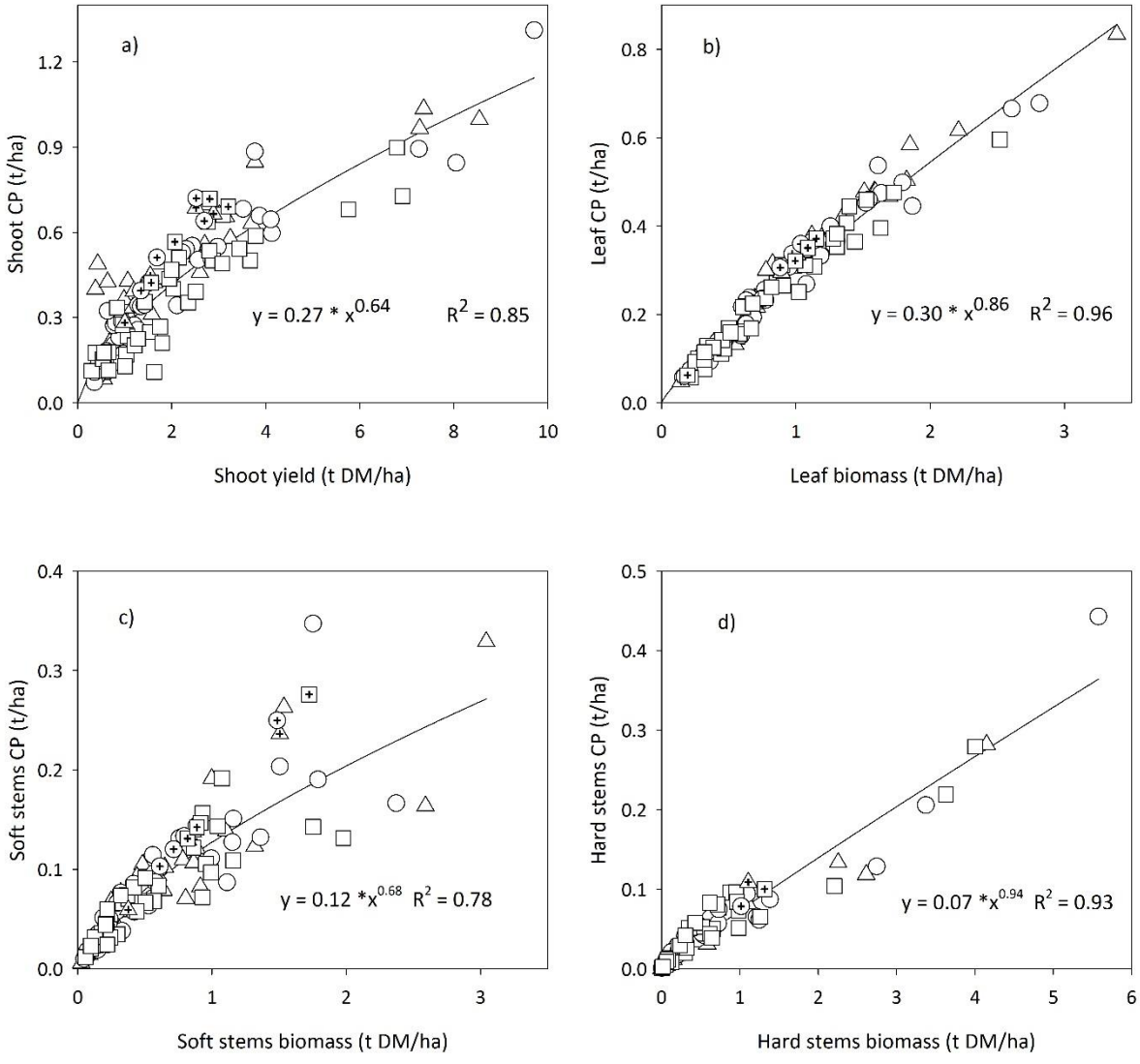


Figure 5.12 Relationship between crude protein (CP) accumulation and biomass accumulation for whole shoot (a), leaf fraction (b), soft stem fraction (c) and hard stem fraction (d) of three lucerne genotypes with fall dormancy (FD) ratings of 2 (Δ), 5 (0) and 10 (□) during seedling establishment and different regrowth cycles over a three growth period in the 2014/15, 2015/16, and 2016/17.

Note: Dotted white symbols represent for seedling lucerne. White symbols represent for regrowth lucerne.

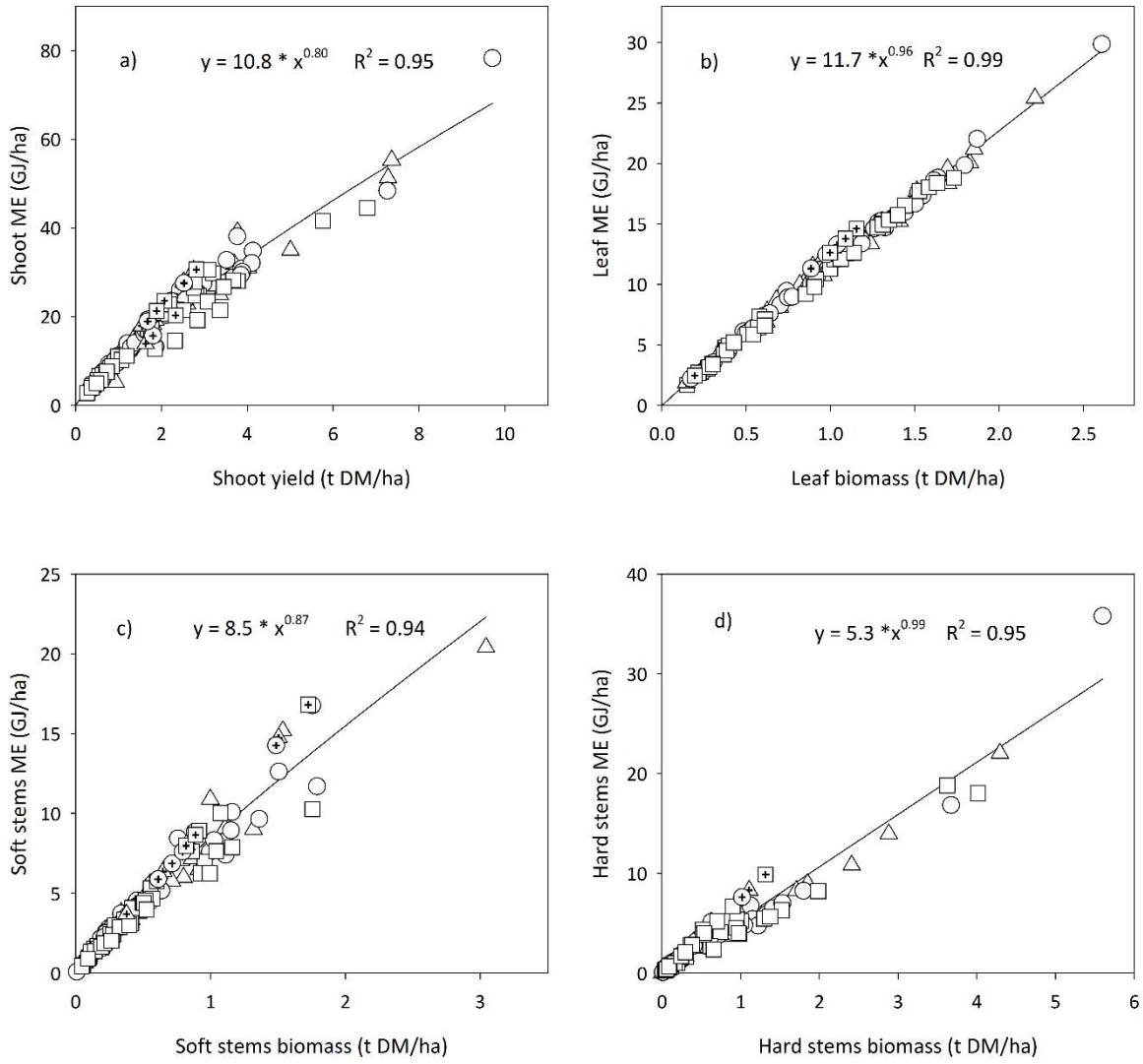


Figure 5.13 Relationship between crude protein (ME) accumulation and biomass accumulation for whole shoot (a), leaf fraction (b), soft stem fraction (c) and hard stem fraction (d) of three lucerne genotypes with fall dormancy (FD) ratings of 2 (Δ), 5 (0) and 10 (□) during seedling establishment and different regrowth cycles over a three growth period in the 2014/15, 2015/16, and 2016/17.

Note: Dotted white symbols represent for seedling lucerne. White symbols represent for regrowth lucerne.

5.3.2.5 Seasonal herbage nutritive characteristics

Figure 5.14 shows CP content and Figure 5.15 shows ME content for each shoot fraction of each genotype within each regrowth cycle throughout the regrowth years.

There was no systematic change in CP and ME concentration among genotypes ($P<0.79$) or between cutting intervals ($P<0.45$). However, CP and ME changed ($P<0.05$) within seasons for all genotypes. For example in DF42_2015/16, crop grown into spring (Cycle 1) had CP and ME concentrations of ～33% and 11.7 MJ/kg DM in the leaf fraction but this decreased to ～30%, and 11.3 MJ/kg DM during the summer period (Cycles 2, 3, 4). Then they increased in autumn (Cycles 5, 6), to similar levels in spring (Figure 5.14, b and 5.15, b). This pattern of change in CP and ME was similar for DF28 and DF82 crops (Figure 5.12 a, c and 5.13 a, c). Overall, the leaf fraction had higher ($P<0.001$) CP and ME contents (c. 31%, 11.7 MJ/kg DM) than soft stem (c. 17%, 9 MJ/kg DM) and hard stem (c. 9%, 6 MJ/kg DM).

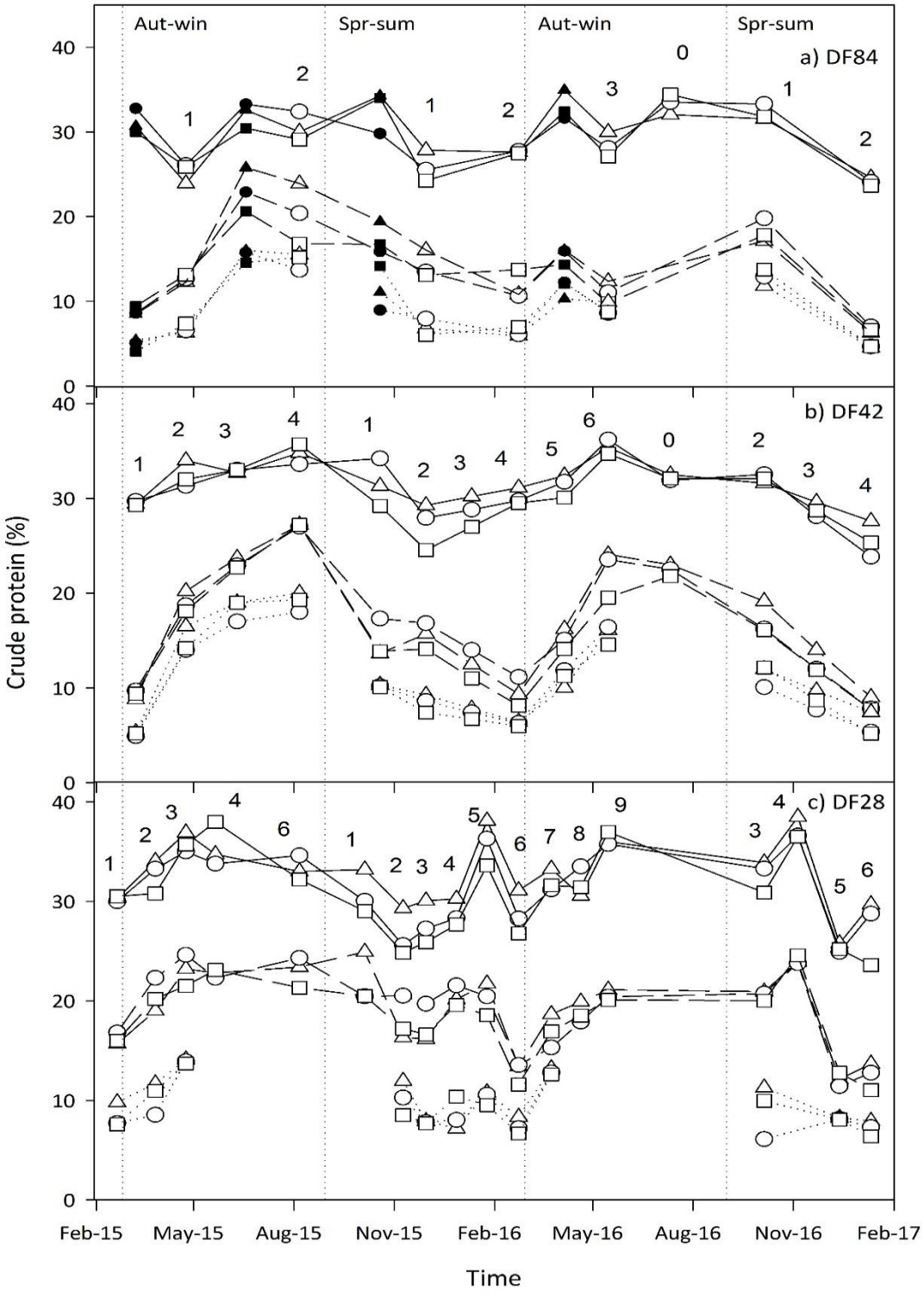


Figure 5.14 Crude protein concentration (CP) of three lucerne genotypes with fall dormancy (FD) ratings of 2 (Δ), 5 (O) and 10 (□) subjected to 28- (c), 42- (b) and 84 day (a) defoliation frequencies (DF) in the 2015; 2015/16 and 2016/17 regrowth years.

Note: Black symbols represent the intermediate points of each 84 day regrowth cycle. Number (0-9) indicates the regrowth cycles. Lines represent for leaf (solid line), soft stem (dash line) and hard stem (dotted line).

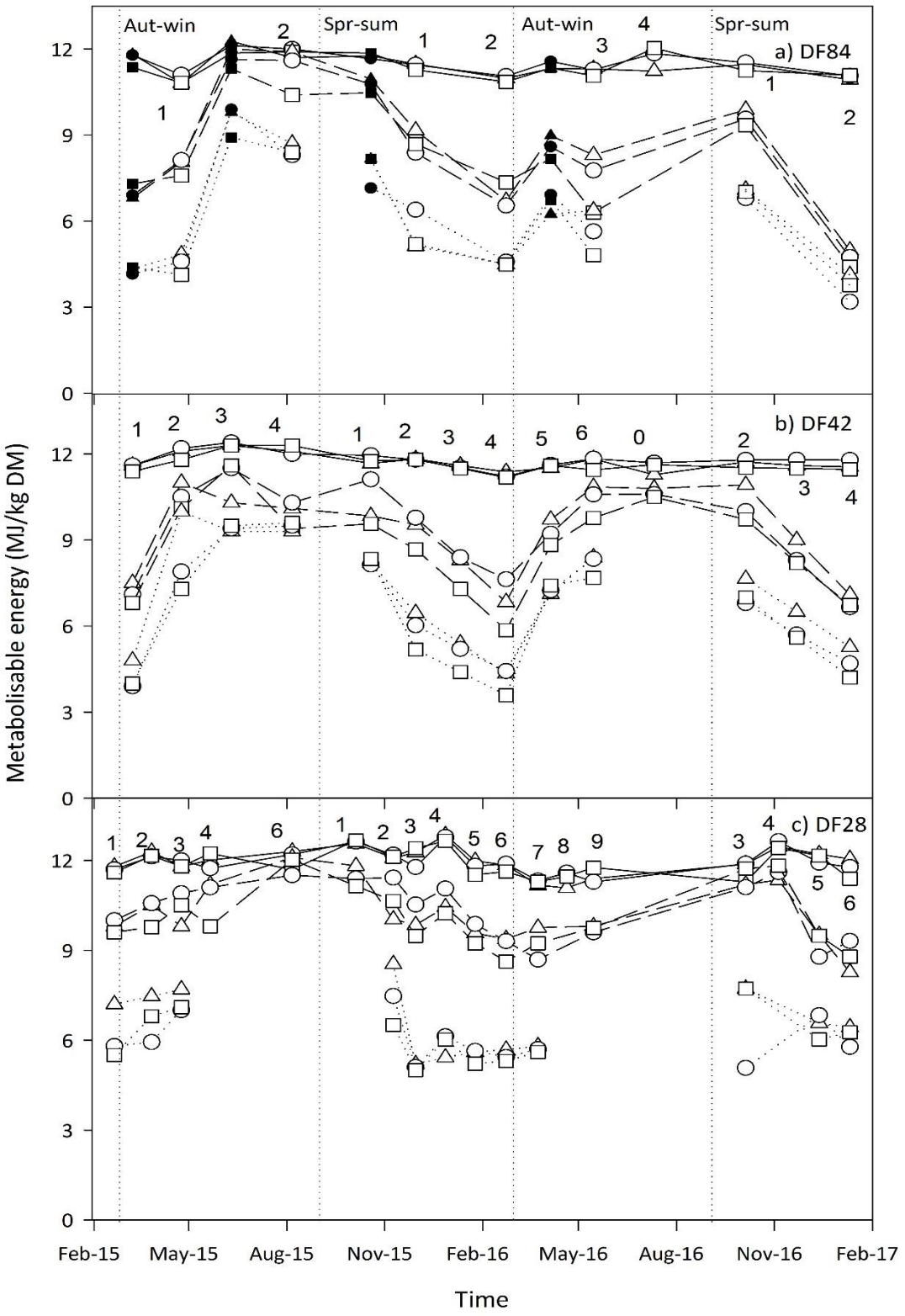


Figure 5.15 Metabolisable energy concentration (ME) of three lucerne genotypes with fall dormancy (FD) ratings of 2 (Δ), 5 (O), and 10 (□) subjected to 28- (c), 42- (b) and 84 day (a) defoliation frequencies (DF) in the 2015; 2015/16 and 2016/17 regrowth years.

Note: Black symbols represent the intermediate points of each 84 day regrowth cycle. Number (0-9) indicates the regrowth cycles. Lines represent for leaf (solid line), soft stem (dash line) and hard stem (dotted line).

5.4 Discussion

Shoot DM differed among FD ratings. The winter-active genotype (FD10) produced more yield and herbage quality in the first year but this advantage did not persist and actually decreased by year 3 with increased defoliation frequency. The use of the three DF regimes was effective in creating lucerne crops of different growth potential among the FD ratings. However, there was no evidence that different FD ratings required different defoliation managements. In addition, quality was unaffected by FD ratings and explained allometrically by the leaf and stem ratio, associated with shoot DM.

5.4.1 Shoot dry matter yield

The total shoot yield in the full regrowth season 2015/16 of the highest yielding DF regimes (DF84 and DF42) of 17.5 – 15.2 t DM/ha was consistent with the national average yield for lucerne of 14 t DM/ha (Douglas, 1986). Varella (2002) reported an annual shoot yield of 17.5 t DM/ha was achieved for lucerne "Kaituna" when working with this crop at Iversen field. However, these yields were considerably lower than previously reported on the location adjacent to Iversen 12 by Brown (2004) and Teixeira (2006) who measured yields exceeding 20 t DM/ha. This suggests the yield in the present study may have been restricted to some extent by soil moisture. A deficit occurred during the exceptional dry period from February to May in 2016. During this time, the soil moisture deficit measured at the experiment site was below the 250 mm target, despite a total amount of 252 mm of water applied (Section 3.3.5). Despite the maximum yield being lower than potential, there were differences in yield potential created by the different DF regimes (Table 5.2). Thus, the main objective of this experiment to create crops of different yield potential among FD ratings was achieved (Section 5.1).

Shoot DM production of the FD10 genotype showed the most change over time and in response to DF (Figure 5.1). In 2015 its total shoot yield was 31% and 16% higher than the FD2 and FD5 genotypes, regardless of DF regimes (Table 5.1). This higher shoot DM production occurred in the autumn-winter regrowth cycles (Figure 5.2). This result is consistent with the range observed on FD ratings in temperate regions of New Zealand by Harvey *et al.* (2014). The advantage in herbage yield during these months only contributed around 8% of the total annual shoot DM yield. Therefore in 2015/16, when the genotypes were grown over a full annual cycle, accumulated shoot DM over seasons showed no difference among genotypes (Figure 5.1, Table 5.1). In the following 2016/17 year, the FD10 genotype started to show a fall in its productivity by the time the experiment ended on 11 January 2017, particularly in the 28 day cutting interval (Table 5.1, Figure 5.1 c). Collectively, the results show a priority of this genotype was shoot production vigorously after sowing (Chapter 4) but this initial advantage was reduced after the full 27 month period of growth. This finding for the FD10 agrees with similar studies on lucerne in temperate (Lodge, 1986) and subtropical regions of Australia (Gramshaw

et al., 1993), and in South America (Ventroni *et al.*, 2010). These authors reported that the yield advantage for the winter active cultivars only appear in the first year.

The greater autumn yield of the FD10 genotype came from faster shoot growth rates than the FD2 and FD5 genotypes from March to the middle of July (Figure 5.3). During this time, temperature and radiation levels are comparatively low (Section 3.2.2). The yield impacts suggesting by the change in shoot growth rates among genotypes of different FD ratings, initiate different strategies in response to the available environment resources. Specifically, the FD10 genotype expanded a larger leaf canopy at establishment (Chapter 4) and during autumn which meant it intercepted more radiation to accumulate total DM. These potential mechanisms will be quantified for the crops in Chapter 6..

There was no interaction between the effect of FD and DF on total herbage yield in 2015 or over the three year study period (Table 5.1). This result is similar to the range observed by Gramshaw *et al.* (1993) on dormancy classes over two years in Queensland, Australia, and recently by Ventroni *et al.* (2010) in South America. The greatest total shoot DM yield was from DF84 crops followed by DF42 crops and lowest from DF28 crops (Table 5.1). Specifically, the crops defoliated at 28 day intervals over the growing season had a 44-49% lower yield than DF42 and DF84 crops. The lower production of DF28 crops was mainly because their shorter regrowth cycle meant they were unable to grow at high linear growth rates for long periods, particularly during spring-summer when shoot growth rates were the highest (Figure 5.3).

For all DF treatments, shoot growth rate increased from winter (July) and reached a maximum in early summer (November-December) and then decreased during the autumn defoliation (March to May) (Figure 5.3). This pattern is consistent with that reported by Teixeira *et al.* (2007a) who observed a seasonal change in shoot growth rates of a 28- and 42 day lucerne "Kaituna" when working at the same location. The seasonal change in shoot growth rate was related to photoperiod direction. When crops were growing into an increasing Pp, growth rate was consistent at around 9.5 and 7.5 kg DM/ha/°Cd for DF84 and DF42 crops, respectively. The 9.5 kg DM/ha/°Cd may represent a physiological maximum for lucerne in this environment in spring. In contrast, crops growing into a decreasing Pp, showed shoot growth rate decreased at a rate of 1.0 (DF84) and 0.86 kg DM/ha/°Cd (DF42) for each hour decrease (Figure 5.4 a - f). It seems likely that the potential shoot growth rate of these crops was also 9.5 kg DM/ha/^{0}Cd but the DF regime had reduced the level of root reserves and altered the expression of growth (Khaiti and Lemaire, 1992; Teixeira *et al.*, 2008). For example, in the same increasing Pp environment the potential shoot growth rates were 7.5 and 3.5 kg DM/ha/^{0}Cd for DF42 and DF28 crops, respectively. Low levels of root reserves are associated with low C and N needed to support shoot regrowth (Avice *et al.*, 1997b). These results suggest that the assimilate supply affected these shoot growth rates. The crops defoliated at 42- and 84 day intervals had sufficient time for canopy

development and responded to the Pp change with different seasonal patterns of growth. However, crops defoliated at 28 day intervals had the flattest photoperiod response (Figure 5.4 g, h, i). In particular, the growth rate of the FD10 genotype did not show a Pp response and was always ~ 2.7 kg DM/ha/^{0}Cd, regardless of photoperiod direction (Figure 5.4 g). This suggests the FD10 genotype had diminished its root reserves faster than other genotypes. Post-defoliation, a lack of underground reserves can reduce photosynthetic capacity and canopy expansion rates of the earliest initiated leaves (Teixeira *et al.*, 2008). Ultimately, this may affect production and persistence of the winter active genotype as shown in Figures 5.1c, 5.2c and 5.3c. Further measurements of underground biomass are required to examine the physiological mechanism of these responses to understand the impact of FD rating on lucerne growth. This physiological mechanism of these lucerne crop responses will be examined in detail in Chapters 6 and 7.

5.4.2 Herbage nutrition

A simple interpretation of the yield results would suggest the longest DF regime should be used to maximise yield. However, the comparison of nutritive characteristics was undertaken to quantify the total CP and ME available for animal consumption. This involved separation of palatable and unpalatable herbage fractions. This showed the ratio of the leaf to stem (LSR) was related to accumulated shoot DM by an allometric relationship. As shoot DM yield increased the LSR decreased in a similar pattern for all treatments across all seasons (Figure 5.7) which was consistent with Lemaire *et al.* (1992). The decrease in LSR was largely accounted for by an increase in the proportion of hard stem that takes place during the growth of crops (Figure 5.7). For practical purposes, grazing at ~3 t DM/ha would optimise the amount of palatable shoot yield and its quality. This is independent of time and suggests an allometrically defined grazing regime for maximise animal production.

With regards to FD ratings, the FD10 genotype had a lower LSR in most autumn-winter regrowth cycles (Figure 5.5 a, b, c) which was mainly explained by an increasing proportion of stem during this time (Figure 5.6). This suggests greater internode extension of the FD10 stem which is consistent with the classification system. For DF regimes, the proportion of leaf fell in all crops that had long regrowth cycles, as illustrated by the rate of decrease in leafiness being greater for DF84 crops (Figure 5.5 a, b, c). The lower LSR of DF84 crops was mainly because the proportion of stem, particularly hard stem increased while proportion of leaf decreased (Figure 5.6).

From an animal production perspective it is the total amount of ME and CP produced that is most important (Waghorn and Barry, 1987). Irrespective of DF regimes, the FD10 genotype produced higher total CP and ME in first year but it was lower than FD2 and FD5 genotypes by the end of third year (Tables 5.2 and 5.3). In this study, crops defoliated at 42 and 84 day intervals produced a higher total CP and ME than a 28 day regrowth crop (Tables 5.2 and 5.3; Figures 5.8 and 5.9). The change in total

CP of shoot fractions was explained by an allometric relationship as DM increased, CP increased in a similar pattern for all treatments throughout growing seasons (Figure 5.12 a - d). Figure 5.12 a shows that the rate of CP accumulation in shoot DM was approximately equal to 0.6 times the growth rate of shoot DM which is close to value of two thirds found by Lemaire *et al.* (1992) for N accumulation in shoot biomass of lucerne crops. Leaf fraction was most nutritious which have a constant of 0.3 t CP per one ton leaf DM followed by soft stem (0.12) and lowest was hard stem of 0.07 t CP/t DM (Figure 5.12 b, c, d). The change in CP among shoot fractions was explained by a decrease of LSR with increasing DM (Figure 5.7). This is because stem fractions (soft and hard stems) contain mainly structural components (Gastal and Lemaire, 2002) which have a low N content than leaf (Figure 5.14). Similarly, the ME in shoot fractions of all lucerne crops was constant of 11.7 GJ ME/t DM for leaf followed by soft stems of 8.5 and hard stems of 5.3 GJ ME/t DM (Figure 5.13 b, c, d). These results indicate that the relationship between yield and quality of lucerne was independent of genotype and predominantly explained allometrically by the LSR, associated with shoot DM.

5.5 Conclusions

Based on the results from this chapter;

- The initial objective of the experiment to create crops of different yield potential by using defoliation treatments was achieved with annual shoot yields ranged from 5.2 t DM/ha in DF28 crops to 17.5 t DM/ha in DF84 crops.
- The FD10 genotype produced 24% more shoot and 24% more CP and ME than the other two genotypes in the first year (2014/15) but this advantage did not persist.
- Under a 28 day defoliation, FD10 had lower shoot growth rates during the spring-summer period in 2016/17 and grew ～3 kg DM/ha/^{0}Cd, lower than the FD2 and FD5 genotype. By the third year (2016/17), the FD10 produced the lowest quality of 1.4 t CP/ha and 63 GJ ME/ha.
- The relationship between yield and quality of lucerne was independent of genotype and predominantly explained allometrically by the LSR, associated with shoot DM.

The following chapter aims to explain these yield differences in terms of radiation interception by quantifying canopy expansion and development of the crops.

Chapter 6 Radiation interception and phenological development

6.1 Introduction

Biomass accumulation can be analysed as the product of the amount of radiation intercepted by the canopy and radiation use efficiency (Equation 2.2, Section 2.3.2). Therefore in Chapter 5, the lower shoot yield observed in DF28 crops that were defoliated more frequencies or the higher shoot yield in autumn of the FD10 genotype can be explained by differences in either R/R_0 and/or RUE. In this chapter these yield differences will be quantified in relation to R/R_0. In Chapter 7, any differences in the RUE for DF regimes and FD ratings will be explored.

Radiation interceptance is modulated by changes in canopy structure and expansion throughout the growth period (Hay and Porter, 2006). This is because morphological changes in canopy structure (*e.g.* canopy leaf angle and optical properties) determine the amount of radiation intercepted per unit of leaf area. This can be quantified by the canopy extinction coefficient (Monsi and Saeki, 2005). The main crop factor that determines the amount of radiation intercepted is canopy expansion. This is quantified by the area of green leaf or leaf area index (LAI) which is driven by environmental variables. In lucerne the LAI has components of stem population, leaf number on the main-stem, branching, senescence, and stem height with each of these component driven by temperature (Robertson *et al.*, 2002) but potentially also modified by photoperiod (Brown *et al.*, 2005b). These responses need to be quantified to explain the dynamics of LAI and quantify changes in radiation interceptance for defoliation regimes and different FD lucerne genotypes.

Another important aspect in crop growth is the quantification of phasic development from vegetative to reproductive because changes in partitioning priority often occur as crops become reproductive (Section 2.2). The time of the transition from the vegetative phase to the reproductive phase varies with temperature (Smith, 1972) but also manipulated by photoperiod Teixeira *et al.* (2011). It is unclear if, or how, phenological development might change with genotypes of different FD ratings. The non-dormant FD10 genotype exhibited faster regrowth in autumn (Chapter 5), consequently it might reach the reproductive phase earlier than the winter-dormant (FD2) and semi-dormant (FD5) genotypes (Lowe, 1985). In contrast, the lower spring regrowth of the FD10 genotype suggests it might take a longer time to reach the reproductive phase than FD2 and FD5 genotypes. The impact of phenological development on partitioning and growth processes is unknown or insufficiently understood to be predictive.

The null hypothesis for this investigate is that phenological development is conservative among FD ratings. The defoliation regimes were used to create crops with different stages of development, to

examine how phenological responses differ with FD ratings and defoliation. Thus, the objective of this chapter is to quantify the physiological responses of both vegetative and reproductive phases of crops with different FD ratings to environmental signals under different defoliation managements. Ultimately, the aim is to use these to explain the yields observed in Chapter 5.

6.2 Material and methods

The description of the experimental design, treatments and agronomic management were presented in Section 3.3. In this chapter, only additional measurements related to results of this chapter are reported.

6.2.1 Phenology of regrowth

Five dominant stems per genotype were tagged per plot to assess (i) the number of fully expanded primary leaves, (ii) stem height (cm), (iii) the number of axillary leaves (branching), the number of senesced leaves and (iv) the timing of bud initiation, bud visible and open flowering at each main-stem. Stems were tagged from the beginning of each regrowth cycle and measurements were taken at 7-10 day intervals until harvest. Reproductive phase was recorded as the date when 50% of tagged stems had initiated buds (swollen part in the meristem) before visible buds, and then open flowers.

6.2.2 Phyllochron

The phyllochron (°Cd) describes the rate of main-stem leaf appearance, and was calculated as the slope of the linear relationship between the number of primary leaves on tagged stems and accumulated thermal time (Section 3.5.2) for each genotype within each regrowth cycle. Phyllochron was displayed in relation to photoperiod at the start of the regrowth period. This is consistent with Sim (2014) who found the phyllochron of primary leaves in lucerne was determined by the direction of photoperiod, rather than the average photoperiod over the entire growth cycle.

6.2.3 Shoot and plant population

Shoot or stem population (stems/m^2) was measured by counting the number of shoots in a 0.2 m^2 quadrat harvested for DM (Section 5.2.1). Plant population (plants/m^2) was measured by counting the number of individual plants excavated from the same quadrat. The crown and root biomass from these plants are reported in Chapter 7.

6.2.4 Canopy expansion

6.2.4.1 Leaf area index

Crop green leaf area index (LAI; m^2/m^2) was measured from a subsample of 10 representative stems which was taken from the quadrat harvested for DM (Section 5.2.1). Leaves were removed from stems

and were separately passed through a leaf area meter (LICOR 3100; Licor Inc. Lincoln, USA). Area sums were recorded regularly and summed at the end to give total leaf area and total stem area of that subsample. The leaf and stem samples were then dried in a forced-air oven set to 60˚C until constant weight. The specific leaf area (SLA) was calculated as the leaf area (cm^2) per unit leaf mass (g). The 27 measurements were taken on seven occasions throughout the regrowth period. Regression of each leaf and stem area against its DM fraction showed the slope was consistent (R^2=0.98) among genotypes (Figure 6.1). This indicates that SLA was constant for all crops.

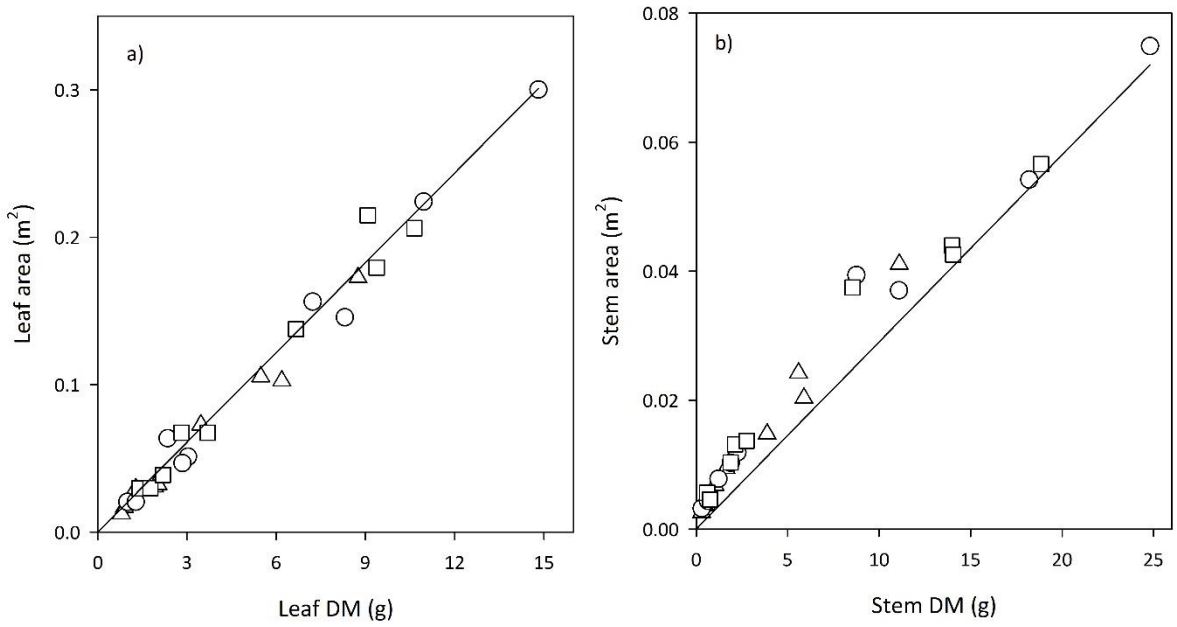


Figure 6.1 Leaf area (a) and stem area (b) of lucerne shoots measured independently by the LICOR 3100 area meter in relation to leaf DM and stem DM of the same shoot fractions of three lucerne genotypes with fall dormancy (FD) ratings of 2 (Δ), 5 (O), and 10 (□).

Note: a) Linear regression (—) y=0.020x; R^2=0.98. b) Linear regression (—) y=0.003x; R^2=0.98. Defoliation regimes/seasons are plotted combined.

Leaf area index at the intermediate points (Section 5.2.1) and at the end of each regrowth cycle was then calculated as:

$LAI = DM_{leaf}/SLA$

Where DM_{leaf} is the total amount of leaf DM (g/m^2) estimated for a given plot (Section 5.2.1).

Daily values of LAI were determined by LAER (Section 6.2.4.2) multiplied by daily accumulated thermal time. Daily thermal time was accumulated using air temperature (T_b = 1°C) as described in Section 3.5.2. To deal with the periods of senescence that occurred in the last stage of each 84 day regrowth cycle, a bi-linear model was used to display LAI for each genotype. The first linear model displays from the start of regrowth until the intermediate point (42 day regrowth) and the second one displays after that to the end of the cycle.

6.2.4.2 Leaf area expansion rate

The average leaf area expansion rate (LAER; $m^2/m^2/°Cd$) was calculated as the slope of the linear regression between LAI against accumulated thermal time for each genotype within each regrowth cycle. The LAER was then plotted against the mean date of each regrowth cycle to display the seasonal pattern. For DF84 crops, only data points at 95% of maximum LAI were used. This method ensured that periods of senescence that limit LAER were excluded from the comparison.

6.2.5 Radiation interception

6.2.5.1 Extinction coefficient

The extinction coefficient (k) was determined from the linear slope between the natural log of canopy radiation interceptance and LAI, measured independently. Interceptance was measured directly, non-destructively using a Sunscan plant canopy analyser (Delta-T Devices Ltd, Burwell, Cambridge, England). The incident solar radiation above canopy (R_0) and transmitted radiation below (R) the canopy was made by seven above and below canopy readings per plot. Readings were taken on 80 occasions for all genotypes from different DF regimes throughout the regrowth seasons.

Sunscan LAI readings were regressed against LAI calculated from destructive measurement (Section 6.2.3.1) and this showed an overestimation of LAI observed from the Sunscan canopy analyser of 24% (Figure 6.2). Sim (2014) reported LAI observed from the Sunscan canopy analyser overestimated actual LAI by 18% when working with an FD5 lucerne "Kaituna" crop at the same location of I12. A difficulty in non-destructive measurement of radiation interceptance with lucerne crops is that the instruments require some canopy height and leaf area before accurate measurements can be taken. This may have prevented accurate reading when measuring incomplete canopies, for DF28 crops and crops at early stages after defoliation.

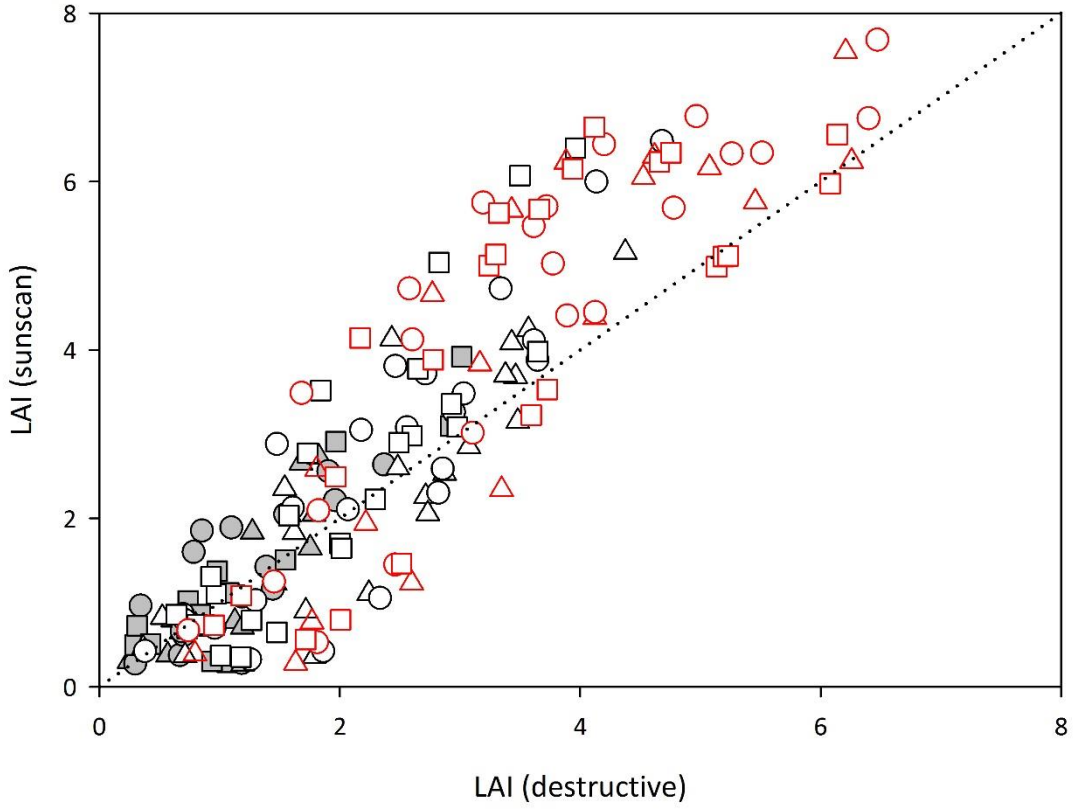


Figure 6.2 Relationship between (LAI) measured non-destructively using the sunscan canopy analyser with LAI calculated from destructive measurement of three lucerne genotypes with fall dormancy (FD) ratings of 2 (Δ), 5 (O), and 10 (□) subjected to 28 (gray symbols), 42 (white symbols)- and 84 (red symbols) day defoliation frequencies (DF) in three regrowth years.

Note: Linear regression y = 1.24x; R^2= 0.83. 1:1 line (·····).

The regression of the natural log of canopy radiation transmission in relation to LAI showed a consistent (R^2=0.93) k value of 0.83 ±0.02 for all genotypes (Figure 6.3). This indicated that all genotypes had a similar canopy structure. Therefore, the difference in the amount of radiation intercepted could be explained by LAI.

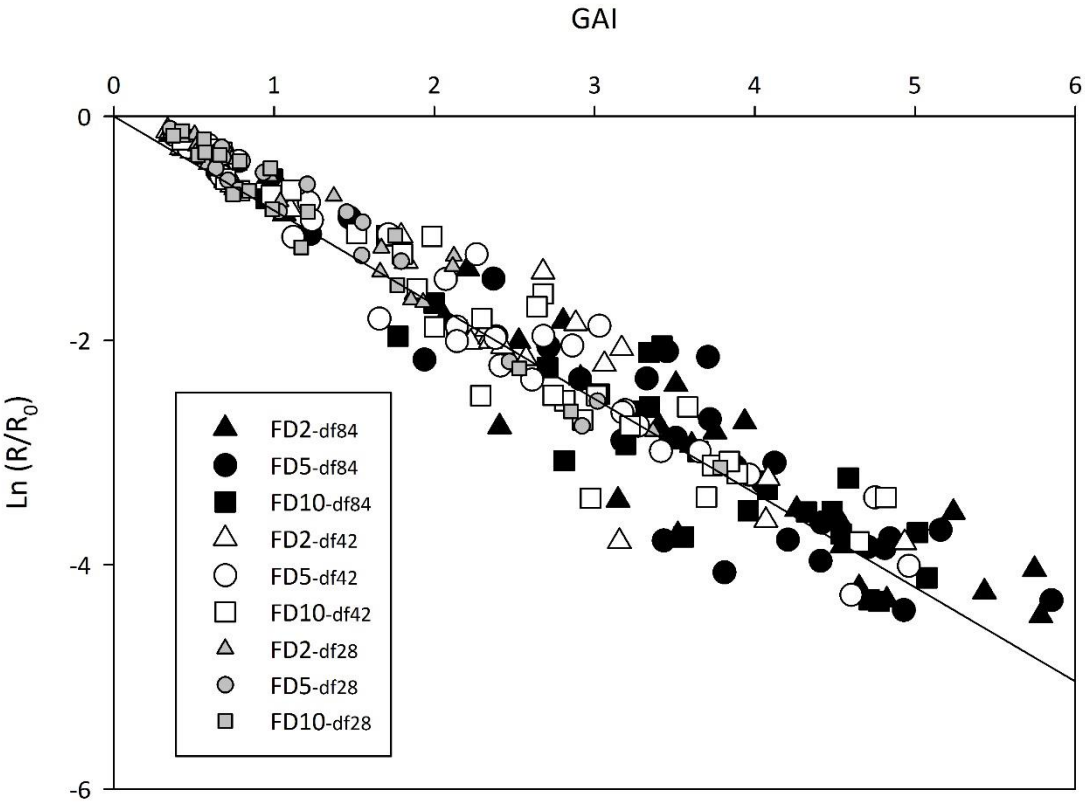


Figure 6.3 The natural log of solar radiation transmission ($Ln(R/R_0)$; measured with sunscan canopy analyser) in relation to leaf area index (LAI; calculated from destructive measurement) of three lucerne genotypes with fall dormancy (FD) ratings of 2 (Δ), 5 (O), and 10 (□) subjected to 28-, 42- and 84 day defoliation frequencies (DF) in three regrowth years.

Note: Linear regression (—) y=0.83x; R^2=0.93.

6.2.5.2 Radiation interception

The accumulated amount of radiation intercepted was calculated by summing daily estimates from each regrowth period. The daily amounts of intercepted radiation (MJ total radiation/m^2) was calculated by using the daily LAI (Section 6.2.3.1) and k (Section 6.2.4.1), which was multiplied by daily incident radiation (R_0).

6.3 Results

6.3.1 Accumulation of intercepted solar radiation

The accumulated intercepted radiation of all treatments and season combinations is displayed in Figure 6.4. In the 2015 regrowth year, intercepted radiation was about 10% higher ($P<0.001$) for the FD10 genotype (1073 MJ/m^2) than that of the FD2 and FD5, regardless of DF regimes. In contrast, there was no effect ($P=0.36$) of FD rating on accumulated intercepted radiation in the second regrowth year (2015/16), when all genotypes intercepted an average of 2610 ±44 MJ/m^2. Interestingly, a separation of radiation interception among FD ratings reappeared in the third regrowth year (2016/17). This occurred particularly in the DF28 regime when the FD10 genotype intercepted 742 MJ/m^2 which was less ($P<0.001$) than the 976 and 1186 MJ/m^2 for the FD5 and FD2 genotypes, respectively.

As expected, DF regime had a stronger influence ($P<0.001$) on accumulated intercepted radiation than FD rating (Figure 6.4 a, b, c). Crops with longer defoliation intervals intercepted more radiation in all regrowth years. For example, in the first year regrowth (2015), DF84 crops intercepted 1372 MJ/m^2 which was higher ($P<0.001$) than the 937 ±32 MJ/m^2 for DF42 crops and the 714 ±32 MJ/m^2 for DF28 crops. A similar pattern occurred in the following regrowth year.

Total accumulated intercepted radiation against shoot DM for the entire regrowth period from January 2015 to January 2017 is displayed in Figure 6.5. Accumulated intercepted radiation explained 94% of the total shoot DM yield of lucerne crops. The slope of the regression indicates an average radiation use efficiency of 0.50 g DM/MJ, but at times individual treatments and growing seasons were not scattered around the line. This suggests radiation use efficiency was not constant and this will be tested for lucerne of different FD ratings and DF regimes in Chapter 7.

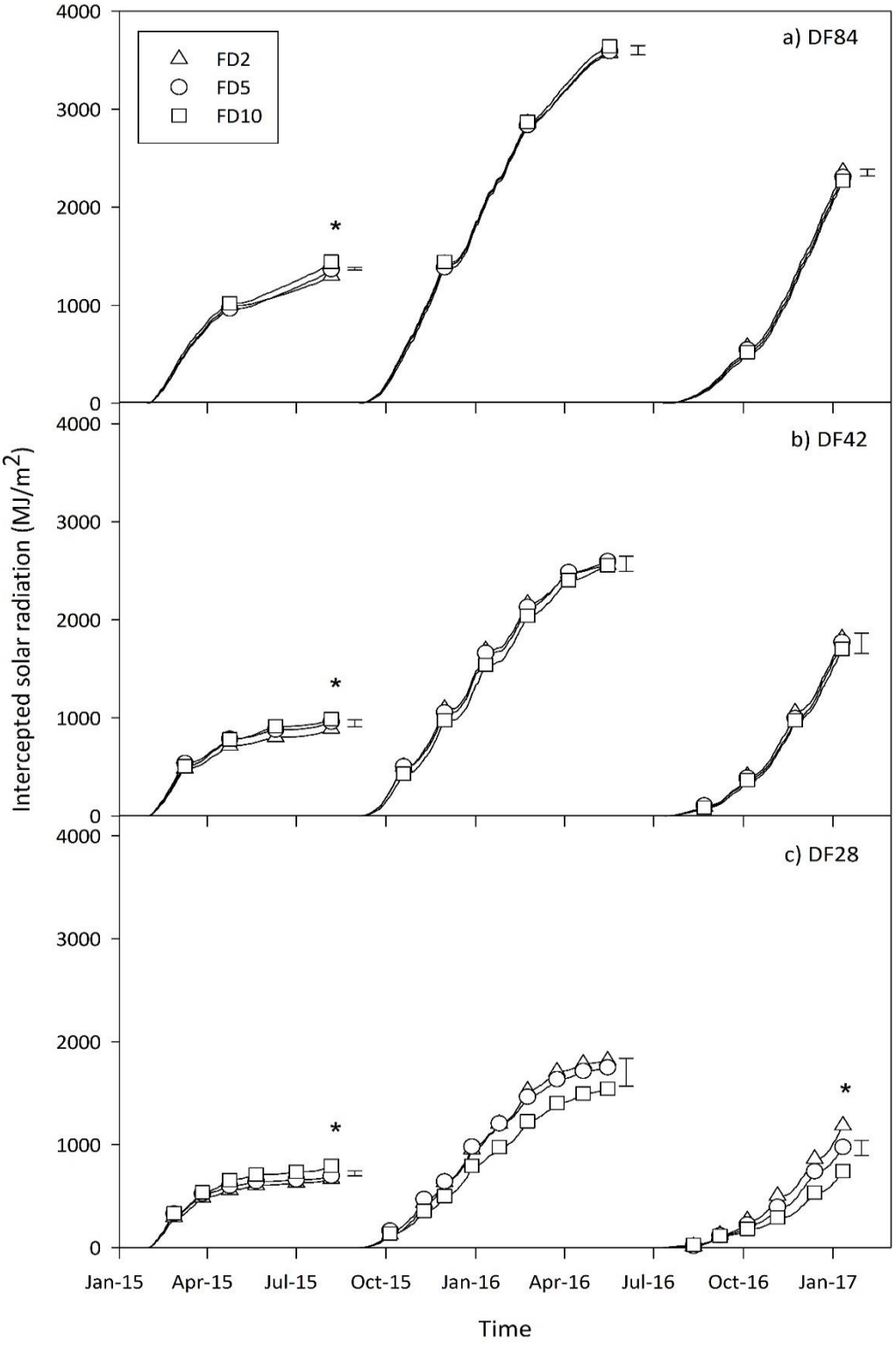


Figure 6.4 Accumulated intercepted radiation of three lucerne genotypes with fall dormancy (FD) ratings of 2 (Δ), 5 (O), and 10 (□) subjected to 28- (c), 42- (b) and 84 day (a) defoliation frequencies (DF) in the 2015; 2015/16 and 2016/17 regrowth years.

Note: Error bars represent LSD (α=0.05) for the final radiation interception. *= P<0.05 when differences occurred among genotypes.

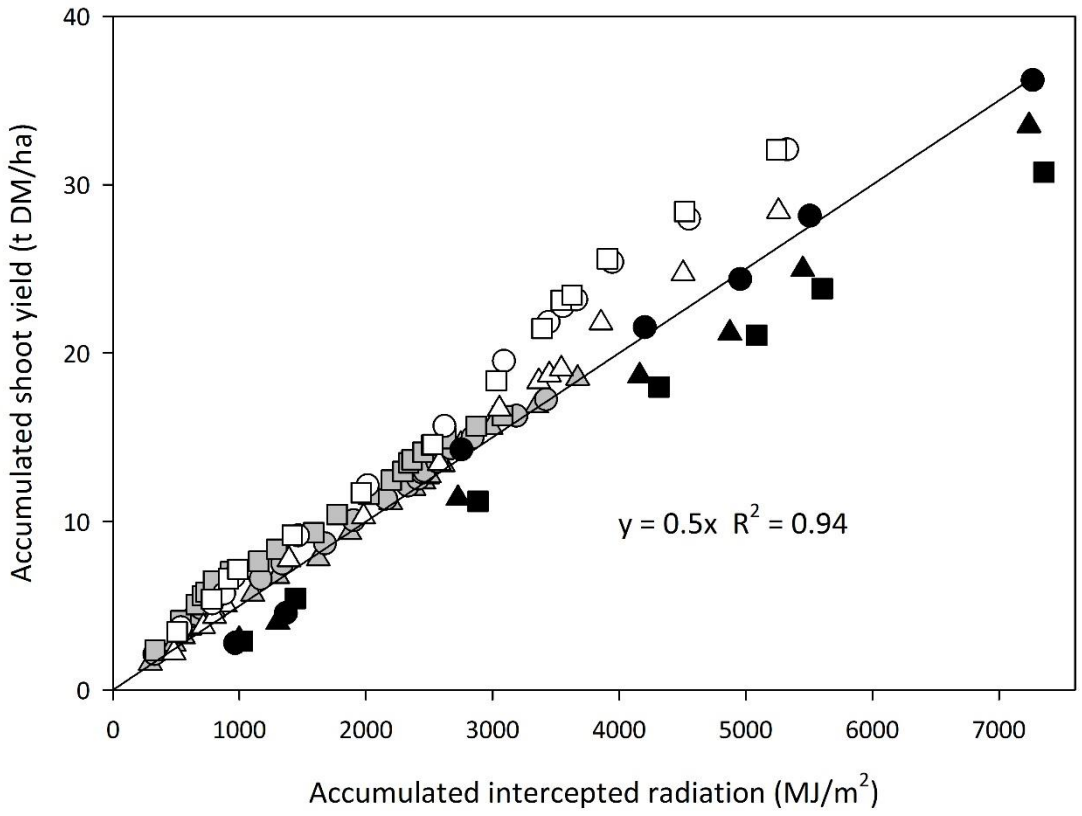


Figure 6.5 Accumulated total shoot dry matter (DM) yield against accumulated intercepted total radiation of three lucerne genotypes with fall dormancy (FD) ratings of 2 (Δ), 5 (O), and 10 (□) subjected to 28- (gray symbols), 42- (white symbols) and 84 day (black symbols) defoliation frequencies (DF) for the overall regrowth period (from January 2015 to January 2017).

The differences in the pattern of radiation interception among genotypes or among DF regimes suggests that either the area of green canopy (LAI) or the efficiency of interception per unit of leaf area (canopy structure) changed during these regrowth seasons. The following sections will examine these components.

6.3.2 Canopy expansion

6.3.2.1 Canopy architecture

The canopy architecture of different crops of genotypes with different FD ratings, subjected to three defoliation regimes, were quantified by the light extinction coefficient with k = 0.83 (Section 6.2.5.1). All genotypes showed a similar (P<0.63) pattern of increasing fractional radiation interception with leaf area index, regardless of DF regimes (Figure 6.6). The relationship demonstrated that all crops intercepted 95% of incident solar radiation when LAI reached to 3.5. This was defined as the critical LAI (LAI_{crit}).

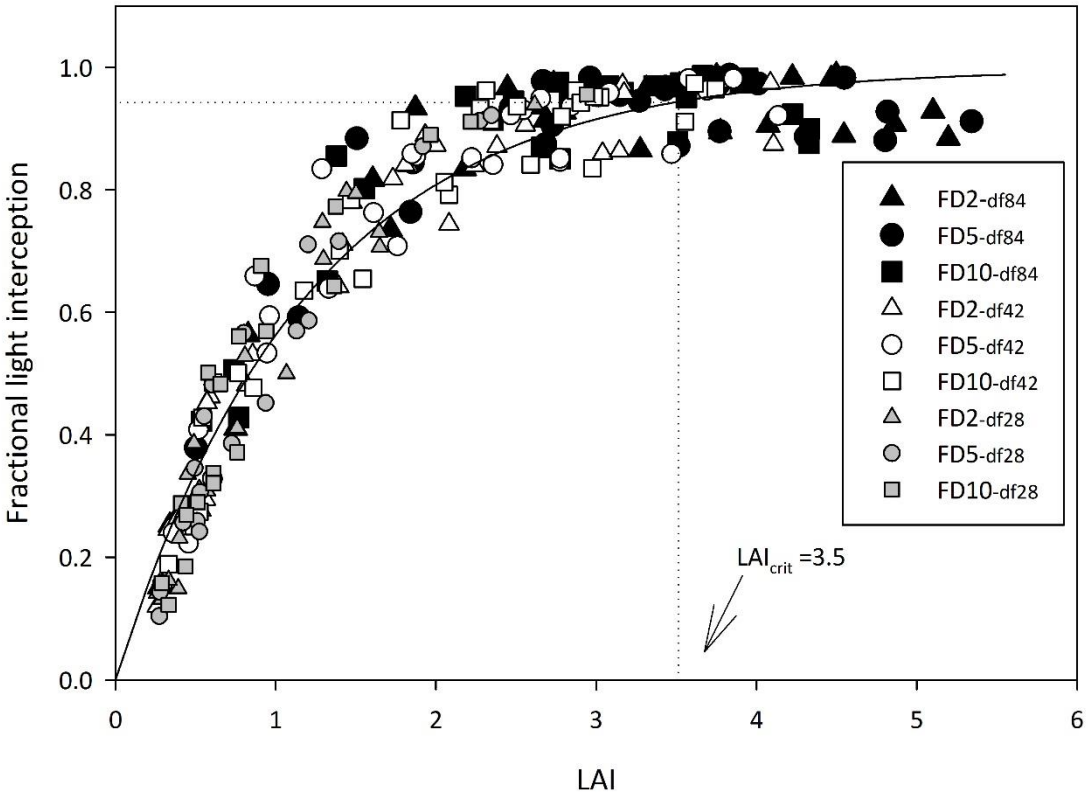


Figure 6.6 Fractional radiation interception against leaf area index (LAI) of three lucerne genotypes with fall dormancy (FD) ratings of 2 (Δ), 5 (O), and 10 (□) subjected to 28-, 42- and 84 day defoliation frequencies (DF) in the 2015; 2015/16 and 2016/17 regrowth years.

Note: LAI calculated from destructive DM samples and fractional radiation interception measured with the SunScan canopy analyser. Regression y = 1- exp(-0.83*LAI) R^2 = 0.94.

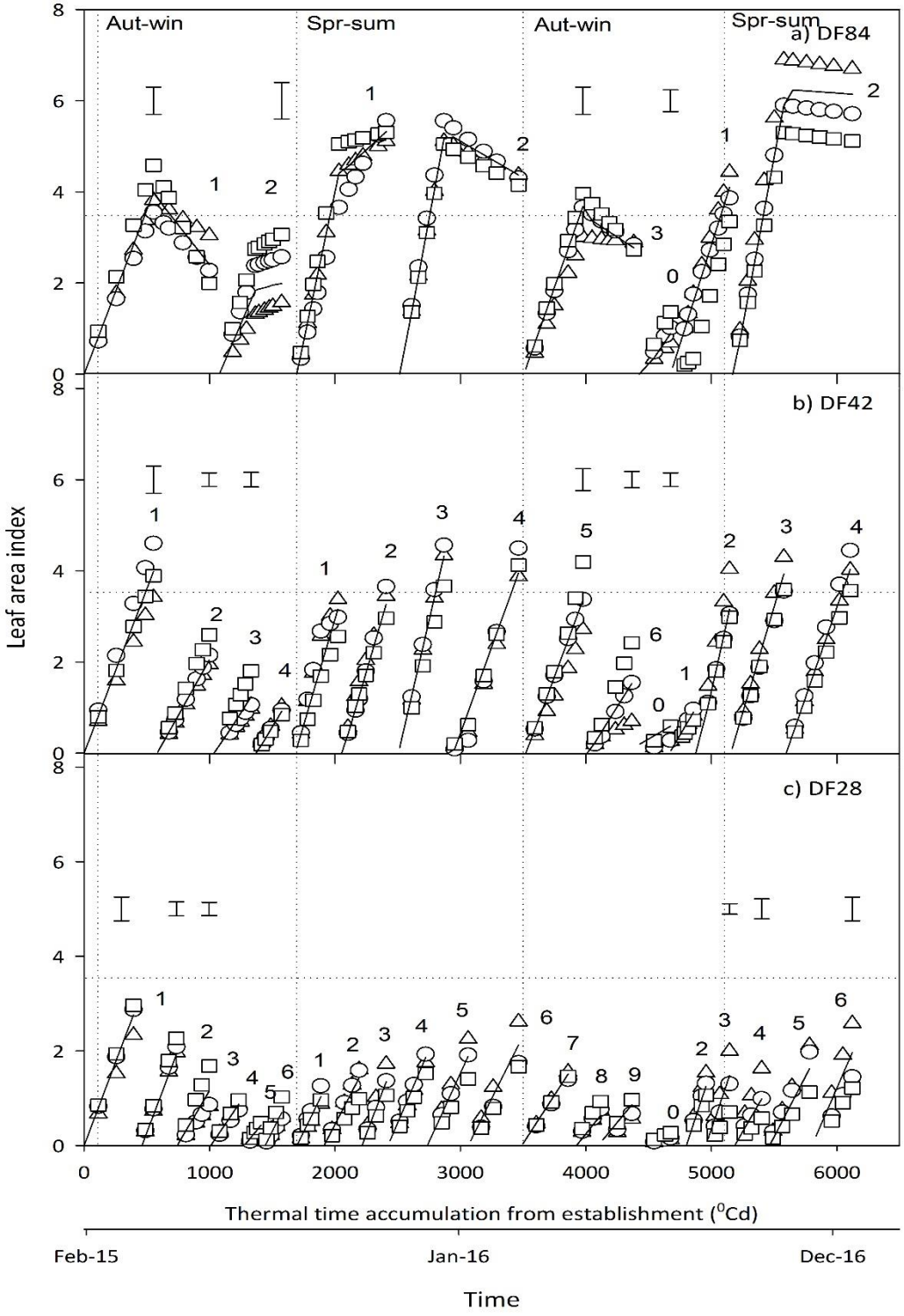


Figure 6.7 Leaf area index of three lucerne genotypes with fall dormancy ratings of 2 (Δ), 5 (O), and 10 (□) subjected to 28- (c), 42- (b) and 84 (a) day defoliation frequencies (DF) in the 2015, 2015/16 and 2016/17 regrowth year at Lincoln University, New Zealand.

Note: Error bars represent LSD (α=0.05) when differences occurred among genotypes. Thermal time accumulated using air temperature (T_b = 1 ^{0}C). Numbers indicate the regrowth cycles. Dotted line represents LAI_{crit} = 3.5.

6.3.2.2 Leaf area index

The canopy expansion pattern of all genotypes displayed strong linear relationships (R^2>0.70) between LAI and accumulated thermal time (Figure 6.7 a; b; c). However, the wide range of slopes indicated temperature was not the only factor driving leaf expansion (Appendix A.2; Table 0.1). In addition, there was also a linear decrease in LAI in the DF84 treatment at the end of the cycles (Cycle 1 in 2015, Cycle 2&3 in 2015/16 and Cycle 2 in 2016/17). This was because senescence started or flowering occurred (Figure 6.7 a).

The effect of FD rating on LAI was apparent in the first autumn-winter cycles in 2015, with the FD10 crops showing a higher LAI (P<0.01). However, during the second autumn-winter cycles in 2015/16, this advantage to FD10 (P<0.01) occurred only for crops defoliated at 42 and 84-day intervals (Figure 6.7 a; b). For crops defoliated at 28-day intervals, FD rating had no effect on LAI during the second autumn cycles. In addition, the FD10 genotype displayed a lower LAI (P<0.05) than the FD2 and FD5 genotypes at the end of the growing cycles in 2016/17 (Figure 6.7 c).

Overall, DF regimes had a strong effect on LAI. Crops in DF84 and DF42 reached LAI_{crit} during most regrowth cycles, with the maximum observed LAI of 7 ±1.4 for DF84 and 4.5 ±0.7 for DF42 during the summer regrowth cycles (Figure 6.7 a; b). In contrast, crops in DF28 did not reach LAI_{crit} throughout any of the regrowth cycles (Figure 6.7 c).

To understand the differences observed in LAI among genotypes and DF regimes, LAI development was regressed against thermal time for each genotype within each regrowth cycle to quantify the rate of leaf area expansion per thermal unit (LAER, $m^2/m^2/°Cd$).

Irrespective of DF regimes, LAER changed seasonally and declined from spring-summer to autumn-winter (Figure 6.8 a, b, c). FD ratings affected LAER during the first autumn-winter in 2015. Specifically FD10 expanded leaf area at an average rate of 0.007 $m^2/m^2/°Cd$ which was faster (P<0.001) than FD5 (0.006) and FD2 (0.005 $m^2/m^2/°Cd$). The effect of FD rating on LAER was carried into the second autumn-winter in 2015/16 (Figure 6.8 a, b), the exception being for crops defoliated at 28 day intervals (Figure 6.8 c). There were no differences (P>0.10) in LAER among genotypes during the spring-summer cycles in 2015/16 and 2016/17. However, LAER differed (P<0.05) among genotypes for DF28 crops in 2016/17, when FD10 had a lower LAER, particularly compared with FD2 genotype (Figure 6.8 c).

For DF regimes, crops defoliated at longer intervals had a faster (P<0.001) LAER. For example in 2015/16, LAER decreased from a maximum of 0.016, 0.012 and 0.006 $m^2/m^2/°Cd$ in spring-summer to a minimum of 0.005, 0.002 and 0.001 $m^2/m^2/°Cd$ in the last autumn-winter for DF84, DF42 and DF28 crops, respectively.

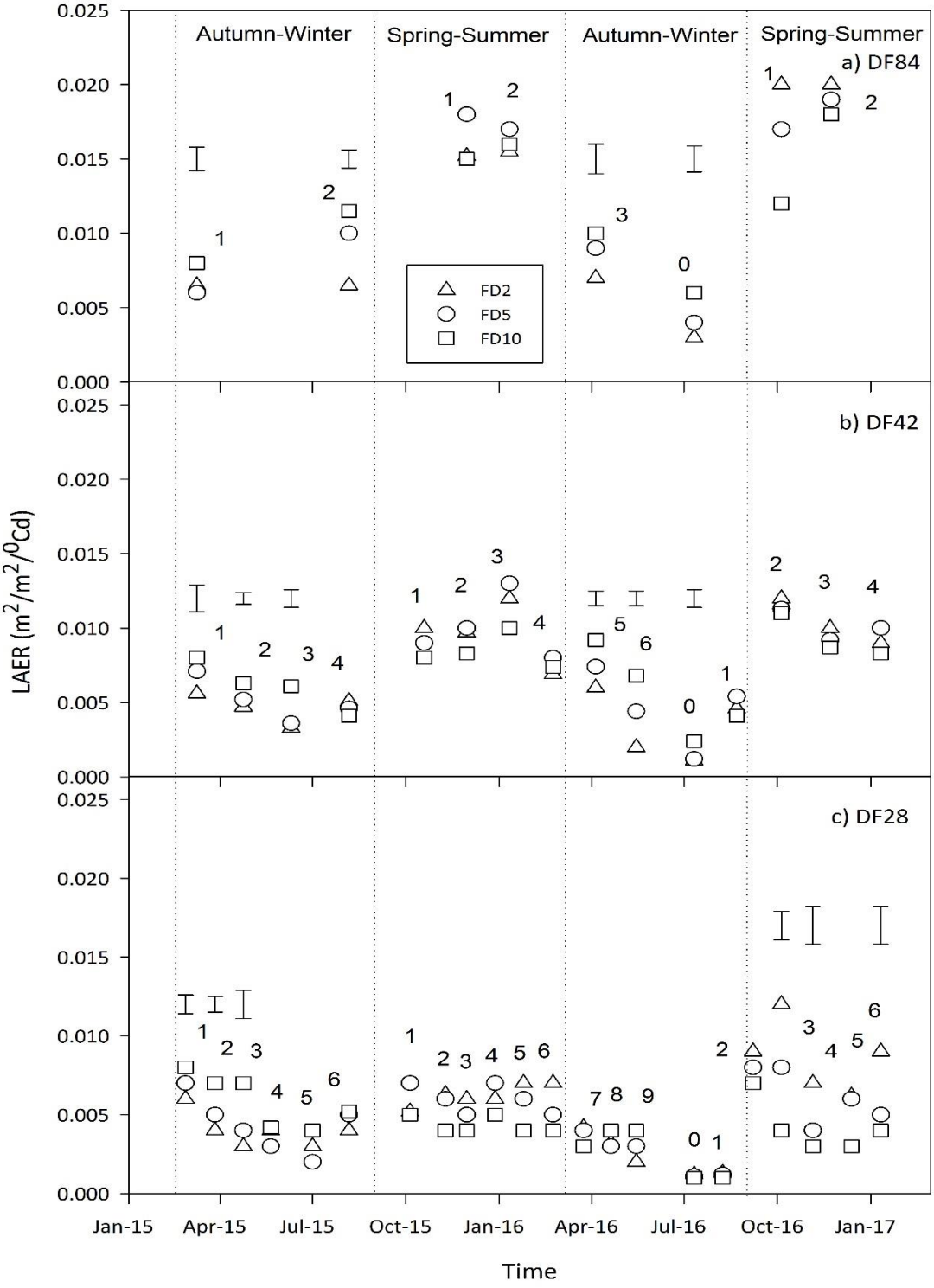


Figure 6.8 Seasonal leaf area expansion rate (LAER) of three lucerne genotypes with fall dormancy (FD) ratings of 2 (Δ), 5 (O), and 10 (□) subjected to 28 (c), 42 (b) and 84 day (a) defoliation frequencies (DF) in the 2015, 2015/16 and 2016/17 regrowth year at Lincoln University, New Zealand.

Note: Error bars represent LSD (α=0.05) when differences occurred among genotypes. Numbers (0-9) indicate the regrowth cycles. Thermal time accumulated using air temperature (T_b = 1 ^{0}C). Calculated physiological parameters for each genotype within each regrowth cycle are presented in Appendix B.1.

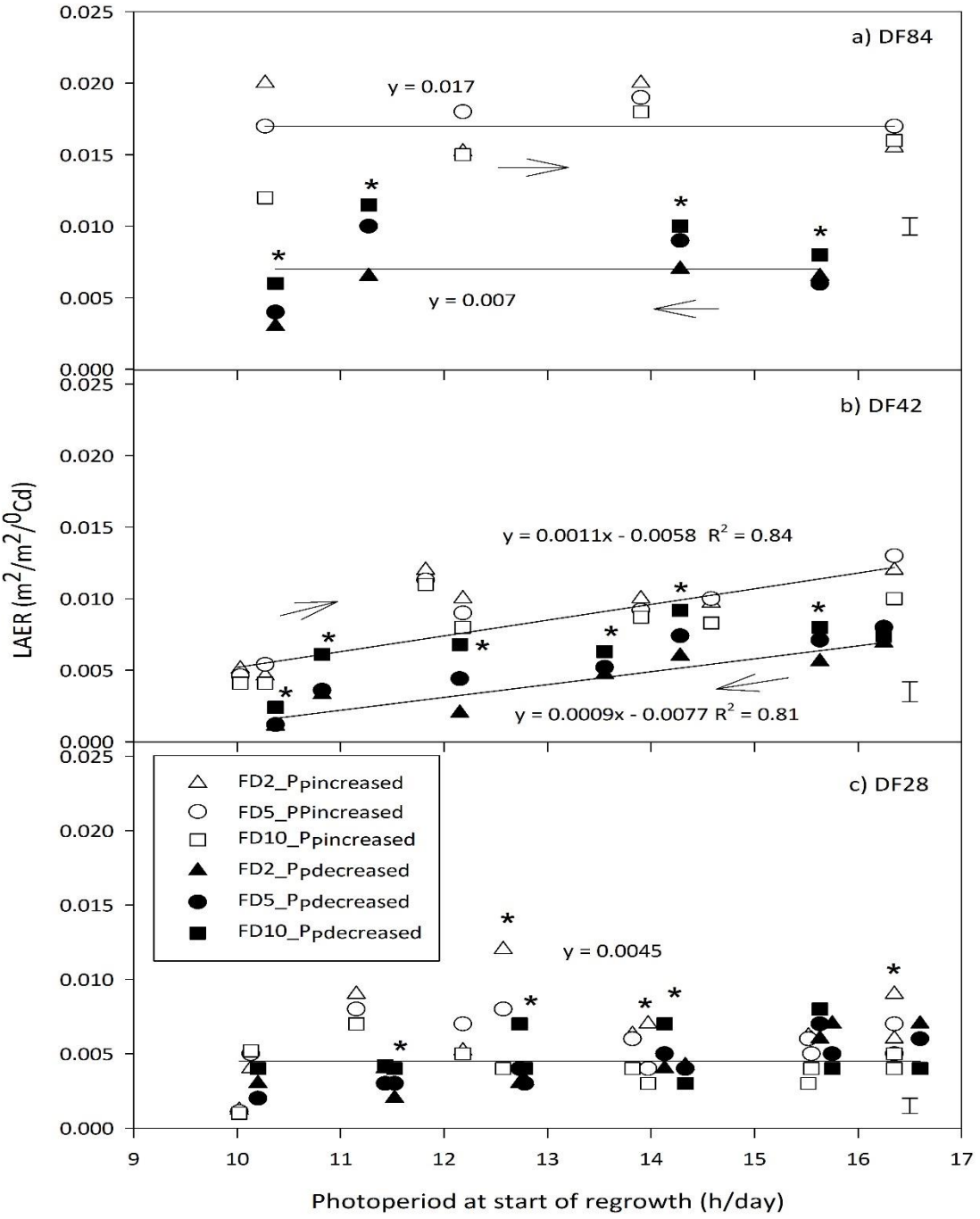


Figure 6.9 Leaf area expansion rate (LAER) of three lucerne genotypes with fall dormancy (FD) ratings of 2 (Δ), 5 (O), and 10 (□) subjected to 28 (c), 42 (b) and 84 day (a) defoliation frequencies (DF) in response to increasing (white symbols) and decreasing (black symbols) photoperiod (Pp) at the start of each regrowth period.

Note: Thermal time accumulated using air temperature (T_b = 1 ^{0}C). Arrows indicate an increasing or decreasing LAER. Solid lines (—) represent regression.* represents P<0.05 when differences occurred among genotypes. Error bars represent LSD (α=0.05) for comparison between increasing and decreasing Pp. Calculated LAER values for each genotype within each regrowth cycle are presented in Appendix B.1.

To explain the seasonal pattern of LAER, the influence of photoperiod (Pp) at the start of each regrowth period was examined (Figure 6.9). When crops in DF84 and DF42 were growing into an increasing Pp from 10 h to 16.5 h, LAER was not different ($P<0.69$) among genotypes. In contrast, when crops were growing into a decreasing Pp from 16.5 h to 10 h, LAER was higher ($P<0.05$) for the FD10 genotype compared with the FD2 and FD5 genotype (Figure 6.8 a, b). For DF28 crops, a similar pattern occurred only in the first regrowth cycles in 2015 when the FD10 genotype had a higher ($P<0.05$) LAER than FD2 and FD5 when photoperiod was decreasing. However, LAER did not differ ($P<0.46$) among genotypes in the following regrowth cycles in 2015/16, regardless of photoperiod. Furthermore, by the final regrowth cycles in 2016/17, FD10 had a lower ($P<0.05$) LAER than the FD2 and FD5 genotypes, despite crops growing in an increasing Pp (Figure 6.9 c). Overall, all genotypes in DF28 crops were fitted on one line with an average LAER of 0.0045 $m^2/m^2/°Cd$, regardless of photoperiod. The reduction in LAER for DF28 crops, particularly for the FD10 genotype (Figure 6.8 c) suggests that the relationship of LAER and Pp was not solely influenced by photoperiod. Others potential causes are discussed in Chapter 7.

The development of individual leaf size for all crops was examined and is shown in Figure 6.10. DF28 crops had the smallest ($P<0.001$) individual leaf area, regardless of photoperiod (Figure 6.10 a, b, c). There was a seasonal effect on the development of the individual leaf. In autumn (15 May 2016), the area of individual leaves was smaller ($P<0.05$) than in early spring (5 October 2016) or early summer (30 November 2015). With regards to FD ratings, FD10 had a larger individual leaf ($P<0.05$) than FD2 when genotypes were growing in a decreasing Pp environment (Figure 6.10 b).

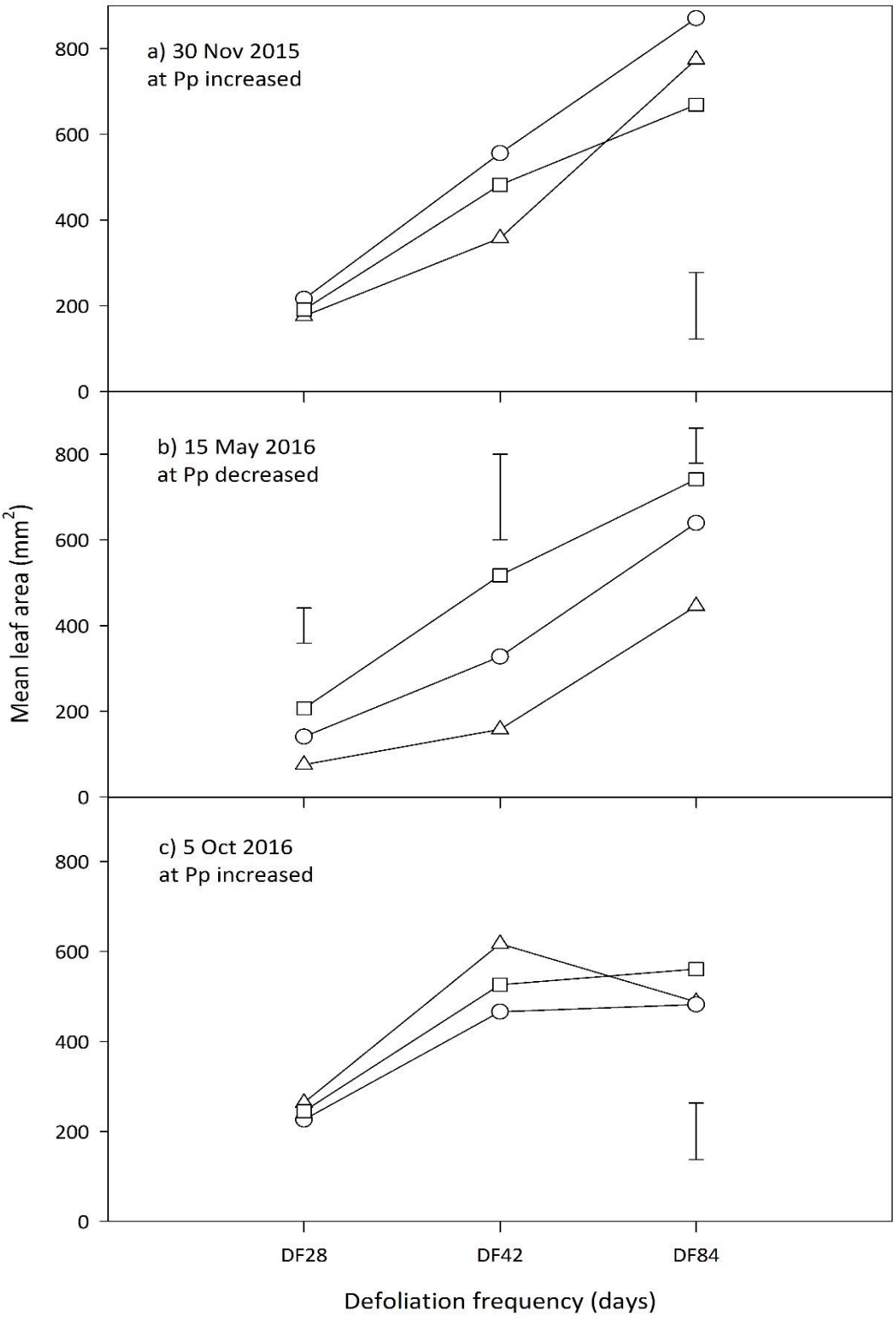


Figure 6.10 Mean leaf area of three lucerne genotypes with fall dormancy (FD) ratings of 2 (Δ), 5 (O), and 10 (□) subjected to 28 (DF28), 42 (DF42) and 84 day (DF84) defoliation frequencies (DF) grown in increasing and decreasing photoperiod (Pp).

Note: Error bars represent LSD (α=0.05) for comparison between DF regimes and among genotypes.

6.3.3 Canopy development

The components of canopy development were quantified to give insight into the mechanisms responsible for the differences in LAER. These included; leaf appearance (phyllochron) and branching, shoot elongation (plant height), leaf senescence and shoot population across FD ratings and DF treatment.

6.3.3.1 Leaf appearance

The number of primary leaves on the main-stem increased linearly in relation to thermal time for all genotypes, regardless of DF regimes (Figure 6.11 a, b, c). However, there was a decrease in the slope of the regression in the latter part of each regrowth cycle in DF84 crops. This bi-linear relationship may reflect senescence, the onset of reproductive development or after a frost, e.g Cycle 2_2015 (Figure 6.11 a). In addition, there was an effect ($P<0.05$) of FD rating on leaf appearance in autumn, when the FD10 genotype expanded 4 more leaves in DF42 (Cycle 6_2015/16) or two more leaves in DF28 (Cycle 2_2015 and Cycle 8_2015/16) than FD2 and FD5 genotypes (Figure 6.11 b, c). Overall, the rate of leaf appearance (primary leaf/°Cd) was consistent ($R^2>0.90$; Appendix A.2; Table 0.2) among genotypes but differed ($P<0.001$) within regrowth cycles.

The change in the rate of leaf appearance was assessed in relation to seasonal variation in phyllochron and showed systematic changes (Figure 6.12). During the spring-summer period, the phyllochron was not different ($P=0.20$) among genotypes at around 30°Cd/primary leaf. Then it increased to over 40°Cd in the later summer-autumn period. In particularly, autumn regrowth cycles showed no difference ($P<0.60$) in phyllochron among genotypes for DF84 crops (Figure 6.12 a), differed ($P<0.05$) for DF42 crops in Cycle 6_2015/16 (Figure 6.11 b) and for DF28 crops in Cycle 2_2015 and Cycles 8, 9_2015/16 (Figure 6.12 c).

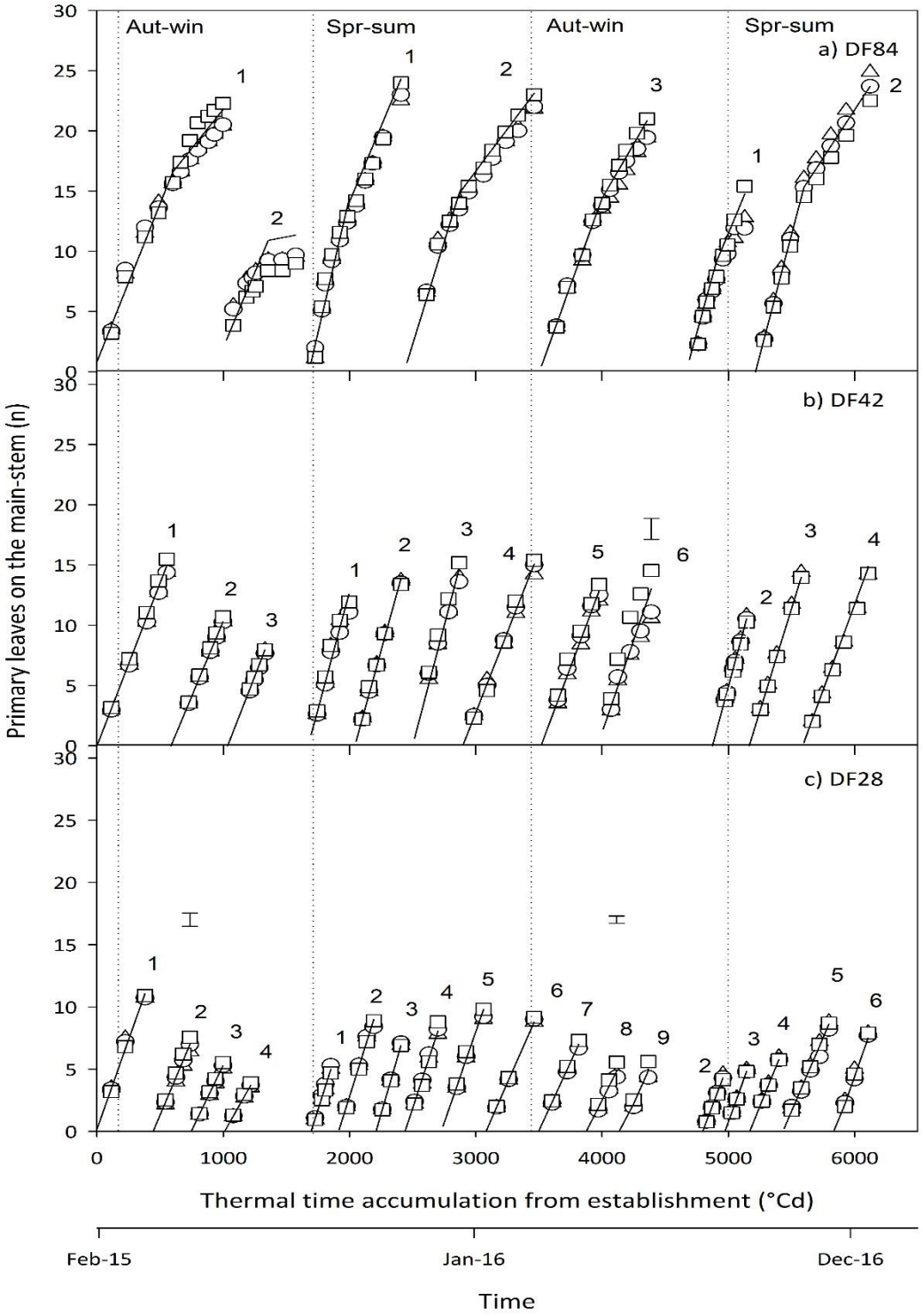


Figure 6.11 Number of primary leaves on the main-shoot during regrowth of three lucerne genotypes with fall dormancy (FD) ratings of 2 (Δ), 5 (O), and 10 (□) subjected to 28- (c), 42- (b) and 84 day (a) defoliation frequencies (DF) in the 2015, 2015/16 and 2016/17 regrowth year at Lincoln University, New Zealand.

Note: Error bars represent LSD (α=0.05) when differences occurred among genotypes. Thermal time accumulated using air temperature (T_b = 1 ^{0}C). Numbers (0-9) indicate the regrowth cycles.

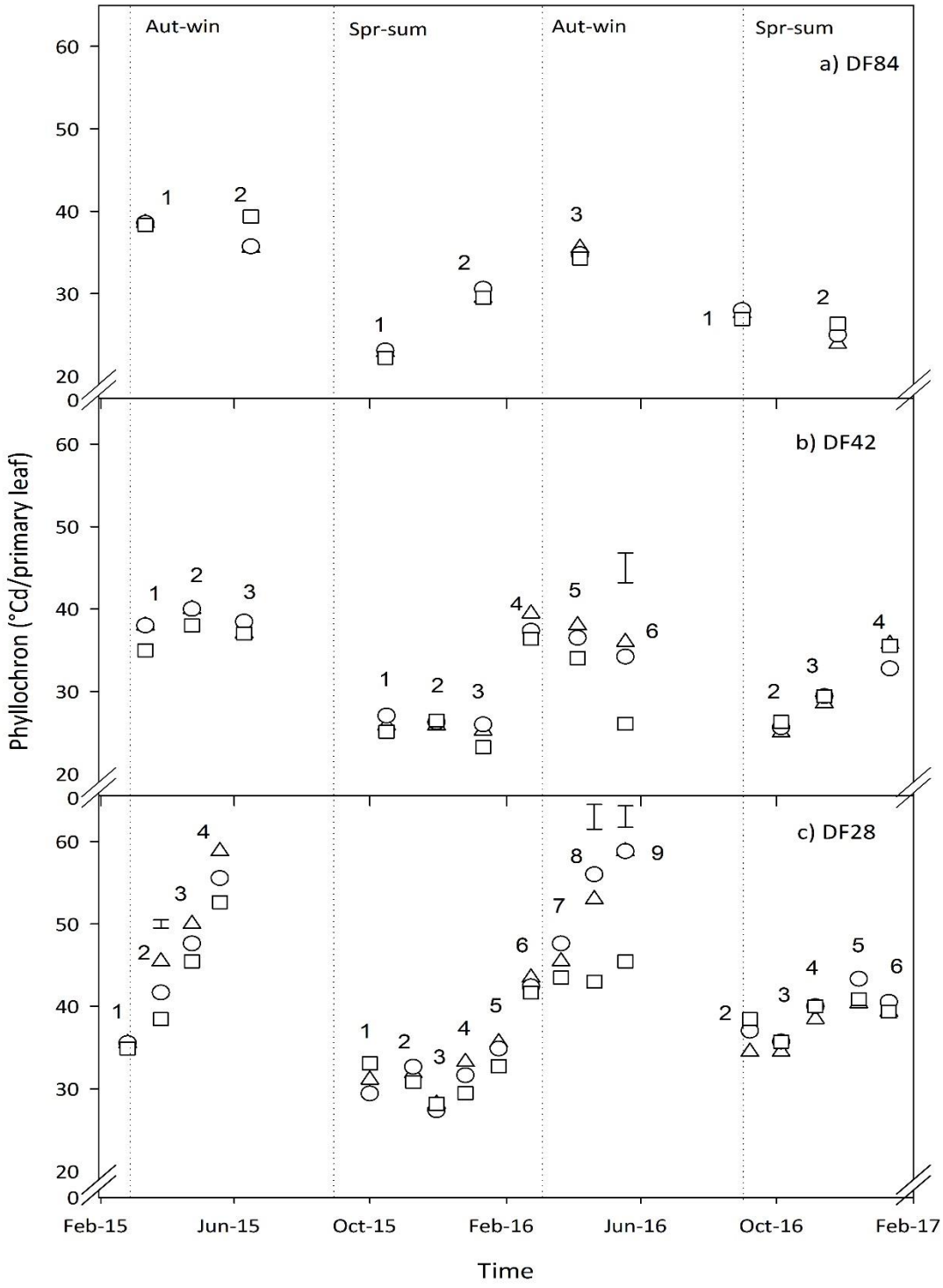


Figure 6.12 Phyllochron of primary leaves on the main-shoot during regrowth of three lucerne genotypes with fall dormancy (FD) ratings of 2 (Δ), 5 (O), and 10 (□) subjected to 28-(c), 42-(b) and 84 day (a) defoliation frequencies (DF) in the 2015, 2015/16 and 2016/17 regrowth year at Lincoln University, New Zealand.

Note: Error bars represent LSD (α=0.05) when differences occurred among genotypes. Thermal time accumulated using air temperature (T_b = 1 ^{0}C). Numbers (0-9) indicate the regrowth cycles.

To investigate the seasonal pattern of phyllochron, the influence of photoperiod (Pp) at the start of regrowth was assessed as a predictor. The linear regressions showed a hysteresis in phyllochron which differed ($P<0.001$) in response to increasing and decreasing Pp (Figure 6.13 a, b, c). Phyllochron displayed a faster rate of ≤ 30°Cd/primary leaf for all genotypes as Pp increased in comparision with when Pp decreased and the phyllochron was always ≥ 30°Cd for all genotypes. Irrespective of DF regimes, when genotypes were grown into increasing photoperiods from 10.5 h to 16.5 h, the phyllochron did not differ ($P<0.65$) among genotypes. In contrast, when genotypes grew into decreasing photoperiods from shorter than 13h in DF42 crops or 15h in DF28 crops, the FD10 genotype had a shorter phyllochron than FD2 and FD5 genotypes (Figure 6.13 b, c). However, the phyllochron was again similar ($P<0.65$) among genotypes when they started their growth period near the shortest day from less than 11 h. In addition, there was a linear increase in the phyllochron at a rate of 3.8°Cd/h for each 1 h decrease in all genotypes in DF28 crops (Figure 6.13 c).

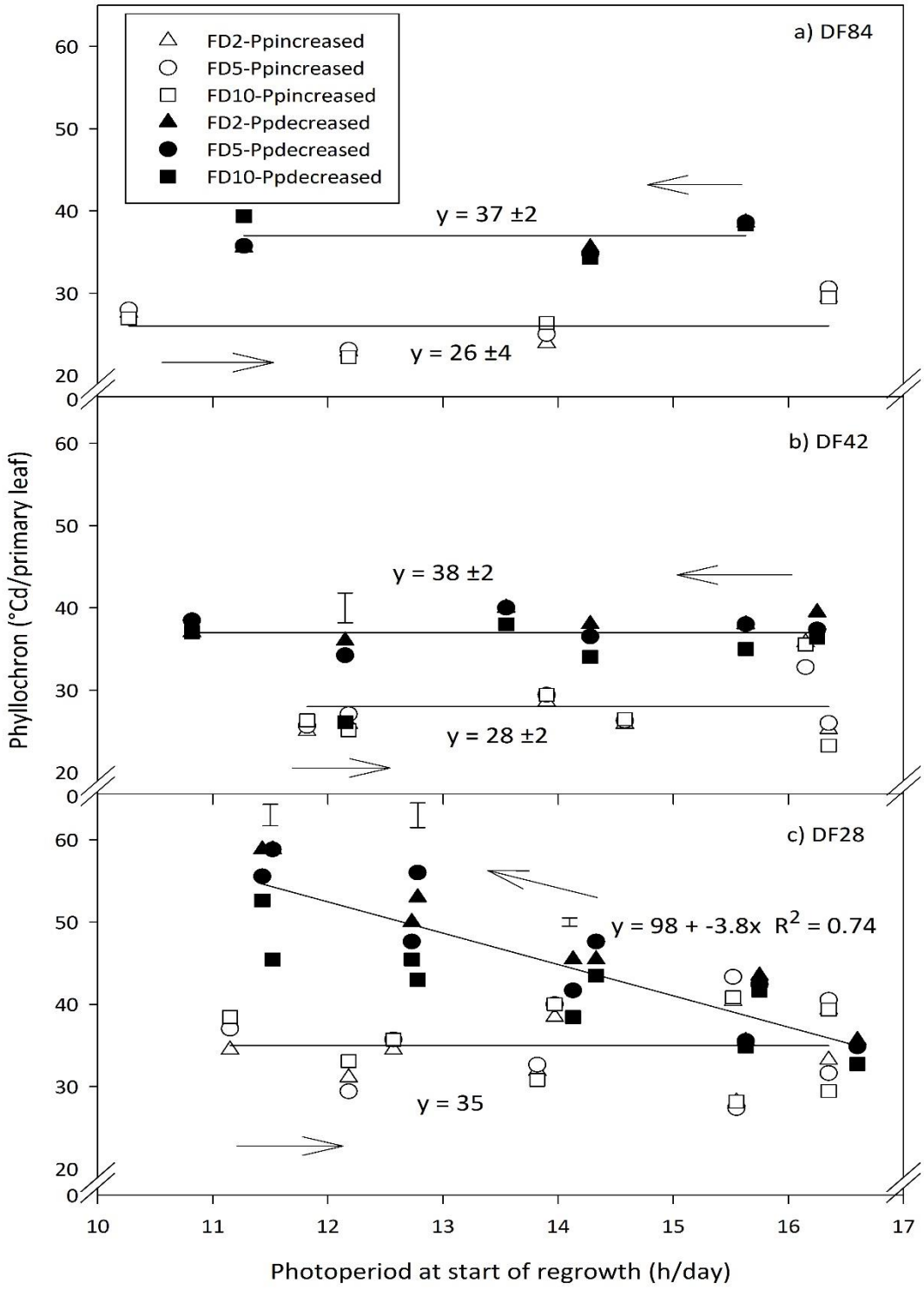


Figure 6.13 Phyllochron of three lucerne genotypes with fall dormancy (FD) ratings of 2 (Δ), 5 (O), and 10 (□) subjected to 28-(c), 42-(b) and 84 day (a) defoliation frequencies (DF) in response to increasing (white symbols) and decreasing (black symbols) photoperiods at start of regrowth.

Note: Error bars represent LSD (α=0.05) when differences occurred among genotypes. Solid lines (—) represent regression. Arrows indicate an increasing or decreasing phyllochron.

6.3.3.2 Axillary leaf appearance on the main-shoot (branching)

The first axillary leaf was initiated when the 4th primary leaf was fully expanded and then progressed linearly (R^2=0.98), consistent with primary leaf appearance for all genotypes, regardless of DF regimes (Figure 6.14). The appearance of axillary leaves was 1.7/primary leaf (P<0.53), for all treatments.

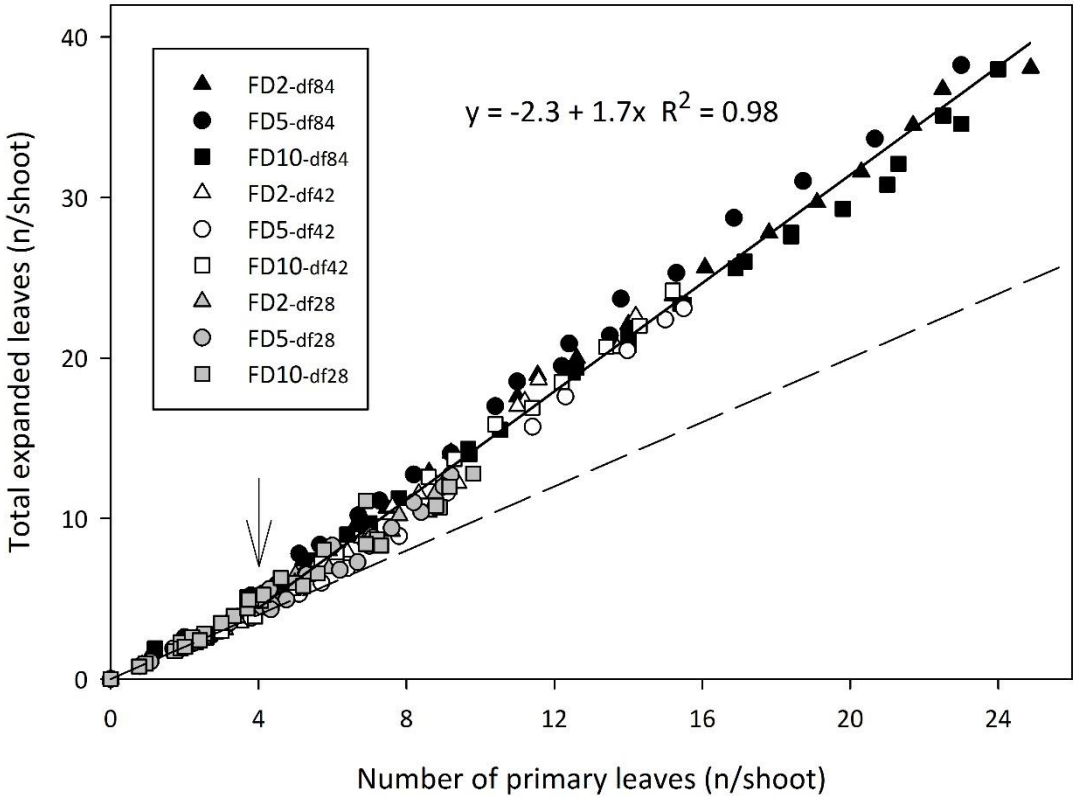


Figure 6.14 Total number of expanded leaves (sum of primary and axillary) in relation to main-stem leaves (primary leaves) on the main-shoot during regrowth of three lucerne genotypes with fall dormancy (FD) ratings of 2 (Δ), 5 (O), and 10 (□) subjected to 28- (gray symbols), 42- (white symbols) and 84 day (black symbols) defoliation frequencies (DF) at Lincoln University, New Zealand.

Note: Dashed line represents primary leaf appearance (x=y). Arrow indicates point when branching started. Solid line represents regression (R^2=0.98).

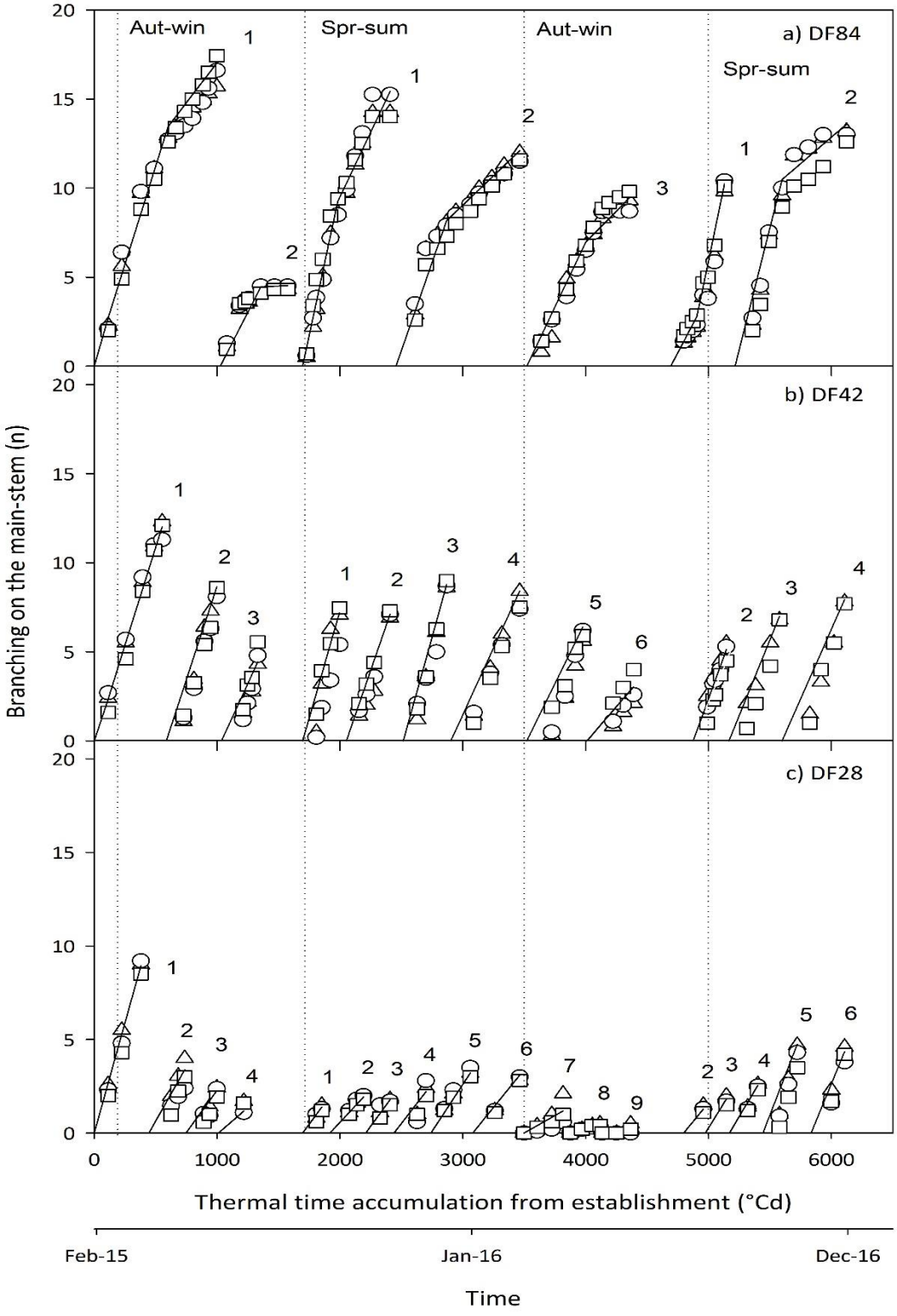


Figure 6.15 Number of axillary leaves (branches) on the main-shoot of three lucerne genotypes with fall dormancy (FD) ratings of 2 (Δ), 5 (O), and 10 (□) subjected to 28- (c), 42- (b) and 84 day (a) defoliation frequencies (DF) in the 2015, 2015/16 and 2016/17 regrowth year at Lincoln University, New Zealand.

Note: Thermal time accumulated using air temperature (T_b = 1 ^{0}C). Numbers (0-9) indicate the regrowth cycles.

Irrespective of DF regimes, the number of axillary branches on the main-stem increased linearly with thermal time for all genotypes (Figure 6.15 a, b, c). The rate of increase in axillary branch number was constant for all genotypes (R^2>0.80) within each regrowth cycle, but the slope of the regression differed (P<0.001) within regrowth cycles, which indicates branching had a strong seasonality, similar to leaf appearance (Appendix A.2; Table 0.3). Spring-summer regrowth cycles increased the total number of branches at a faster (P<0.001) rate than autumn-winter. For example in the DF42 crops, branching ranged from a maximum of 12 axillary branches in spring-summer to a minimum of 5 in autumn-winter (Figure 6.15 b). A similar pattern also occurred in the DF84 and DF28 (Figure 6.15 a, c). However, there was also a decrease in the slope of the regression in the later part of each regrowth cycle in DF84 crops (Figure 6.15 a), similar to leaf appearance (Figure 6.11 a).

6.3.3.3 Plant height

Shoot elongation was related to temperature as shown in Figure 6.16 (a, b, c). From the beginning of the experiment, the rate of increase in the shoot height was constant in thermal time (R^2>0.70) but differed (P<0.05) among genotypes within regrowth cycles (Appendix A.2; Table 0.4). In the first autumn-winter in 2015, stem expansion rate of FD10 was 0.99 mm/°Cd which was faster (P<0.05) than FD5 (0.70) and FD2 (0.53 mm/°Cd). As a consequence, the tallest plants were FD10 followed by FD5 and FD2, regardless of DF regimes. However, in the following spring-summer cycle in 2015/16, crops defoliated at 28 day intervals showed plant height was not different (P<0.43) among genotypes (Figure 6.16 c). At the end of the experiment, the rate of shoot elongation was constant (P<0.65) for all genotypes in spring-summer cycles in 2016/17 (Figure 6.16 a, b, c). The rate of shoot elongation also followed a seasonal pattern, similar to leaf appearance (Figure 6.11) and branching (Figure 6.15).

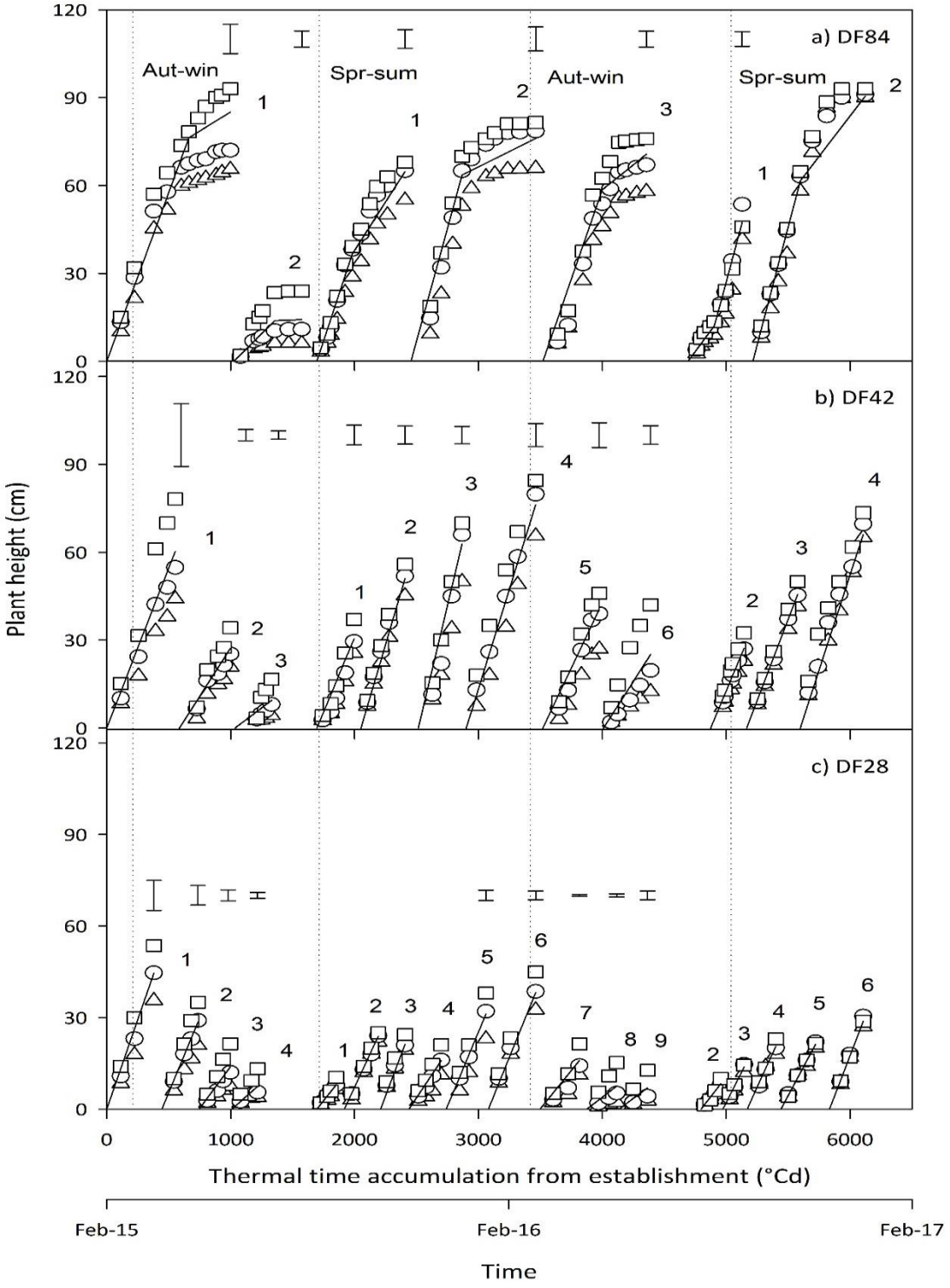


Figure 6.16 Shoot height (cm) of three lucerne genotypes with fall dormancy (FD) ratings of 2 (Δ), 5 (O), and 10 (□) subjected to 28- (c), 42- (b) and 84 day (a) defoliation frequencies (DF) in the 2015, 2015/16 and 2016/17 regrowth year at Lincoln University, New Zealand.

Note: Error bars represent LSD (α=0.05) when differences occurred among genotypes. Thermal time accumulated using air temperature (T_b = 1 ^{0}C). Numbers (0-9) indicate the regrowth cycles.

6.3.3.4 Senescence of primary leaves

Leaf senescence was described in relation to (R^2=0.98) the number of primary leaves on the main-shoot but was also affected by the direction of photoperiod (Pp) at the start of the regrowth cycle (Figure 6.17). This demonstrated that, when genotypes were growing in an increasing Pp, senescence commenced at the time of appearance of the 5th primary leaf on the main-stem (Figure 6.17 a). At this stage, senescence occurred at a rate of 0.74 leaves for each primary leaf that appeared. In contrast, when genotypes were growing in a decreasing Pp, the first leaf senesced at the time of appearance of the 7th primary leaf on the main-stem, and then proceeded at a rate of 0.89 leaves/primary leave (Figure 6.17 b).

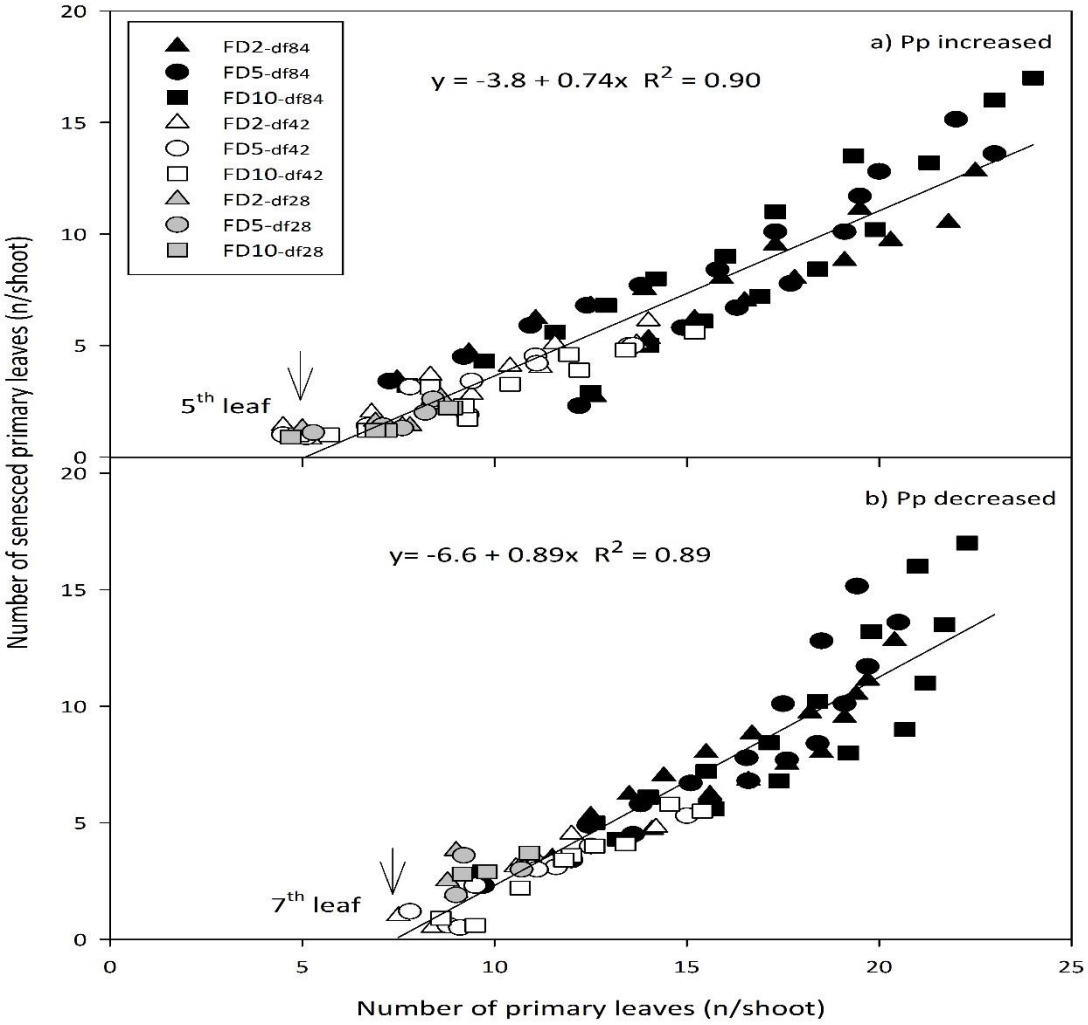


Figure 6.17 Relationship between primary leaf senescence and primary leaf appearance of three lucerne genotypes with fall dormancy (FD) ratings of 2 (Δ), 5 (O), and 10 (□) subjected to 28-(gray symbols), 42-(white symbols) and 84 (black symbols) day defoliation frequencies (DF) in response to increasing (a) and decreasing photoperiods at start of each regrowth period.

Note: Arrows indicate at the time of senescence commenced. Solid lines (—) represent regression.

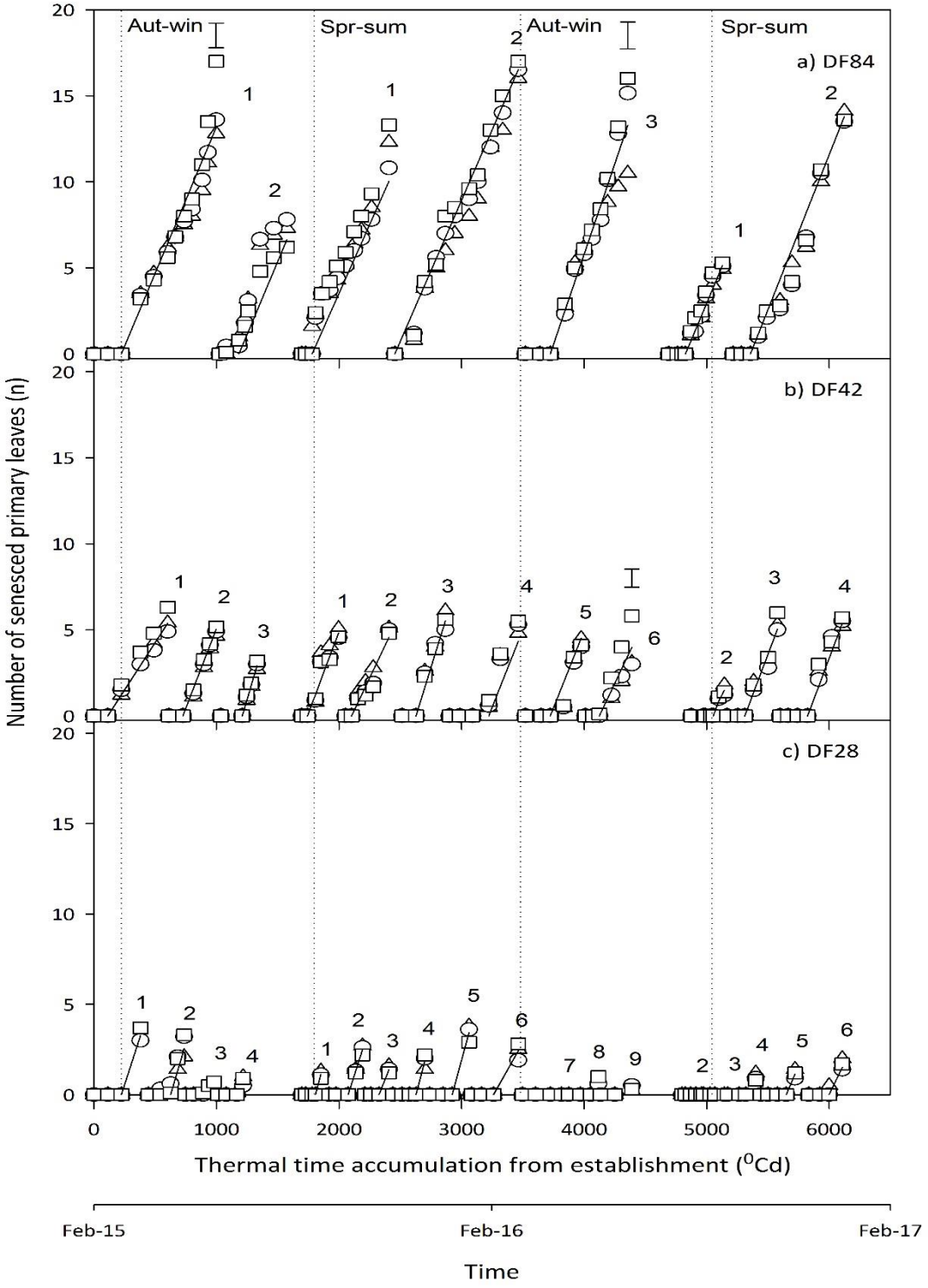


Figure 6.18 Number of senesced primary leaves on the main-shoot of three lucerne genotypes with fall dormancy (FD) ratings of 2 (Δ), 5 (O), and 10 (□) subjected to 28- (c), 42- (b) and 84 day (a) defoliation frequencies (DF) in the 2015, 2015/16 and 2016/17 regrowth year at Lincoln University, New Zealand.

Note: Error bars represent LSD (α=0.05) when differences occurred among genotypes. Thermal time accumulated using air temperature (T_b = 1 ^{0}C). Numbers (0-9) indicate the regrowth cycles.

After the first senesced leaf appeared, temperature was the main driver of subsequent leaf senescence. This was shown by the linear relationship (R^2>0.80) between the accumulated number of senesced leaves and accumulated thermal time within each regrowth cycle (Figure 6.18 a, b, c) (Appendix A.2; Table 0.5). In most cases, senescence rate was constant for all genotypes (R^2>0.80) within and among regrowth cycles. The exception was in the latter part of autumn regrowth cycles in DF84 crops (Cycle 1_2015 and Cycle 3_2015/16) and in DF42 crops (Cycle 6_2015/16), when the FD10 and FD5 genotypes senesced at a faster rate (P<0.05) than FD2.

6.3.3.5 Plant population

Plant population measured at the end of each regrowth cycle for all treatments is shown in Figure 6.19. Plant population followed the same pattern of decline throughout the growing seasons, but there were differences in final plant population among genotypes (p<0.001) and within DF regimes (p<0.05) (Table 6.1). Therefore, plant population of each genotype was investigated further and there was a differential response depending on DF regime (Figure 6.20).

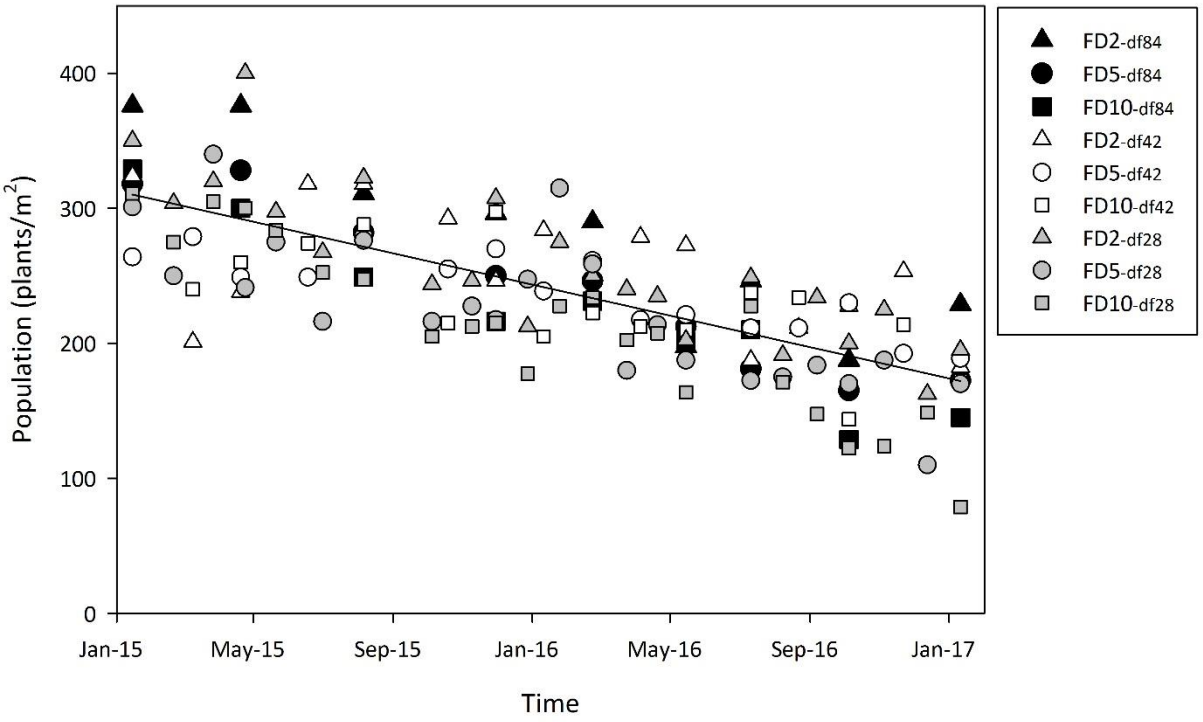


Figure 6.19 Plant population of three lucerne genotypes with fall dormancy (FD) ratings of 2 (Δ), 5 (O), and 10 (□) subjected to 28- (gray symbols), 42- (white symbols) and 84 day (black symbols) defoliation frequencies (DF) in the 2015, 2015/16 and 2016/17 regrowth year at Lincoln University, New Zealand.

Note: Linear regression (——) y= 329 - 0.19x (R^2=0.58).

Table 6.1 Plant population (plants/m^2) of lucerne genotypes with different fall dormancy (FD) ratings over a three regrowth period, defoliated at 28, 42 or 84 day intervals.

	Initial plant population at the start of DF application (15 January 2015) plants/m^2	Final plant population (11 January 2017) plants/m^2
FD2	328	213_b
FD5	295	171_a
FD10	316	144_a
P <	0.52	0.001
SEM	28	15
DF28	322	153_a
DF42	298	201_b
DF84	319	175_a
P <	0.24	0.04
SEM	13	12
FD x DF		
P<	0.85	0.23
SEM	43	25

The linear declines (Figure 6.20 a, b) demonstrated that plant population decreased at the same rate for all genotypes in a DF84 (0.23) and DF42 (0.12 plants/day) regime. However, under a 28 DF regime, the FD10 genotype declined at a rate of about 0.29 plants/day which was faster ($P<0.05$) than the 0.21 plants/day of FD2 and FD5 genotype (Figure 6.20 c). For DF regimes, plant population for the DF28 and DF84 declined at a rate of about 0.23 plants/day which was faster ($P<0.001$) than the 0.12 plants/day for the DF42 treatment (Figure 6.20 a, b, c). This meant at the end of the experiment DF42 averaged 201 plants/m^2 compared with 164 plants/m^2 for 28 and 84 day treatments (Table 6.1).

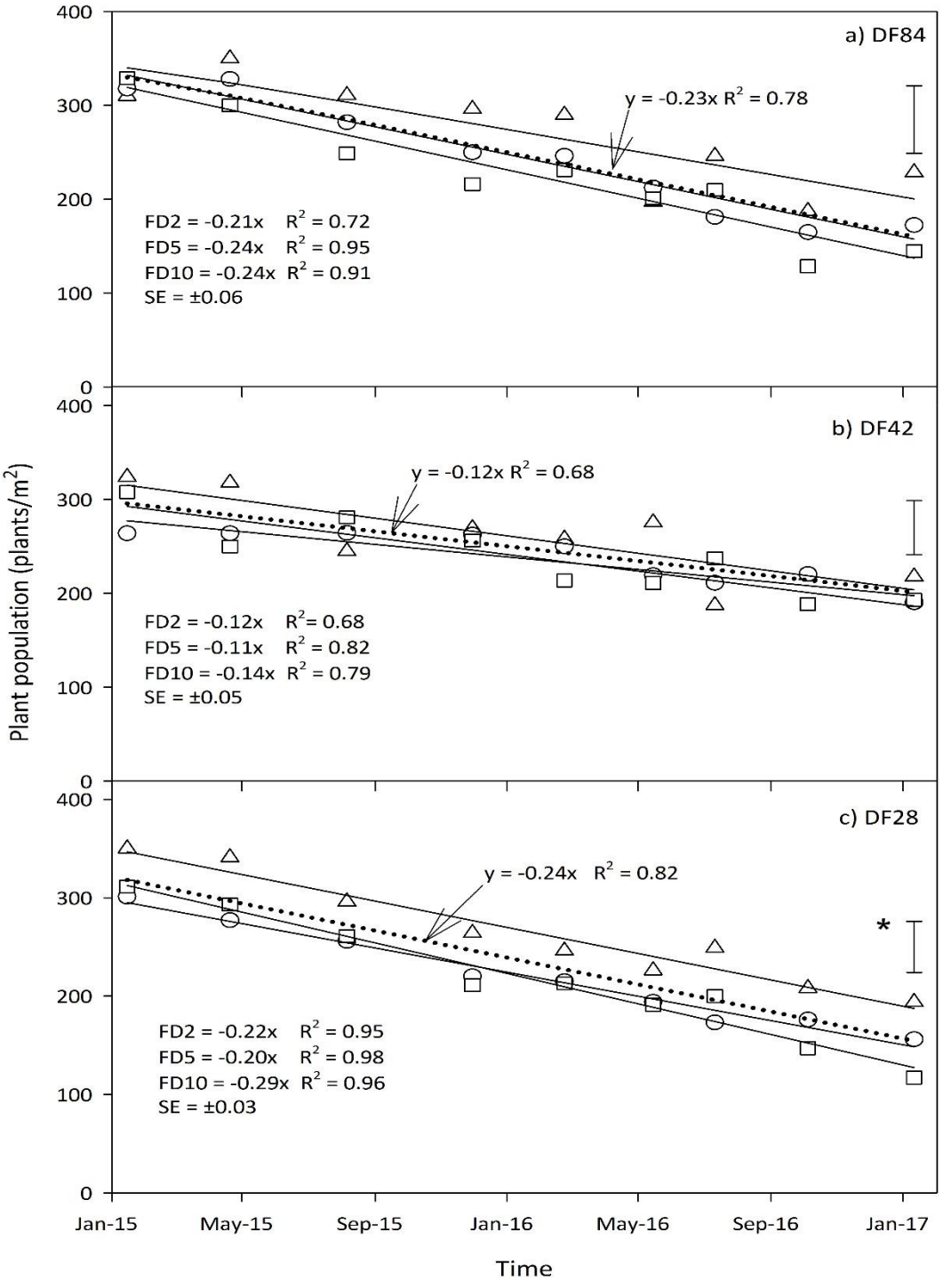


Figure 6.20 Plant population over time for three lucerne genotypes with fall dormancy (FD) ratings of 2 (Δ), 5 (O), and 10 (□) subjected to 28- (c), 42- (b) and 84 day (a) defoliation frequencies (DF) in the 2015, 2015/16 and 2016/17 regrowth year at Lincoln University, New Zealand.

Note: Data points are the average plant population of each two regrowth cycles for DF42 and three regrowth cycles for DF28 to align with DF84. Solid lines (—) represent regression for each genotype. Dotted lines (····) represent regression for all genotypes. Error bars represent LSD (α=0.05) for the final plant population. * represents P<0.05 when differences occurred among genotypes.

6.3.3.6 Shoot population

Shoot population of all lucerne genotypes ranged from 500 to 1000 stems/m^2 with an average of 700 stems/m^2, irrespective of plant population (Figure 6.21). However, under a DF28 regime FD10 was no longer maintaining 700 stems/m^2, when this genotype was at <120 plants/m^2 at the end of experiment.

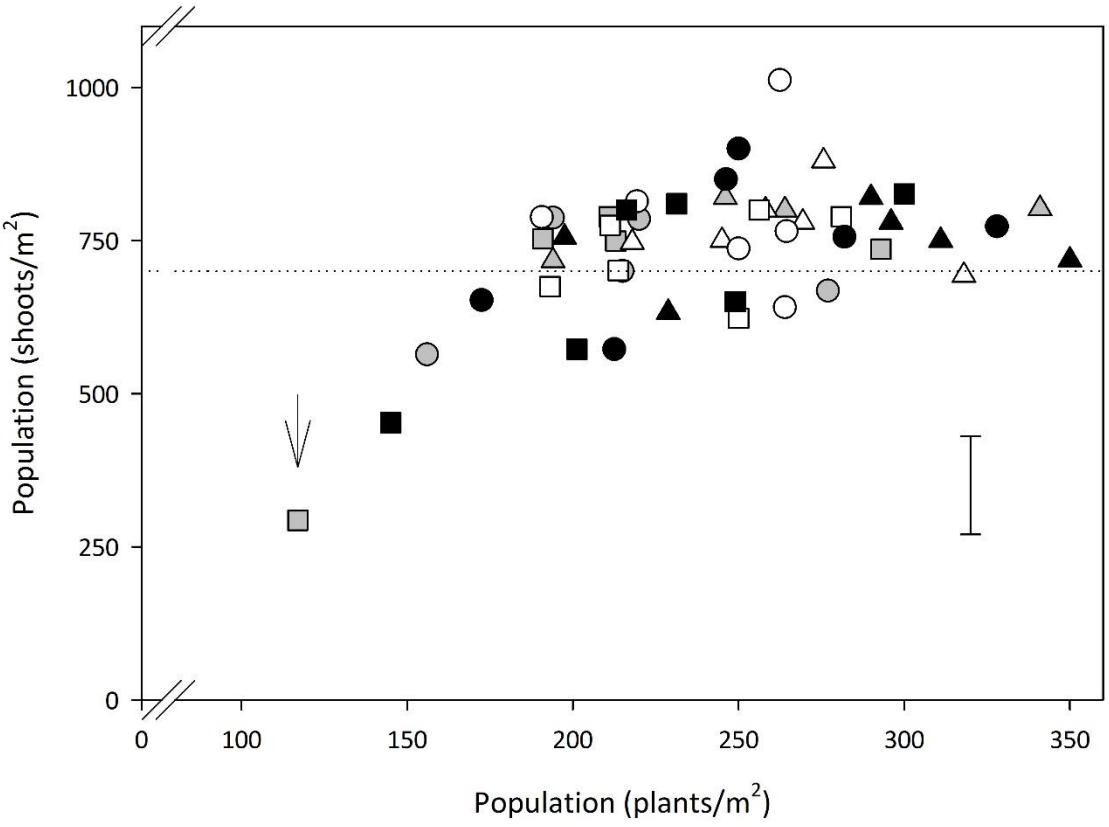


Figure 6.21 Shoot population against plant population of three lucerne genotypes with fall dormancy (FD) ratings of 2 (Δ), 5 (O), and 10 (□) subjected to 28- (gray symbols), 42- (white symbols) and 84 day (black symbols) defoliation frequencies (DF) in the 2015, 2015/16 and 2016/17 regrowth year at Lincoln University, New Zealand.

Note: Data points are the average shoot and plant population of each two regrowth cycles for DF42 and three regrowth cycles for DF28 to compare with DF84. Dotted lines (····) represents 700 stems/m^2. Error bars represent one SEM. Arrow indicates FD10 is at 250 stems/m^2 under a DF28 regime, at the end of the experiment.

To understand the mechanisms behind the changes in shoot population, the influence of plant population on shoots/plant was examined (Figure 6.22). An exponential model (R^2=0.55) described the increase in shoots/plant when plant population decreased to ≥150 plants/m^2 and this was unaffected (P<0.43) by genotype or DF regimes. Shoots/plant increased from about 2.2 at 350 plants/m^2 in January 2015 to 4.0 shoots/plant at 156 plants/m^2 (at the end of experiment) in January 2017. This pattern maintained the shoot population of about 700 stems/m^2 for the duration of this experiment. Under the DF28 regime, FD10 was only able to produce 2.5 shoots/plant when plant population decreased to <120 plants/m^2. This gave only 300 shoots/m^2 for FD10 at the end of experiment in January 2017.

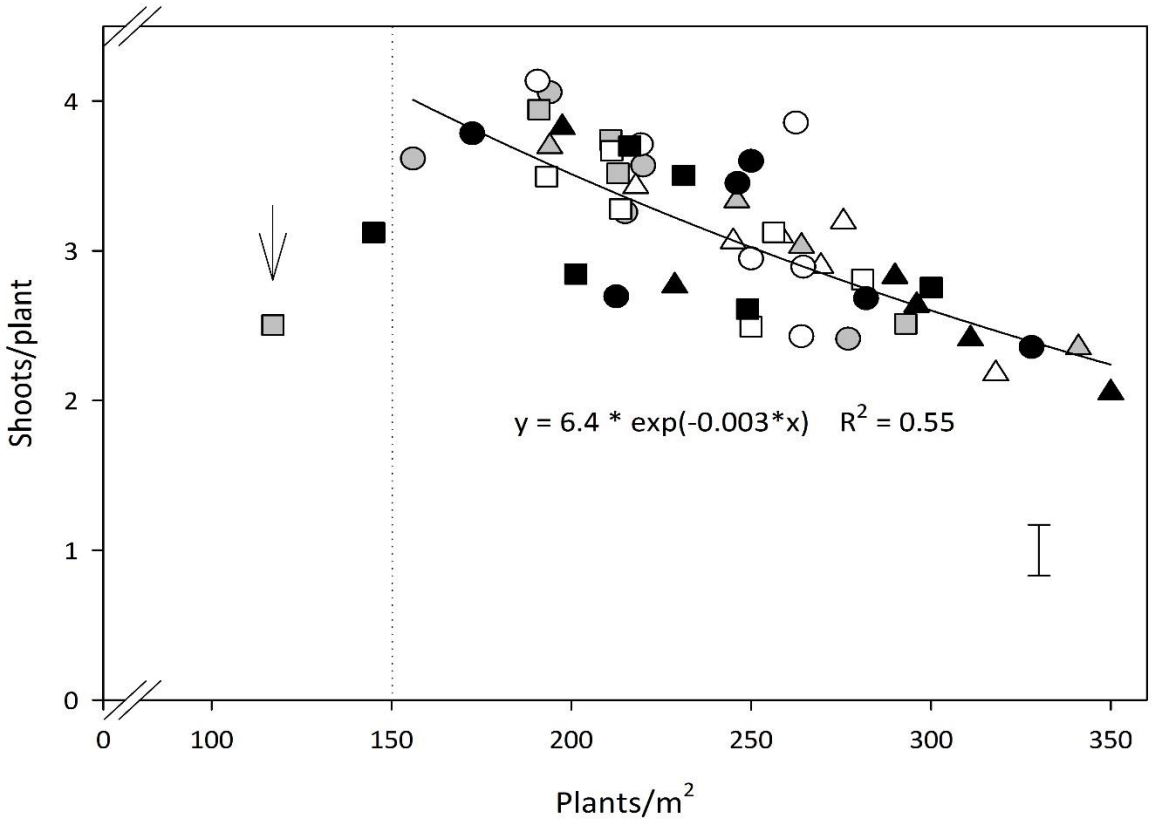


Figure 6.22 Shoots/plant against plant/m^2 of three lucerne genotypes with fall dormancy (FD) ratings of 2 (Δ), 5 (O), and 10 (□) subjected to 28- (gray symbols), 42- (white symbols) and 84 day (black symbols) defoliation frequencies (DF) in the 2015, 2015/16 and 2016/17 regrowth year at Lincoln University, New Zealand.

Note: Exponential solid line (——). Dotted line (····) represents a plant population of 150 plants/m^2. Arrow indicates FD10 with only 2.5 shoots/plant at plant population of <120 plants/m^2. Error bars represent one SEM.

6.3.4 Reproductive development

The time to reach 50% bud initiation is shown in Figure 6.23. For all genotypes, the number of days to reach bud initiation was fewer in summer than in early spring and autumn. For example, when the regrowth cycles started in September 2015, all genotypes required 45 days to reach 50% bud initiation while 23 days were needed when the regrowth cycles started in December 2015 or 2016. However, when all genotypes were grown in autumn, only FD10 reached bud initiation at about 41 days. As a result, genotypes that received a 28-day cutting interval only reached bud initiation in the summer regrowth period.

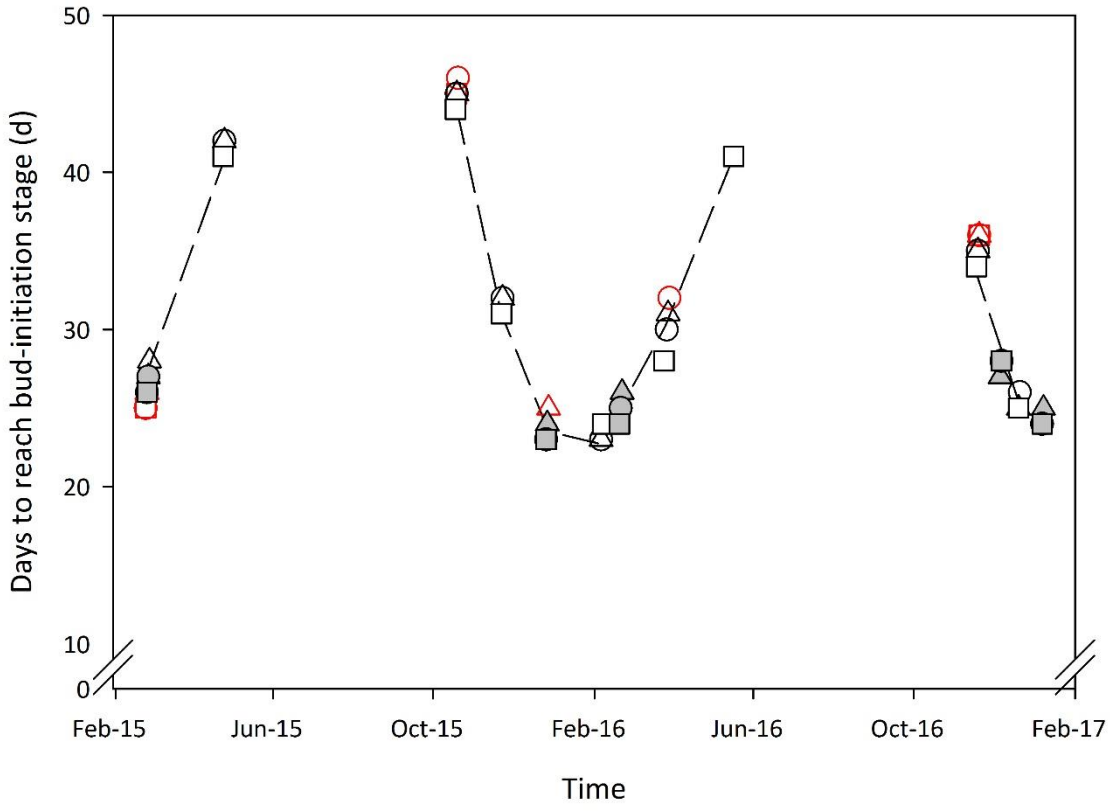


Figure 6.23 Number of days to reach the bud-initiation stage for three lucerne genotypes with fall dormancy (FD) ratings of 2 (Δ), 5 (O), and 10 (□) subjected to 28- (gray symbols), 42- (white symbols) and 84 day (red symbols) defoliation frequencies (DF) in the 2015, 2015/16 and 2016/17 regrowth year at Lincoln University, New Zealand.

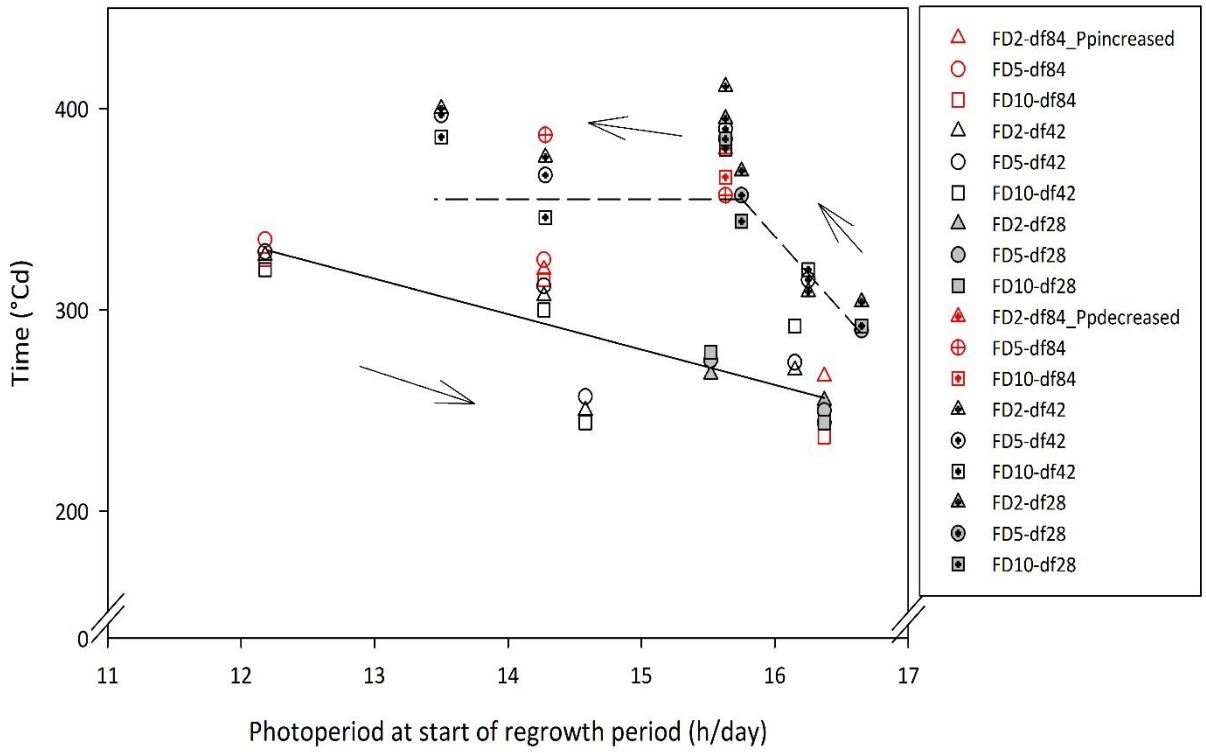


Figure 6.24 Thermal time requirement for 50% bud-initiation for three lucerne genotypes with fall dormancy (FD) ratings of 2 (Δ), 5 (O), and 10 (□) subjected to 28-, 42- and 84 day defoliation frequencies (DF) in response to increasing (symbols_Ppincreased) and decreasing (symbols_Ppdecreased) photoperiods during regrowth year at Lincoln University, New Zealand.

Note: Thermal time accumulated using air temperature (T_b = 1 ^{0}C). Linear regression solid line (——) y=544 -18x (R^2=0.70). Linear regression dashed line (----) y= 1527 – 74x (R^2=0.93). Dashed line (-----) y =350. Arrows represent the direction of photoperiod.

To explain the seasonal pattern of bud-initiation, the influence of photoperiod (Pp) at the start of the regrowth period on the thermal time requirement for bud initiation was investigated (Figure 6.24). The thermal time required to reach 50% bud initiation was consistent (P<0.65) among genotypes, but it responded to increasing and decreasing photoperiod. When genotypes were grown into increasing Pp, time to reach 50% bud initiation decreased (P<0.01) from 327°Cd at 12 h to 237°Cd at 16.4 h, an 18°Cd decrease for each additional daylight hour. When genotypes were grown into decreasing Pp, time to reach 50% bud initiation increased at a faster (P<0.01) rate of 74°Cd per hour from 290°Cd at 16.6 h to 350°Cd at 15.7 h, then it remained around 350°Cd below 15.7 h.

After bud-initiation, temperature was the main factor that led to the appearance of buds (bud visible), regardless of the direction of Pp. This is shown by the linear relationship (R^2>0.75) between the thermal

time to bud-initiation and thermal time required to reach visual bud stage (Figure 6.25). Based on the trend of the linear model (the solid line), the thermal time requirement from bud-initiation to bud visible was 12°Cd (the dash line), when genotypes were grown into increasing photoperiod. In contrast, it required 98°Cd to reach bud visible, when genotypes were growing into decreasing photoperiod (dotted line). This caused a longer time to reach flowering during the autumn-winter cycle. In addition, frosts occurred in the cool months that may damage buds and prevent flowering. This may be why in the DF84 crops, flowering was not apparent in the autumn-winter cycle in year 2015 (Cycle 1 and 2) and year 2015/16 (Cycle 3).

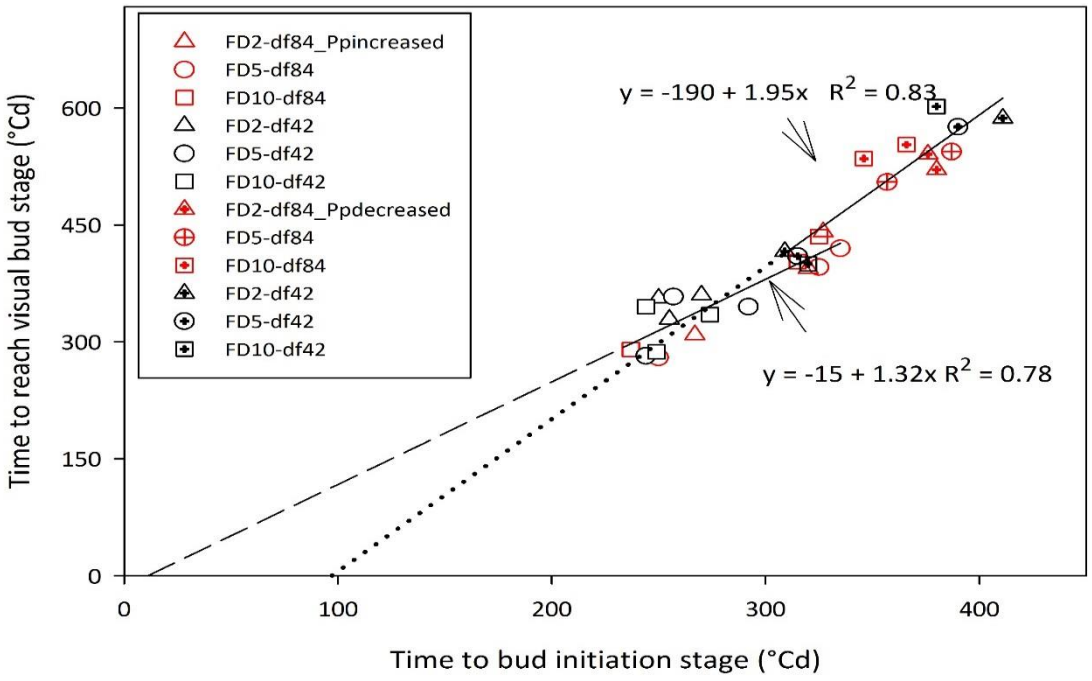


Figure 6.25 Thermal time requirement for 50% bud-initiation in relation to 50% buds visible for three lucerne genotypes with fall dormancy (FD) ratings of 2 (Δ), 5 (O), and 10 (□) subjected to 42- and 84 day defoliation frequencies (DF) in response to increasing (symbols_Ppincreased) and decreasing (symbols_Ppdecreased) photoperiods during regrowth year at Lincoln University, New Zealand.

Note: Thermal time accumulated using air temperature (T_b = 1 ^{0}C). Dash line (– – –) represents for the y-intercept of 0°Cd at x=12°Cd. Dotted line (····) represents the y-intercept of 0°Cd at x=98°Cd.

The number of nodes at the time of early bud visible appears related to the direction of photoperiod (Figure 6.26). When genotypes were growing in an increasing Pp, stems had about 16 nodes when they flowered in a 12h photoperiod but 11 nodes when the photoperiod was 16.4h. This indicated a linear decrease of 1.15 nodes for each additional daylight hour. When genotypes were growing in a decreasing Pp, the number of nodes at bud visible increased at a faster ($P<0.05$) rate of 7.8 per hour from 11 nodes at 16.3 h to 15 nodes at 15.6 h. It then remained around 15 nodes even when the photoperiod dropped below 15.6h. For all crops, the minimum number node sets the earliest time to bud visible which was around 10 nodes, regardless of Pp. This suggests that at least 9 nodes were required for crops to finish their vegetative phase and transition to the reproductive phase.

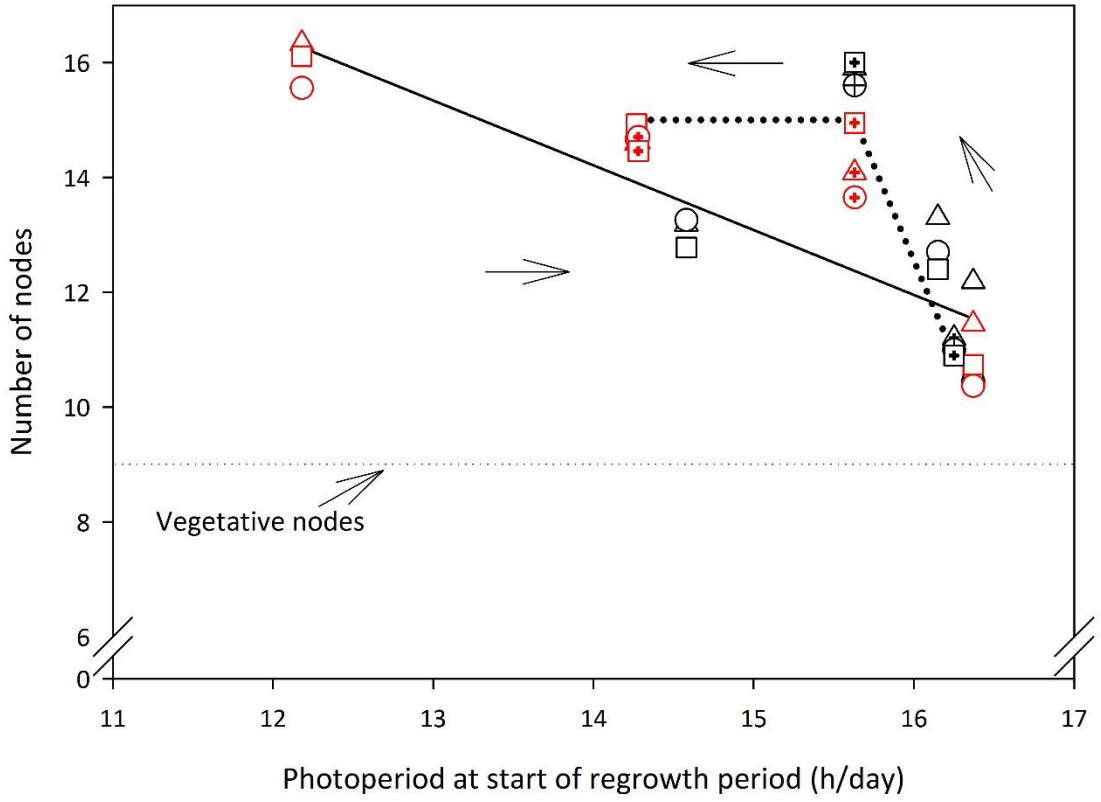


Figure 6.26 Number of nodes to first bud-visible for three lucerne genotypes with fall dormancy (FD) ratings of 2 (Δ), 5 (O), and 10 (□) subjected to 42- (white symbols) and 84 day (red symbols) defoliation frequencies (DF) in response to increasing (non-dotted symbols) and decreasing (dotted- symbols) photoperiods during regrowth year at Lincoln University, New Zealand.

Note: Linear regression solid line (——) y= 30.5 -1.15x (R^2=0.72). Linear regression dotted line (····) y= 138 – 7.8x (R^2=0.99). Dotted line (····) y =15. Arrows represent the direction of photoperiod.

6.4 Discussion

These results indicate that phenological development (phyllochron, branching, canopy structure and leaf senescence) and reproductive development (flowering) were conservative among FD ratings. In contrast, vegetative growth (leaf area expansion and stem elongation) was most closely correlated with fall dormancy ratings, particular in atumn period.

6.4.1 Radiation interception

The amount of radiation intercepted by the canopy explained 94% of the differences in accumulated shoot DM yield among lucerne crops (Figure 6.5). Because the fraction of radiation intercepted increased exponentially with LAI (Figure 6.6), a reduction in canopy expansion reduced the amount of energy captured and used for growth. Therefore, lower shoot yield in DF28 crops was mainly attributed to the lower in amount of radiation intercepted (Figure 6.4 a, b, c). Similarly, the greater autumn yield or the lower spring growth of the FD10 genotype were also explained by the higher/lower amount of radiation intercepted by this genotype, relative to the other two.

Nevertheless, shoot yield of lucerne crops also depends on the efficiency of conversion of intercepted radiation into biomass (RUE) and on partitioning this biomass into shoot and root organs (Lemaire *et al.*, 1992; Teixeira *et al.*, 2008). The linear relationship between total shoot DM yield and total accumulated intercepted radiation in Figure 6.5 suggests that there may have been seasonal and treatment differences in RUE for shoots and total (shoots plus roots) biomass. This physiological mechanism will be examined in Chapter 7.

To understand the processes that caused the different patterns of radiation interception among genotypes or between DF regimes the components of canopy formation were quantified.

6.4.2 Canopy architecture

The canopy architecture was quantified by the light extinction coefficient (k) which defined the efficiency of interception per unit of leaf area (Hay and Porter, 2006). In this study, no differences in canopy architecture were found among genotypes or between DF regimes (Figure 6.3). All crops had a similar k value of 0.83 and this is consistent with previous reports that found little variation in k among genotypes (Gosse *et al.*, 1988; Thiébeau *et al.*, 2011) or between defoliation treatments (Teixeira *et al.*, 2007b). This high and stable k for all crops indicated that canopy structure was unaffected by genotypes and defoliation treatments. Therefore, the difference in the amount of radiation intercepted could be explained by variation of LAI rather than canopy architecture.

6.4.3 Canopy expansion

DF28 crops intercepted less radiation because harvests occurred before canopy closure to the critical leaf area index (LAI_{crit}) of 3.5 (Figure 6.7 a, b, c). Also, this caused a subsequent delay in time to reach complete radiation interceptance (Figure 6.6) and therefore reduced shoot growth rate (Section 5.3.1.3) and yield (Section 5.3.1.1). The lower LAI in DF28 crops was explained predominantly by slower leaf area expansion rate (LAER). This was 50 and 62% lower during the main spring-summer growth periods than DF42 and DF84 crops, respectively (Figure 6.8 a, b, c). This is consistent with the observation by Teixeira *et al.* (2007b), who reported a slower LAER for a 28 than a 42 day lucerne crop grown in a similar environment.

With regards to FD ratings, greater autumn growth of FD10 appeared related to the LAI (Figure 6.7) and plant height (Figure 6.16). This strategy of elongating shoot length resulted in higher shoot yield (Section 5.3.1.1) but also produced a higher un-palatable proportion (Section 5.3.2.1) because of increased lignification to support the extra height (Christian *et al.*, 1970). Higher LAI for FD10 was explained by LAER which was 22% faster during autumn than FD2 and FD5 (Figure 6.8). However, all genotypes had a similar LAER during the main spring-summer growth (Figure 6.8). This explains why there were no differences in LAI (Figure 6.7), and therefore no differences in amounts of radiation intercepted and yield during this time. The seasonal change in the pattern of LAER appears related to photoperiod at the start of each regrowth cycle. For example, LAER was consistent for all genotypes when they were growing in an increasing Pp (Figure 6.9 a, b). In contrast, LAER was faster for FD10 than FD2 and FD5 genotypes when crops were growing in a decreasing Pp (Figure 6.9 a, b). Nevertheless, the priority of autumn LAER for FD10 was less consistent in a 28 day regime (Figure 6.8 c). This is demonstrated by these results which showed no differences in the slope of the regression between LAER and Pp (Figure 6.9 c). By the final regrowth season (11 January 2017), FD10 experienced a slower LAER than FD2 despite crops growing in an increasing Pp (Figure 6.8 c). This suggests LAER was not solely driven by photoperiod and potential other causes are discussed in Chapter 7.

The development of the individual leaf area mainly explained the differences in LAER (Figure 6.10). Crops defoliated at 28 day intervals had the smallest individual leaf area which was 50 and 65% smaller than DF42 and DF84 crops. Leaf growth depends strongly on the availability of N for cell division and expansion (Avice *et al.*, 1996). Increased defoliation frequency has been shown previously to reduce endogenous N in taproots, across a range of FD ratings (Gramshaw *et al.*, 1993; Avice *et al.*, 1997a; Meuriot *et al.*, 2005). Therefore, lower individual leaf size in DF28 crops could be due to less N underground reserves which can reduce photosynthetic capacity and canopy expansion rates of the earliest initiated leaves (Teixeira *et al.*, 2008).

To understand the mechanisms responsible for the differences in LAER, the components of canopy development processes (leaf appearance and branching, and shoot population) were quantified.

6.4.4 Canopy developmental processes

Leaf appearance was influenced by DF regimes but was less influenced by FD ratings. Primary leaf appearance, quantified by phyllochron was consistent at ≤30°Cd/primary leaf for all crops experiencing an increasing Pp (Figure 6.13). This suggests temperature was the main driver of primary leaf appearance during the spring-summer. This is illustrated in Figure 6.12 which shows no differences in phyllochron among genotypes or between DF regimes during this time. Fick *et al.* (1988) and recently Teixeira *et al.* (2007b) reported phyllochron remained constant during spring/summer regardless of defoliation treatments or genotypes. However, phyllochron increased to ≥30°Cd/primary leaf for all crops experiencing a decreasing Pp (Figure 6.13). This is consistent with previous reports of lucerne grown in a similar environment (Brown *et al.*, 2005b; Teixeira *et al.*, 2007b; Sim, 2014). A longer phyllochron during the autumn period suggests that primary leaf appearance could not be explained solely by photoperiod and potentially there are other causes. A possibility suggested by Brown *et al.* (2005b) is that the supply of carbon to shoot growth is limited to meet potential demand for forming new basal leaves. This is because the biomass demand from crown and taproot organs imposes a strong competition for assimilate during the autumn period (Teixeira *et al.*, 2007c) which limits C and N supply to shoots (Avice *et al.*, 1997b). This is demonstrated in Figure 6.13 whereby crops with shortest regrowth cycles (DF28) are expected to have limited root storage (sink). This may have reduced new basal bud initiation and therefore increased the phyllochron for all genotypes at a rate of 3.8°Cd/h for each 1 hour decrease in photoperiod (Figure 6.13 c).

Nevertheless, branching rate was driven by temperature and conservative for all crops (Figure 6.15). Crops produced their first axillary leaf when the 4th primary leaf was fully expanded and then progressed linearly consistent with primary leaf appearance (Figure 6.14). It is known that in dicotyledonous crops, branching development is influenced by plant population (Hay and Porter, 2006) which then determines shoot population. This is because the distribution of radiation quality and quantity are altered by shading around plants and there is a decrease in the spectral radiation (e.g. the red/far red ratio) which can restrict branch development (Thompson, 1993). In this study, shoot population was consistent for all crops (Figure 6.21), which were likely maintained by changes in shoot number per plant (Figure 6.22). Therefore, similar shoot populations could be expected in that all crops have the same shading effect and consequently similar branching.

However, developmental processes are known to be affected by assimilate supply under extreme pressure (Grant and Barthram, 1991). This may explain the less consistent results for the FD10 genotype over the 24 month period of growth. Under a 28 DF regime, the FD10 population declined at

a rate of 0.29 plants/day which was faster than the FD2 or FD5 population (Figure 6.20 c). As a consequence of faster self-thinning, it had only 120 plants/m^2 by 11 January 2017. At this time, FD10 was unable to maintain a high stem population (Figure 6.21). Therefore, the lower shoot yield during the spring period for FD10 could be attributed to its lower LAI (Figure 6.7 c) and therefore less radiation interception and biomass accumulation.

6.4.5 Leaf senescence

The rate of primary leaf senescence was driven by temperature and was consistent for all crops (Figure 6.18). It is known that stresses including N deficiency can reduce the lifespan of leaves (Hay and Porter, 2006). However, the limited root storage created in DF28 crops did not enhance the remobilisation of assimilate source from older leaves to form a new one. The primary leaf senescence response appears related to the direction of photoperiod at the start of regrowth. When genotypes were growing in an increasing Pp, senescence commenced at the time of appearance of the 5th primary leaves on the main-stem (Figure 6.17 a). In contrast, when genotypes were growing in a decreasing Pp, the first senesced leaf occurred at the time of appearance of the 7th primary leaf on the main-stem (Figure 6.17 b). This suggests the seasonal recycling of the resource could promote the earlier death of the leaves. Time to first leaf senescence was longer in autumn which may be caused by less partitioning of assimilates to storage organs during this time (Teixeira *et al.*, 2007c).

6.4.6 Reproductive development

The rate of reproductive development was consistently slower in a decreasing Pp and faster in an increasing Pp environment (Figure 6.24). This field observation was consistent with classic treatment of lucerne a long-day plant as observed in a previous field trial (Teixeira *et al.*, 2011) and control environment conditions (Major *et al.*, 1991). The linear regression shown in Figure 6.24 indicates a minimum requirement of 237°Cd and 350°Cd for genotypes to finish their vegetative phase when they grew into increasing or decreasing Pp, respectively. Given a phyllochron of 28°Cd in an increasing Pp and 37°Cd in a decreasing Pp, this would equal to 8 - 9 primary leaves before transition to reproductive phase (Figure 6.26). It is known that a genotype must be finished the vegetative phase before it transitions to the reproductive phase (Major, 1980). The slower phyllochron in a decreasing Pp environment (Figure 6.13) could lengthen the time to produce sufficient leaves for crops to complete their vegetative phase. Therefore, a slower rate of development vegetative in a decreasing Pp environment could delay the time to reach the reproductive phase for genotypes growing during this period (Figure 6.24). In autumn 2016 from a 42 day regime, only FD10 reached bud initiation (Figure 6.23) due to the faster phyllochron (Figure 6.13 b) of this genotype which consequently finished its period of juvenility and transited to the reproductive phase earlier than the FD2 and FD5 genotypes.

The transition from bud initiation to bud visible was driven by temperature but was also influenced by the direction of Pp. In an increasing Pp, the thermal time from bud-initiation to bud visible was 12°Cd but it increased to 98°Cd when genotypes grew into a decreasing Pp (Figure 6.25). For example, at a Pp shorter than 15.5h, 15 nodes would appear at time of bud visible in all crops. In contrast, at a Pp longer than 15.5h, a minimum of 12 nodes had formed to set bud visible (Figure 6.26). This caused a longer time to reach flowering when genotypes grew in a shorter Pp and is consistent with literature of a long-day plant grown under control environmental conditions (Major *et al.*, 1991).

The practical implication of this result is that grazing or cutting management decisions based on the time of flowering should be adapted across dormancy groupings and defoliation regimes. For example, historic recommendations to harvest lucerne at 10% flowering (Smith, 1972) will result in crops of different yield and age being harvested in spring, summer and autumn. Furthermore, more recent suggestions to ignore the 10% flowering and only allow lucerne to flower in autumn (Moot *et al.*, 2003) need a caveat that flowering may not occur later in autumn. The aim of this latter recommendation is to encourage the replenishment of root reserves. In the next chapter we will see how partitioning is affected by photoperiod at flowering.

6.5 Conclusions

Based on the results from this chapter;

- Accumulated amounts of radiation intercepted explained most (R^2=0.94) of the differences in DM accumulation among genotypes and among DF regimes.

- The differences in radiation intercepted were mainly due to differences in the development of individual leaf area, through changes in leaf area expansion rates, which were always smaller in DF28 crops.

- Canopy structure was unaffected by DF regimes or FD ratings and k had a consistent value of 0.83 for all crops.

- Phyllochron was conservative but was related to the direction of Pp. It was ≤30°Cd with an increasing Pp and ≥30°Cd with a decreasing Pp. Branching, shoot population and leaf senescence were consistent for all crops. These values could be used in of crop simulation models.

- With regards to FD ratings, the higher autumn shoot yield of the FD10 genotype came from a faster stem elongation rate and greater individual leaf area that allowed more radiation to be intercepted and therefore more biomass accumulation. Lower spring yield in FD10 was mainly due to fewer shoots per plant which meant it was unable to maintain the 700 stems/m^2 population needed to maximise yield.

- Environmental factors (temperature and Pp) had a pronounced influence on the phasic transition and development of regrowth lucerne crops. In a decreasing Pp environment, crops needed a longer time to complete the vegetative phase before transition to the reproductive phase than in an increasing Pp. This is because, the slower phyllochron in the shorter Pp created a delay in the time to produce the potential leaf number required for crops to complete the vegetative phase. As a consequence, time to flowering was longer in a decreasing Pp.

In the following chapter the efficiency of conversion of radiation intercepted in terms of shoot DM and total DM (shoots plus roots) will be examined.

Chapter 7 Root dry matter, RUE and biomass partitioning

7.1 Introduction

In Chapter 6 the differences in shoot yield among DF treatments and among genotypes were explained by differences in amounts of radiation intercepted by the canopy (R^2=0.94) with an assumed annual RUE for shoot dry matter (RUE_{shoot}) of 0.5 g DM/MJ total solar intercepted radiation. However, RUE_{shoot} may differ in response to seasons because the partitioning of biomass to taproot and crown (P_{root}) changes within regrowth cycles and between seasons as discussed in Section 2.5.

In Chapter 5, non-dormant (FD10) lucerne exhibits higher shoot growth rates in autumn (Section 5.3.1, Figure 5.3). This differences in shoot growth rate might influence the partitioning of dry matter to crown and taproot and ultimately may affect production and persistence of lucerne crops. The physiological mechanisms involved in these processes are unknown or insufficiently quantified to be predictive.

Thus, the objective of this chapter is to investigate whether yield differences observed in Chapter 5 were also associated with variations of RUE and partitioning of dry matter by analysing RUE_{shoot}, RUE_{total} and P_{root}. The defoliation regimes were used to create crops with different levels of root reserves, to examine how the physiological responses differ among FD ratings.

7.2 Material and methods

The description of the experimental design, treatments and agronomic management were presented in Section 3.3. In this chapter, only additional measurements related to results of this chapter are reported.

7.2.1 Sampling of crown and taproot dry matter (DM)

Samples of crowns and taproots were taken at the end of each regrowth cycle by using 0.2 m^2 quadrat placed randomly in each plot. During year 1 (2015) and year 2 (2015/16), intermediate measurements were also taken at 28-day or 14 day intervals before the 42-day regrowth crops were harvested. Similarly, for 84-day regrowth cycles, intermediate measurements were taken at the mid-point after 42-days. Shoot samples were initially harvested using hand shears to cut all shoots just above crown height (Section 5.1.2). A root sample (crowns + taproots) was then obtained from the same quadrat by digging a trench to a depth of 300 mm. Materials were washed clean of soil and crowns were separated from taproots at the transition zone between tissues. Taproots were trimmed to 300 mm then samples were dried in a forced-air oven set to 60°C until a constant weight was achieved.

7.2.2 Radiation use efficiency for shoot DM

Radiation use efficiency (RUE_{shoot}; g DM/MJ intercepted total solar radiation) was calculated by the slope of the regression between mean shoot dry matter (g DM/m^2) against the amounts of accumulated intercepted solar radiation (MJ/m^2) for each regrowth period. Measurement of shoot dry matter was described in Section 5.2.1. The amount of solar radiation intercepted was estimated as presented in Section 6.2.5.

7.2.3 Radiation use efficiency for total DM

Radiation use efficiency for total DM (RUE_{total}) represented the efficiency of conversion of radiation energy into total crop DM. Total crop DM was calculated as the sum of shoot DM (DM_{shoot}) plus crown and 300 mm of taproot DM (DM_{root}). When DM_{root} was stable or declined, RUE_{total} was omitted for that regrowth cycle because, at this time, reserves can be mobilised from the root mass and allocated to the above ground fraction (Teixeira *et al.*, 2007b). This resulted in 23 estimates of RUE_{total} from 42 available regrowth cycles.

7.2.4 Dry matter partitioning to crown and taproot

Fractional dry matter partitioning to crown and taproot (P_{root}) was calculated as the reciprocal of the relationship between RUE_{shoot} and RUE_{total} as proposed by Brown *et al.* (2006) and is presented below;

$$P_{root} = 1 - RUE_{shoot}/RUE_{total}$$

Fractional partitioning was plotted against the photoperiod at start of each regrowth period (Pp) and air temperature (T_{air}) to test how these influence P_{root}. This analysis was segmented into periods of increasing versus decreasing Pp, because the photoperiod direction change may influence the partitioning response of lucerne (Brown *et al.*, 2005b) and has been shown to affect crop development (Chapter 6).

7.3 Results

7.3.1 Crown and taproot dry matter (DM)

Figure 7.1 shows the linear relationship (R^2=0.83) between crown DM and taproot DM for all genotypes and DF regimes over all regrowth periods. This strong relationship suggested that both perennial organs of all genotypes responded in a similar way to environment signals and defoliation treatments. Thus, for all subsequent analyses crown and taproot DM were summed to represent below-ground dry matter “root DM” as distinguished from above-ground dry matter “shoot DM”.

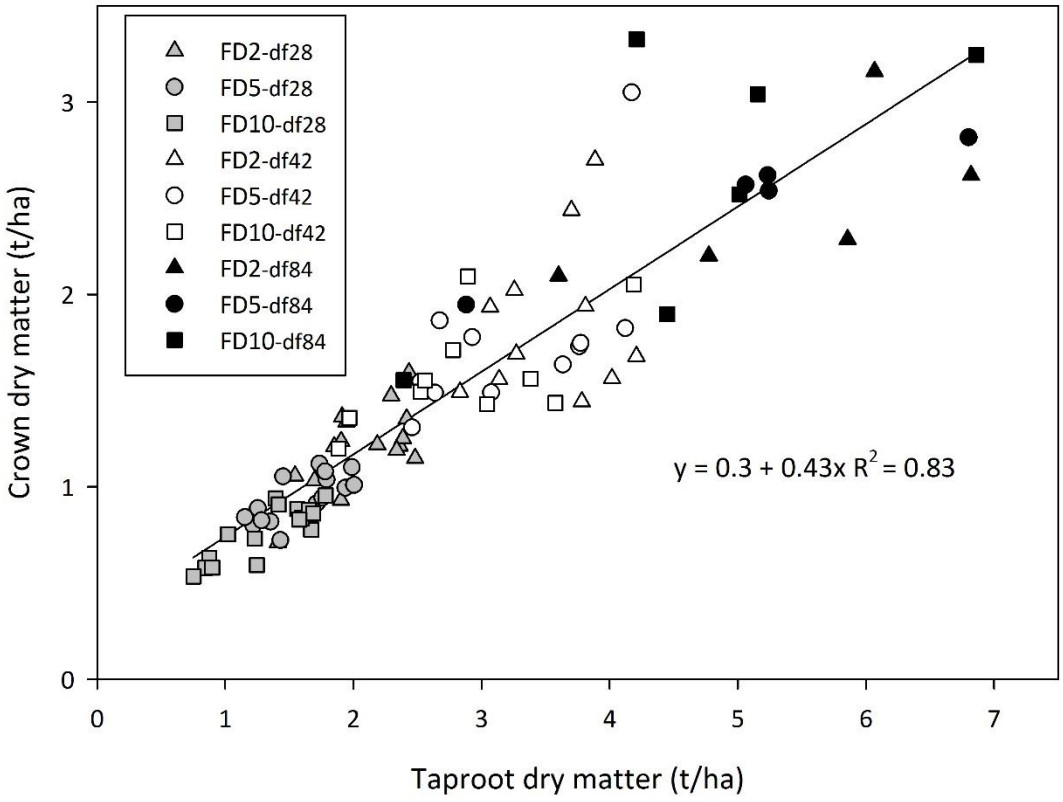


Figure 7.1 Relationship between crown dry matter (DM) and taproot DM to 30 cm depth of three lucerne genotypes with fall dormancy (FD) ratings of 2 (Δ), 5 (O), and 10 (□) subjected to 28- (gray symbols), 42- (white symbols) and 84 day (black symbols) defoliation frequencies (DF) in the 2015; 2015/16 and 2016/17 regrowth years.

7.3.2 Seasonal root dry matter (DM)

Figure 7.2 shows the seasonal patterns of root DM of each genotype and defoliation regime throughout the regrowth years.

Root DM changed ($P<0.01$) through each growth season, being greatest ($P<0.01$) during autumn and lowest during spring for all DF regimes. DF84 crops always had higher ($P<0.001$) root DM followed by DF42 crops and the lowest root DM was in DF28 crops. For example, in autumn 2015/16, maximum root DM in DF84 crops was 9.7 t DM/ha (Cycle 3) compared with 5.5 t DM/ha for DF42 (Cycles 5 and 6) and 2.9 t DM/ha (Cycles 7, 8 and 9) for DF28 crops (Figure 7.2 a, b, c). Over the three regrowth years, DF regimes accumulated root DM in excess of 3.0 t DM/ha for all 42 day regrowth cycles and 6.0 t DM/ha for all 84 day regrowth cycles (Figure 7.2 a, b). In contrast, the root DM of all genotypes in the 28 day regrowth treatment was ～3.0 t DM/ha, with the exception of the first DF28-Cycles 5 and 6 in August 2015 (Figure 7.2 c).

Irrespective of DF regimes, in the first autumn-winter (2015) all genotypes showed an increase in root DM accumulation from summer reaching maximum root weight in autumn (June 2015). During this period, FD10 grown in the 42 day regrowth cycle had a higher ($p<0.05$) root yield than FD2 and FD5 in Cycle 2 (Figure 7.2 b).

In the following spring-summer (2015/16), the root biomass from the previous autumn-winter season declined rapidly to minimum values for all genotypes in spring before increasing again in summer (Figure 7.2 a, b, c). For example in DF42 crops, the last cycle in the previous autumn-winter season (Cycle 4) had an average root yield of 7.8 t DM/ha for all genotypes. From this time, root biomass decreased ($P<0.001$) for all genotypes to a minimum of 3.7 t DM/ha in spring (October 2015) and then increased ($P<0.001$) to be 5.6 t DM/ha in summer (January 2016) (Figure 7.2 b). The pattern of root biomass change during this period was similar in the DF84 and DF28 crops (Figure 7.2 a, c).

The separation of root weight among genotypes occurred in the autumn-winter (2015/16) with lower ($p<0.05$) root biomass recorded for the FD10 genotype, particularly in DF28 crops (Figure 7.2 c). Under a 28 day defoliation regime, the FD10 genotype was unable to recharge to 3.0 t DM/ha in autumn (Cycle 7, March 2016). This decline persisted during winter and throughout the next spring-summer regrowth. By the end of the experiment on 11 January 2017, FD10 had the lowest ($p<0.05$) root biomass of 1.5 t DM/ha compared with 3.7 t DM/ha for the FD2 and FD5 genotypes. Interestingly, under a 42 day defoliation regime, FD10 produced a higher ($p<0.05$) root yield in autumn (Cycle 5, April 2016) but declined faster ($p<0.05$) throughout winter and spring than the FD2 genotype (Figure 7.2 b). However, in the summer period, root DM increased to 6.0 t DM/ha for FD10, similar to the other genotypes. In addition, genotypes grown on 84 day regrowth cycles had similar root biomass throughout regrowth seasons (Figure 7.2 a).

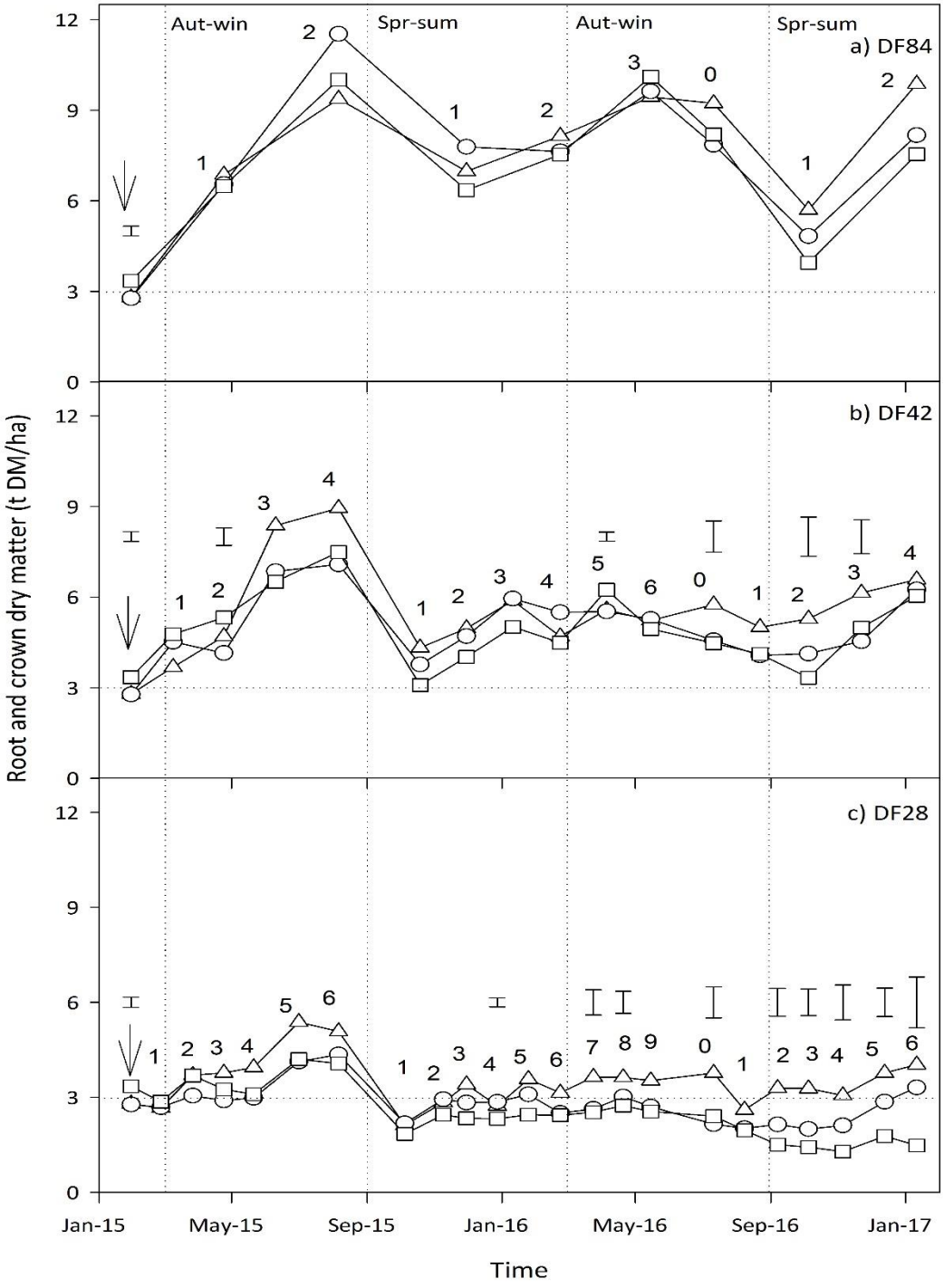


Figure 7.2 Seasonal crown plus taproot dry matter (DM) at the end of each regrowth cycle of three lucerne genotypes with fall dormancy (FD) ratings of 2 (Δ), 5 (O), and 10 (□) subjected to 28- (c), 42- (b) and 84 day (a) defoliation frequencies (DF) in the 2015, 2015/16 and 2016/17 regrowth year at Lincoln University, New Zealand.

Note: Error bars represent LSD (α=0.05) when differences occurred among genotypes. Numbers (0-9) indicate the regrowth cycles. Dotted line (····) represents average root DM of 3.0 t DM/ha. Arrows indicate root DM for all genotypes at the end of seedling phase.

7.3.3 Seasonal shoot RUE (RUE_{shoot})

The RUE_{shoot} of three FD ratings is shown in Figure 7.3 for each regrowth cycle throughout the three regrowth years.

For DF regimes, crops defoliated at 84 day intervals did not follow a seasonal pattern with an overall average ($p<0.18$) of 0.79 g DM/MJ (Figure 7.3 a). However, RUE_{shoot} in DF42 crops changed ($p<0.05$) seasonally, being lower in winter and higher in autumn (Figure 7.3 b). For example, the RUE_{shoot} of DF42 crops increased ($p<0.001$) from 0.56 g DM/MJ in October 2015 (early spring) to 0.73 g DM/MJ in late May 2016 (autumn) before decreased to 0.37 g DM/MJ in August 2016 (winter). Crops grown under a 28 day defoliation regime experienced a decline in RUE_{shoot}. From the beginning of the experiment in February 2015 (late summer), the RUE_{shoot} of DF28 crops was 0.61 g DM/MJ which was higher ($p<0.001$) than 0.44 g DM/MJ by the end of the experiment on January 2017 (mid-summer) (Figure 7.3 c). Overall, DF84 crops always had the highest ($P<0.001$) RUE_{shoot}, followed by DF42 crops and the lowest RUE_{shoot} was in DF28 crops. For example, during spring-summer 2015/16, RUE_{shoot} in DF84 crops at 0.78 g DM/MJ was higher ($P<0.001$) than the 0.56 g DM/MJ for DF42 crops and 0.45 g DM/MJ for DF28 crops (Figure 7.3 a, b, c).

With regards to FD ratings, the FD10 genotype defoliated with a 42- and 84 day intervals during autumn had a 40% higher ($p<0.05$) RUE_{shoot} than FD2 genotype (Figure 7.3 a, b). However, the advantage in RUE_{shoot} of the winter-active (FD10) genotype during colder months was not consistent in DF28 crops (Figure 7.3 c). Under a 28 day defoliation regime, this genotype had higher ($p<0.05$) RUE_{shoot} in the first autumn regrowth in April 2015 (Cycle 2). But the RUE_{shoot} was not different ($p<0.65$) among genotypes in the following regrowth cycles (Figure 7.3 c).

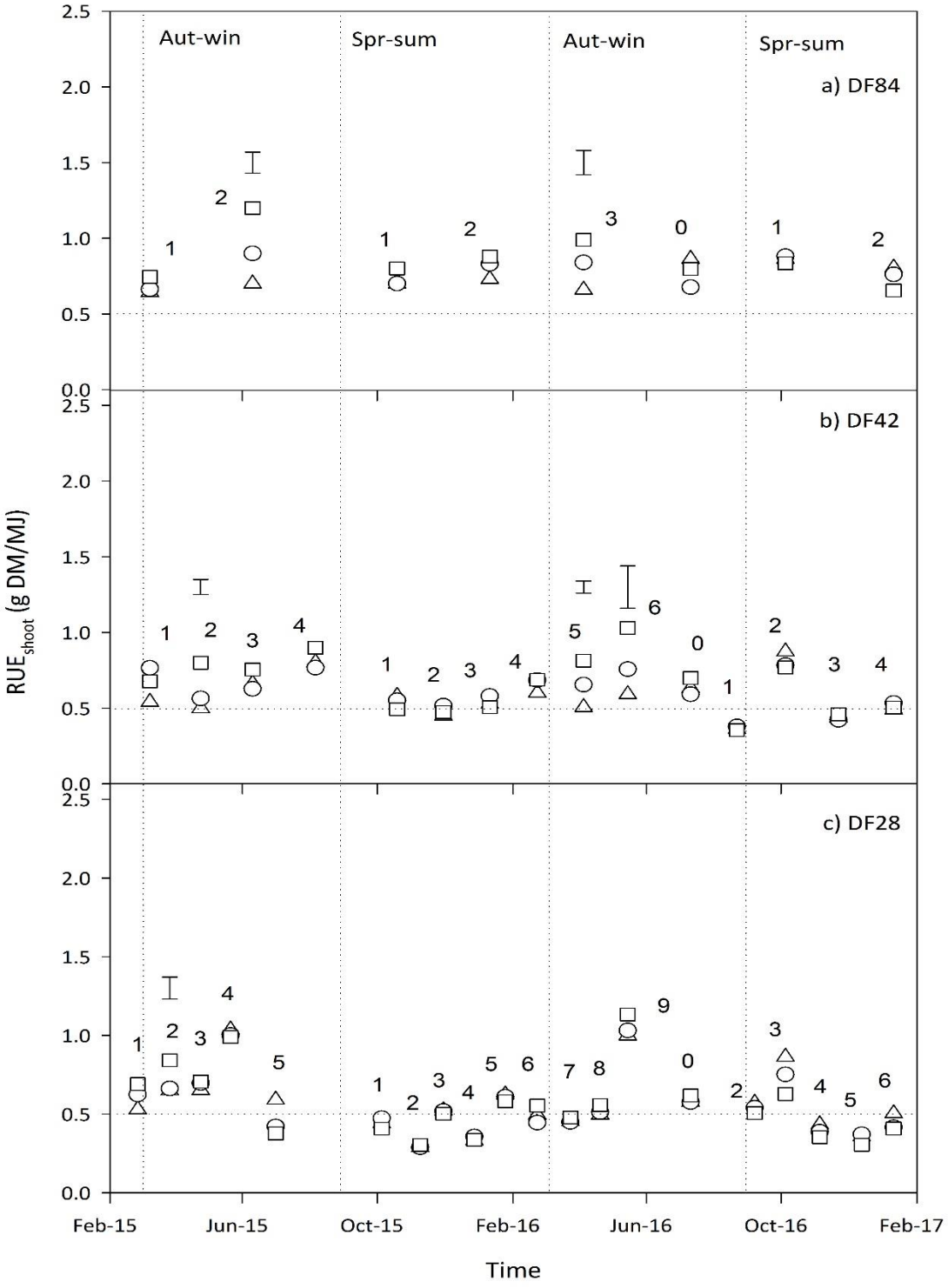


Figure 7.3 Seasonal radiation use efficiency for shoot yield (RUE_{shoot}) of three lucerne genotypes with fall dormancy (FD) ratings of 2 (Δ), 5 (O), and 10 (□) subjected to 28- (c), 42- (b) and 84 day (a) defoliation frequencies (DF) in the 2015, 2015/16 and 2016/17 regrowth year at Lincoln University, New Zealand.

Note: Error bars represent LSD (α=0.05) when differences occurred among genotypes. Numbers (0-9) indicate the regrowth cycles. Dotted line (····) represents average RUE_{shoot} of 0.50 g DM/MJ.

7.3.4 Radiation use efficiency for total dry matter (RUE_{total})

Mean RUE_{total} was 1.21 g DM/MJ for DF84 crops compared with 1.03 g DM/MJ for DF42 crops and 0.73 g DM/MJ for DF28 crops.

To investigate possible temperature effects, RUE_{total} values were plotted against the mean air temperature (Figure 7.4). RUE_{total} of all genotypes in the DF84 regime decreased ($p<0.001$) with T_{air} at 0.09 g DM/MJ/°C from 8 to 18°C (Figure 7.4 a). However, RUE_{total} of genotypes defoliated with a 42 and 28 day intervals responded differently with air temperature (Figure 7.4 b, c). For example, the RUE_{total} of the FD2 genotype under the DF42 regime followed the same pattern of response to T_{air} as in the DF84 regime (Figure 7.4 b). This showed RUE_{total} of the FD2 genotype decreased ($p<0.05$) at 0.23 g DM/MJ/°C as T_{air} ranged from 8 - 18 °C. Whereas, the RUE_{total} of FD5 genotype increased at 0.06 g DM/MJ/°C as T_{air} ranged from 12 - 18 °C. Nevertheless, the RUE_{total} of FD10 genotype did not follow the linear response to T_{air} with an average of 0.89 g DM/MJ, regardless of temperature. For DF28 regime, the RUE_{total} of FD2 genotype still followed the same pattern response to T_{air} as in DF42 and DF84 regimes where RUE_{total} decreased at 0.06 g DM/MJ/°C from 9 – 18 °C (Figure 7.4 c). However, the RUE_{total} of FD5 and FD10 genotypes did not follow the linear response to T_{air}, with an average of 0.60 g DM/MJ, regardless of temperature.

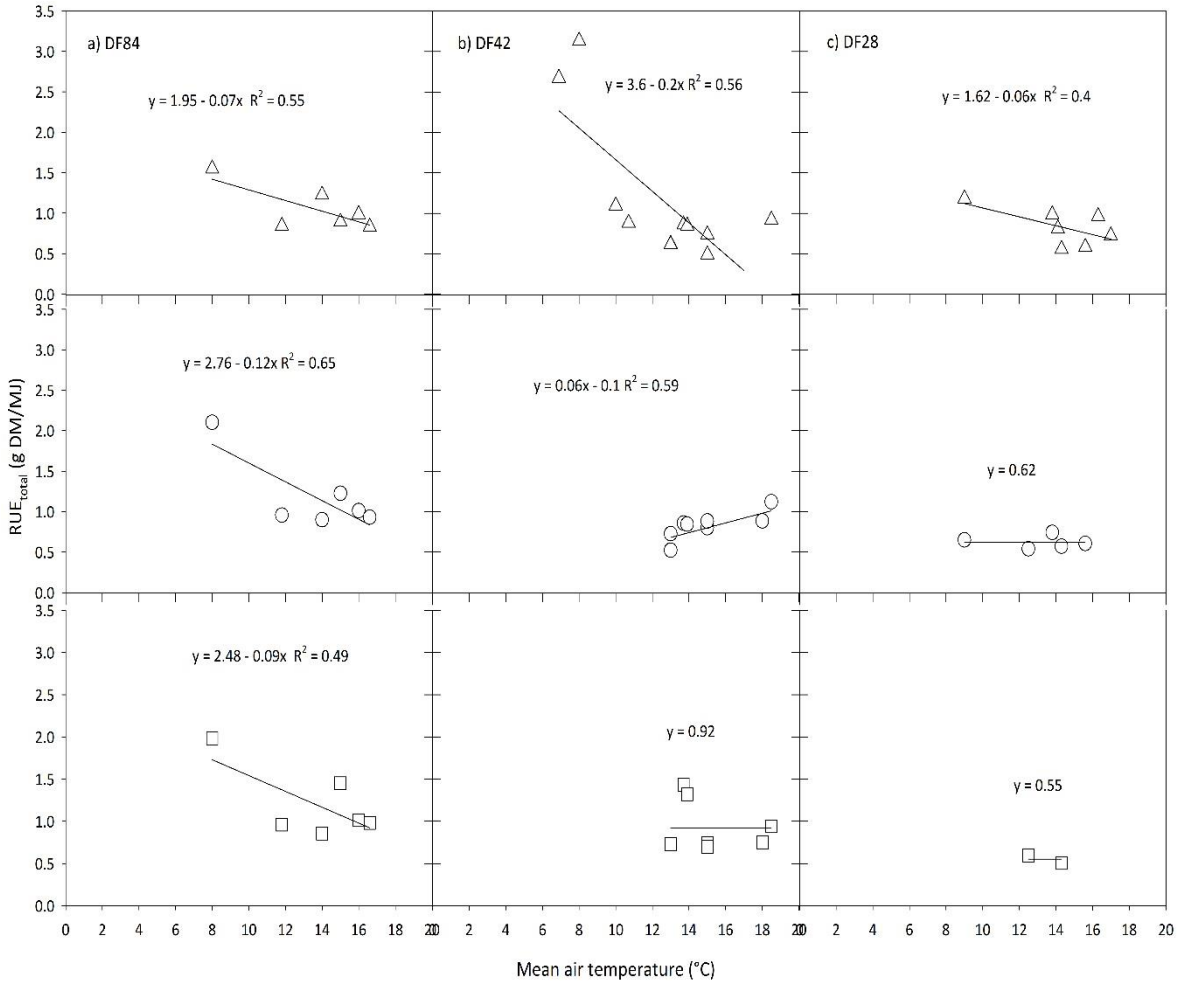


Figure 7.4 Total radiation use efficiency (RUE_{total}) against mean air temperature of three lucerne genotypes with fall dormancy (FD) ratings of 2 (Δ), 5 (O), and 10 (□) subjected to 28- (c), 42- (b) and 84 day (a) defoliation frequencies (DF) in the 2015, 2015/16 and 2016/17 regrowth year at Lincoln University, New Zealand.

7.3.5 Fractional partitioning of dry matter (DM) to crown plus taproots (P_{root}) in relation to temperature and photoperiod

The fractional partitioning of DM to crown plus taproot was calculated for each genotype within each regrowth cycle and plotted against the mean air temperature (T_{air}) (Figure 7.5).

In the DF84 regime, the P_{root} of all genotypes was poorly associated with T_{air} (Figure 7.5 a). For example, at the same T_{air} of 8.0 °C, the P_{root} values ranged from 0.00 to 0.52 for all genotypes. This implies that the P_{root} was not solely influenced by air temperature when this genotype grew in the 84 day defoliation regime. In this study, the P_{root} = 0.00 at T_{air} = 8.2 °C occurred in October 2016 (early spring). Whereas, at the same T_{air} but in August 2015 (winter) the P_{root} increased to ～0.52 for all genotypes. This suggests photoperiod could be a stronger factor that affected P_{root} rather than T_{air} in the DF84 regime.

In the DF42 regime, the fractional partitioning of DM to perennial organs of the different genotypes followed a different pattern of response to T_{air} (Figure 7.5 b). The P_{root} of the FD2 genotype decreased (R^2=0.58) at 0.06/°C with T_{air} over a temperature range from 7 to 15 °C and then reduced to 0.0/°C when temperature was >15 °C. The higher P_{root} at T_{air} = 18.5 °C occurred in March 2015 (autumn). In contrast, at the same T_{air} condition, FD5 genotype did not partition DM into root until ≤10 °C, but then P_{root} increased (R^2=0.51) at a rate of 0.03/°C when T_{air} > 10 °C. In comparison with the same T_{air}, the FD10 genotype did not accumulate DM to root when T_{air} <10.7 °C, similar to FD5 genotype. The P_{root} of FD10 genotype increased to 0.4 until T_{air} = 13 °C and then decreased (R^2=0.52) at a rate of 0.03/°C when T_{air} >13 °C.

In the DF28 regime, all most regrowth cycles from the FD2 genotype tended to partition DM into root (Figure 7.5 c). The P_{root} of the FD2 genotype decreased (R^2=0.43) at a rate of 0.04/°C as temperature ranged from 7 to >18 °C. In contrast, the higher FD ratings showed fewer temperature responses. Specifically, the FD10 genotype had only three regrowth cycles which partitioned DM into root, throughout three regrowth years.

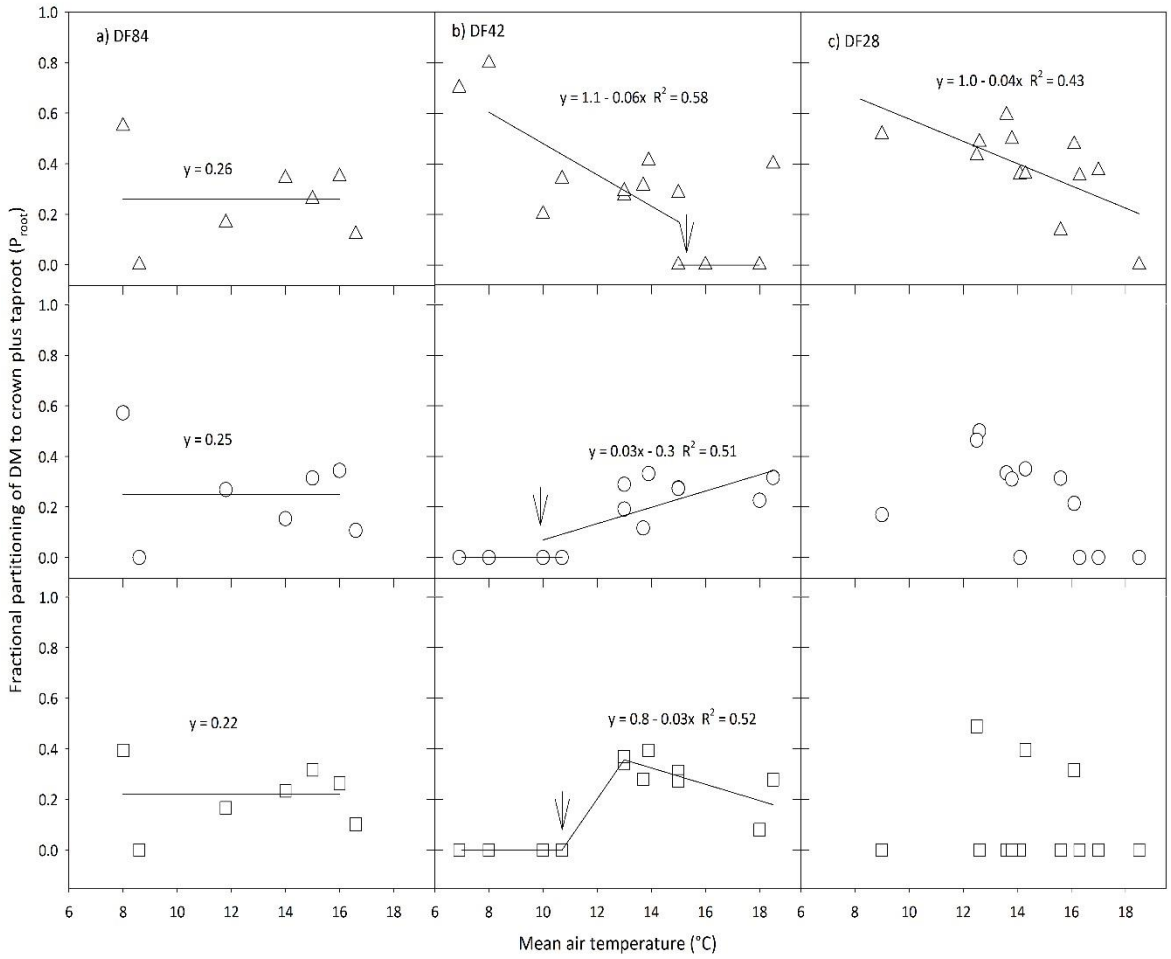


Figure 7.5 Fractional partitioning of dry matter (DM) to crown plus taproot (P_{root}) against mean air temperature of three lucerne genotypes with fall dormancy (FD) ratings of 2 (Δ), 5 (O), and 10 (□) subjected to 28- (c), 42- (b) and 84 day (a) defoliation frequencies (DF) in the 2015, 2015/16 and 2016/17 regrowth year at Lincoln University, New Zealand.

Note: Arrows indicate genotype started or stopped partitioning of DM into root.

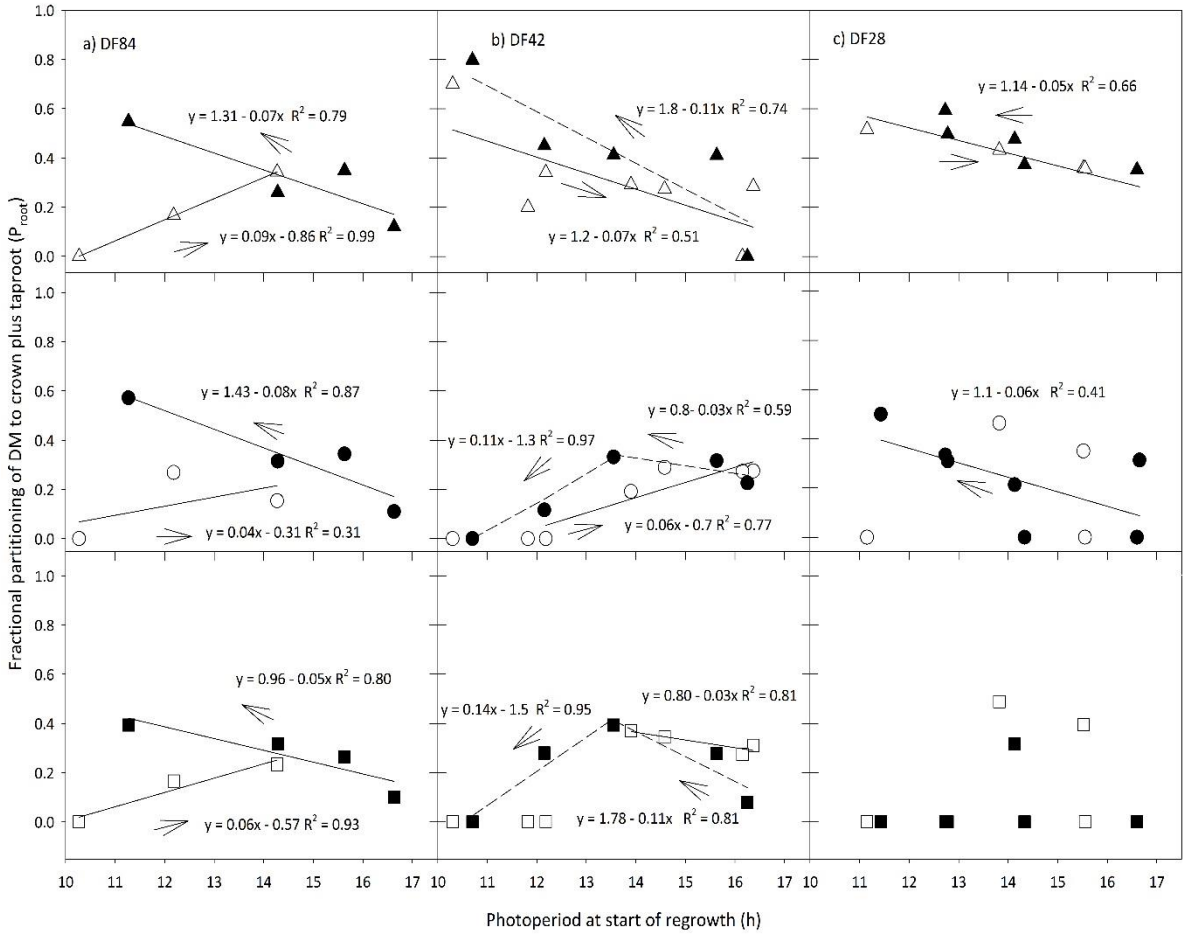


Figure 7.6 Fractional partitioning of dry matter (DM) to crown plus taproot (P_{root}) of three lucerne genotypes with fall dormancy (FD) ratings of 2 (Δ), 5 (O), and 10 (□) subjected to 28- (c), 42- (b) and 84 day (a) defoliation frequencies (DF) in response to increasing (white symbols) and decreasing (black symbols) photoperiod (Pp) at the start of each regrowth period.

Note: Arrows indicate an increasing or decreasing Pp.

To analyse the patterns of P_{root}, the influence of photoperiod (Pp) at the start of each regrowth period was also examined (Figure 7.6).

In the DF84 regime, the P_{root} of all genotypes followed a similar pattern of responses to photoperiod (Figure 7.6 a). When genotypes were growing into an increasing Pp, P_{root} increased ($P<0.01$) from 0.00 at a Pp of 10.3 h to ～0.27 at a Pp of 14.5 h. This implies that for each increment of one hour of Pp there was an increase of 0.06 in the partitioning of DM to perennial organs. In contrast, when genotypes were growing into a decreasing Pp, P_{root} increased ($p<0.01$) at a rate of 0.07 per one hour decrease from 0.10 at 16.5 h to ～0.50 at 11 h (Figure 7.6 a).

In the DF42 regime, the fractional partitioning of DM to perennial organs in different genotypes followed a different pattern of photoperiod responses (Figure 7.6 b). For example, values of P_{root} decreased ($p<0.01$) with an increasing Pp at a rate of 0.07 per one hour for the FD2 genotype. As Pp

declined, FD2 genotype increased P_{root} ($p<0.01$) at a rate of 0.11 per one hour from 0.15 at 16.5 h to ～0.80 at 10.5 h. In contrast, at the same increasing Pp, the FD5 genotype did not partition DM into root until the Pp was longer than 12 h, then P_{root} increased ($p<0.01$) with Pp >12 h at a rate of 0.06/h. As Pp declined from 16.5 h to 13.5 h, FD5 genotype increased P_{root} ($P<0.05$) at a rate of 0.03/h but then P_{root} declined sharply at a rate of 0.11/h when the Pp was shorter than 13.5 h. In comparison at the same increasing Pp, the FD10 genotype did not accumulate DM to root when Pp <12 h, similar to FD5 genotype. When Pp >13.5 h, FD10 genotype tended to decrease P_{root} from 0.37 at a Pp of 13.5 to 0.27 at a Pp of 16.5 h. In a decreasing Pp, FD10 genotype increased P_{root} ($p<0.001$) at a rate of 0.11/h from 0.08 at a Pp of 16.5 h to 0.39 at Pp of 13.5 h. However, P_{root} of this genotype decreased ($p<0.001$) at a rate of 0.14/h when the Pp was shorter than 13.5 and was 0.00 at a Pp of 10.5 h.

In DF28 regime, FD2 genotype tended to increase the partitioning of DM into root when the Pp was getting shorter and decrease P_{root} when the Pp was getting longer (Figure 7.6 c). However, the higher FD ratings showed less photoperiod response. Specifically, for FD10 genotype, 18 of the 21 regrowth cycles showed no DM partitioned into roots, regardless of Pp direction.

7.4 Discussion

Yield differences observed in Chapter 5 were also explained by RUE. Lower RUE was associated with lower root reserves created by DF regimes. The difference in P_{root} among genotypes was possibly due to different in base photoperiod response. The FD2 genotype showed the most response to Pp direction. In contrast, the FD10 genotype had a higher base photoperiod and therefore had less time to recharge root reserves than the FD2 genotype, FD5 was intermediate. The following sections discuss the mechanisms that explain any differences in root reserves (DM_{root}), RUE, and P_{root} of crops with different FD ratings in responses to DF regimes and environmental signals.

7.4.1 Dry matter (DM) accumulation in root

DM accumulation to crowns and taproots responded similarly to seasonal factors and DF regimes (Figure 7.1), which indicates both were important storage organs in lucerne. However, taproot DM increased at more than twice the rate of crowns. This suggest that taproots to 30 cm depth represent a larger fraction of root DM than crowns, as previously observed by Fornasier *et al.* (2003) and recently by Teixeira *et al.* (2007c).

The effect of frequent defoliations on crown plus taproot DM (DM_{root}) was evident after the seedling phase when DF regimes were applied in February 2015 (Figure 7.2). For example, during the first seven months after the application of DF treatments (February – August 2015), DM_{root} in DF28 crops was 4.5 t DM/ha in comparison with 7.5 t DM/ha in the DF42 and 10.5 t DM/ha in the DF84 crops, respectively. This indicates the short regrowth cycles caused a major reduction in the accumulation of biomass into root, which reduced DM_{root} by 40 ～ 60% in relation to DF42 and DF84 regimes. Similarly, Teixeira *et al.* (2007c) observed a 40% reduction in perennial reserves when their cutting interval was shifted from 42 to 28 days.

There were also seasonal patterns of change in lucerne DM_{root}, regardless of DF treatments and the amounts of root reserves (Figure 7.2 a, b, c). All genotypes showed an increase in root DM accumulation from early spring, reaching a maximum DM_{root} in autumn before a decrease during winter to a minimum in early spring. A similar seasonal accumulation and depletion of DM_{root} was previously reported by Dhont *et al.* (2002) who observed a 50% increase in root DM during autumn in Canada. Teixeira *et al.* (2007c) reported a 45% decline in DM_{root} during spring when working with their FD5 crops at the same location as the current experiment at Lincoln University. The seasonal pattern indicates that biomass was preferentially allocated into roots during late summer-autumn. This suggests the biomass demand from crown and taproot organs imposed strong competition for assimilate during the autumn period (Teixeira *et al.*, 2007c). This limits C and N supply to support shoot growth (Avice *et al.*, 1997b), and therefore is consistent with the reduced shoot growth rates (Section

5.3.1.3; Figure 5.3) during autumn. During winter/spring, DM_{root} decreased in all crops, probably as the root reserves were remobilised to support shoot regrowth in early spring (Volenec *et al.*, 1996; Teixeira *et al.*, 2007c). They therefore contributed to the increased shoot growth rates during this season (Section 5.3.1.3; Figure 5.3).

With regard to FD ratings, the DM_{root} of the FD10 genotype showed the most change over time and in response to defoliation frequency (Figure 7.2 a, b, c). The effect of defoliation treatments on FD ratings was most evident in the second autumn-winter of growth (2015/16). Specifically, in the DF28 regime DM_{root} of FD10 was consistently <2.0 t DM/ha in comparison with ~3.0 t DM/ha for FD2 and FD5 genotypes (Figure 7.2 c). Based on a DM_{root} of ~3.3 t DM/ha for FD10 at the beginning of the experiment (Section 4.3.2) in February 2015, the FD10 genotype declined at 2.4 kg DM/ha/day in root reserves throughout the full 24 months of regrowth.

Under the 42 day defoliation regime in autumn, the FD10 genotype accumulated DM_{root} of ~19.0 kg DM/ha/day more than the FD2 genotype. However, the FD10 genotype declined at ~11.3 kg DM/ha/day faster than FD2 genotype throughout the winter and spring period (Figure 7.2 b). The DM_{root} advantage of the winter-active (FD10) genotype appeared in the short autumn period when growth is insufficient to compensate for what was lost through the longer winter-spring growth. Therefore, the FD10 genotype had lower root reserves during this time. However, in the summer period (higher temperature), root DM increased to 6.0 t DM/ha for FD10 which was not different ($p<0.52$) to the other genotypes. In addition, genotypes grown under the 84 day regrowth cycles had similar root biomass throughout the regrowth seasons (Figure 7.2 a). This indicates that frequent defoliation had a major influence on the partitioning of DM to perennial organs in all genotypes, possibly in response to photoperiod and/or lower temperature (Khaiti and Lemaire, 1992; Teixeira *et al.*, 2008). This will be discussed in the following section.

7.4.2 Radiation use efficiency for shoot (RUE_{shoot}), shoot plus root (RUE_{total}) and dry matter (DM) partitioning in roots (P_{root})

The lower RUE_{shoot} observed in the 28 day defoliation regime (Figure 7.3) was associated with lower amounts of perennial reserves in DF28 crops (Figure 7.2), possibly due to depleted N reserves. For lucerne, frequent defoliation has been shown to diminish the amount of endogenous N in taproots (Graber *et al.*, 1927; Reynolds and Smith, 1962). Post-defoliation, a lack of endogenous N in perennial reserves can limit the supply of N to shoots in the early stages of leaf initiation and therefore reduce RUE_{shoot} (Avice *et al.*, 1997a). It can be expected that the amount of N reserves in DF28 crops was lower than other DF regimes. In this study, RUE_{shoot} was found to be less sensitive to the seasonal signals. This can be seen in the DF84 regime where RUE_{shoot} of crops did not follow a seasonal pattern with an overall average of 0.79 g DM/MJ throughout seasons (Figure 7.3 a). In contrast, Teixeira *et al.* (2008)

suggested that environmental signals exerted a stronger control than the availability of N, created by DF. However, it is also known that RUE differs following phasic development. Specifically, maximum RUE is attained in the vegetative phase and declines during the reproductive phase, due to N mobilisation from leaves into reproductive organs and roots (Sinclair and Muchow, 1999). It is expected that frequent defoliation at a 42 day interval in Canterbury, New Zealand would be insufficient for lucerne crops to complete their growth cycle to full flowering, and this may limit their potential physiological performance. The constant RUE_{shoot} in DF84 crops indicates that crops grown under the 84 day interval completed their life cycle, regardless of seasons. This was demonstrated by the observation that full flowering only occurred in the DF84 regime (Chapter 6).

The seasonal differences in lucerne DM_{root}, were caused by changes in RUE_{total} and DM partitioning in roots (P_{root}). Both air temperature (T_{air}) and photoperiod at the start of each regrowth period (Pp) were tested for associations with RUE_{total} and P_{root} (Figures 7.4, 7.5 and 7.6). This was because these environmental factors are associated with N and C partitioning between shoot and root of lucerne crops (Noquet *et al.*, 2001; Brown *et al.*, 2006). Both RUE_{total}, and P_{root} were poorly associated with T_{air} and Pp in DF28 crops (Figures 7.4 c, 7.5 c and 7.6 c). This suggests that, DF regimes altered the response of P_{root} to temperature and photoperiod. Under a 28 day regime, the crops had insufficient time to respond to the environment signals, possibly because the crop did not complete its growing cycle. This was illustrated in Figure 6.26 in Section 6.3.4, DF28 crops did not have a minimum 10 nodes before these crops can flower. This interrupted the allocation of DM into roots, particularly when crops grew in a decreasing temperature or shortening photoperiod environment (Figures 7.5 c and 7.6 c). Therefore this limited the availability of reserves and remobilise for early spring growth.

With regards to FD ratings, the different in DM_{root} among genotypes was mainly caused by changes in P_{root} in response to Pp. There were clear genotype differences in the seasonal pattern of DM partitioning (Figure 7.6 b). Specifically, with an increasing Pp, P_{root} of FD2 decreased from 0.70 at 10 h to 0.15 at 16 h. As Pp declined, P_{root} of FD2 increased from 0.15 at 16 h to 0.80 at 10 h. In contrast, at the same increasing Pp, the FD10 genotype did not partition DM to roots until the Pp was getting longer than 12 h. In a decreasing Pp, P_{root} of FD10 increased from 0.08 at 16 h to 0.39 at 13h, when the Pp was getting shorter than 13h, its P_{root} declined towards to 0.0 at 16h. The P_{root} in different genotypes followed different patterns of photoperiod responses. This suggests that the physiological mechanisms responsible for partitioning of different genotypes, was possibly due to changes in base photoperiod of the genotypes. Under a changing Pp environment, the FD2 genotype showed the most response to Pp direction. This suggests this dormant genotype has a low base photoperiod and therefore achieved sufficient biomass into root reserves at all times of year (Figure 7.2). In contrast, the winter-active (FD10) genotype had a higher base photoperiod. Therefore, the FD10 had less time to recharge root reserves compared with the FD2 genotype. This explains a faster decline at 11.3 kg DM/ha/day in the

amount of root reserves for FD10 when this genotype was growing during winter/spring regrowth period (Figure 7.2 b). Specifically, under extreme pressure, the FD10 genotype did not partition DM into roots when in a shortening photoperiod environment (Figure 7.6 c). This indicates that under defoliation stress different genotypes have different strategies in response to the available environment resources. Physiologically, plant adaptation to the available environmental resources is a prerequisite for starvation avoidance and survival (Smith and Stitt, 2007). In lucerne, winter survival and tolerance to defoliation frequency are predominantly required for these genotypes to be successful on farms (Smith, 1972). In this study, the FD10 genotype showed the most vulnerability to frequent cutting and therefore can be expected to be less persistent than other genotypes, particularly compared with the FD2 genotype.

7.5 Conclusions

Based on the results from this Chapter;

- The DF regimes effectively created differences in the amounts of root reserves (DM_{root}) among genotypes (～2.5 to 9.0 t DM/ha).
- Frequent defoliation with a 28 day cycle reduced the amount of DM_{root} to 40～60% of the maximum.
- Defoliation regimes with higher amounts of DM_{root} had greater RUE_{shoot}. Crops grown under a 28 day defoliation regime declined in RUE_{shoot}, from 0.61 g DM/MJ in February 2015 to 0.44 g DM/MJ by January 2017.
- More frequent defoliation resulted in a decline in P_{root} and therefore reduction of 2.4 kg DM/ha/day in DM_{root} for the FD10 genotype. Consequently, this genotype declined its root reserves over time to 1.5 t DM/ha by the end of the experiment on January 2017. This may explain its less consistent yield results over the 27 month period of growth.

Chapter 8 General discussion

8.1 Introduction

The aim of this thesis was to understand differences in the growth and development of lucerne genotypes with fall dormancy (FD) ratings of FD2, FD5 and FD10. To do this, one field experiment involving three lucerne genotypes were defoliated at three DF regimes of DF28-, DF42-, and DF84 days. Measurements were taken over two years from the seedling phase in October 2014 to January 2017. The defoliation regimes were used to create different levels of root reserves, to examine how this affected the yield and quality of crops with the different FD ratings (Chapters 4 and 5). Differences in the agronomic performance were then explained physiologically. This was done through quantification of radiation interception, canopy expansion and development (Chapter 6), and RUE and biomass partitioning (Chapter 7) in response to environmental factors. This general discussion summaries the key physiological results from chapters and uses this data to discuss the productivity and persistence of the genotypes with refinement to their use on farms.

8.2 Agronomic performance and implications

In Chapter 4, by the end of the seedling phase, the FD10 genotype had a 20% higher shoot and 16% greater root biomass than the other two genotypes. These results highlighted a priority of this genotype to vigorous shoot production immediately after emergence. It remained to be seen if this yield advantage was maintained during future regrowth cycles of the established crops. Therefore, Chapter 5 investigated the yield and quality responses of crops of different FD ratings when they were grown in changing environmental conditions under the different defoliation managements.

In Chapter 5, the use of the three DF regimes was effective in creating lucerne crops of different yield potential among the FD ratings. The greatest total shoot DM yield was from DF84 crops followed by DF42 crops and the lowest was from DF28 crops (Table 5.1). Specifically, the crops defoliated at 28 day intervals over the growing season had a 44-49% lower yield than DF42 and DF84 crops. The reduction in shoot DM production of DF28 crops was mainly because shorter regrowth cycles, they were unable to grow at high linear rates for long periods, particularly during favourable spring-summer conditions when shoot growth rates were highest (Figure 5.3). The seasonal change in shoot growth rate appeared related to mean air temperature which was high during spring-summer and low during autumn-winter (Section 3.2.2). Generally, the rates of growth increased with increasing temperature but potentially this was also modified by photoperiod (Pp). For example, when crops were growing into an increasing Pp, growth rate was consistent at around 8.8 and 7.5 kg DM/ha/°Cd for DF84 and DF42 crops, respectively (Figure 5.4 a, b). In contrast, when these crops were growing into a decreasing

Pp, growth rate decreased at a rate of 1.2 (DF84) and 0.88 kg DM/ha/°Cd (DF42) for each hour decrease (Figure 5.4 a, b). However, crops defoliated at 28 day intervals did not show a Pp response, and were always below 3.5 kg DM/ha/^{0}Cd regardless of the direction of photoperiod change (Figure 5.4 c). The physiological mechanisms responsible for these changes will be discussed in detail in Sections 8.3.

With regards to FD ratings, the FD10 genotype showed the most change in yield production over time and due to the effect of defoliation frequency (Figure 5.1). FD10 produced the highest shoot yield after sowing (Figure 4.2), but the yield avantage was less consistent over the 24 month period of regrowth (Table 5.1). Higher shoot DM production for this genotype also occurred in the autumn-winter period but this advantage contributed only 8% of the total annual shoot DM (Figure 5.2). The greater autumn yield from FD10 came from faster shoot growth rates than the FD2 and FD5 genotypes from March to the middle of July (Figure 5.3). During this time, temperature and radiation levels are low (Section 3.2.2). This indicates that different genotypes had different strategies in response to the available environment resources. Despite the yield advantage and growth rate advantage to FD10 in autumn this did not translate to a higher annual yield because it had lower growth in the main spring production period, particularly under a DF28 regime (Figures 5.1 c and 5.3 c).

The yield results alone suggest the longest DF regime should be used to maximise yield. However, from an animal nutrition perspective not all forage is of equal value. Therefore, a comparison of nutritional characteristics was also undertaken to quantify the total CP and ME readily available for animal consumption. This involved separation of palatable and unpalatable herbage fractions. This showed the FD10 genotype produced higher total CP in autumn but it was lower than FD2 and FD5 genotypes during spring-summer (Figure 5.10). Therefore accumulated CP over the regrowth periods gave a lower total CP for the FD10 genotype (Table 5.2). The total ME showed a similar pattern as CP (Figure 5.11). There was no interaction between FD and DF for total CP and ME (Table 5.2 and 5.3). In this study, crops defoliated at 42 and 84 day intervals gave a higher total CP and ME than a 28 day regrowth crop. The change in total CP and ME was explained by an allometric relationship as DM increased, CP and ME increased in a similar pattern for all treatments throughout growing seasons (Figures 5.12 and 5.13 a - d). Leaf fraction have higher quality than the soft and hard stem fractions (Figures 5.12 and 5.13), because stem fractions (soft and hard stems) contain mainly structural components (Gastal and Lemaire, 2002) which have a low N and ME contents than leaf (Figures 5.14 and 5.15). The change in CP among shoot fractions was explained by a decrease of LSR with increasing DM (Figure 5.7). These results indicate that the relationship between yield and quality of lucerne was independent of genotype and predominantly explained allometrically by the LSR, associated with shoot DM. These systematic changes enabled functional relationships to be quantified between yield and quality across treatments. These could be used for crop management and in crop simulation models to predict yield and quality of lucerne crops.

There was no evidence that different FD ratings required different defoliation management. This is important on farm, because a similar grazing management could be used for all genotypes. This thesis also demonstrated the spring-summer growth resulted in greater shoot yield and quality than the autumn-winter growth. Therefore, from a yield and quality perspective, the optimum grazing management should prioritize spring-summer to maximise productivity and let crops recharge below-ground in autumn, particularly for the FD10 genotype. This is consistent with previous recommendations based on "Kaituna" lucerne (Moot *et al.*, 2003). Finally, with regards to FD ratings, the winter-active genotype provided more herbage in the colder months but was less consistent, particularly with the increased defoliation frequency. In lucerne, winter survival and tolerance to defoliation frequency are predominant requirements for genotypes to be successful on farms in temperate climates. In this study, the FD10 genotype showed the most vulnerability to frequent cutting and therefore was less persistent than the other genotypes, particularly compared with the FD2 genotype. The following section discusses the physiological mechanisms that explain the agronomic performance among genotypes and between defoliation treatments.

8.3 Physiological performance and implications

For lucerne, yield forming processes are mainly driven by temperature and solar radiation (Fick *et al.*, 1988) and can be estimated as the product of radiation intercepted by the canopy (R/R_0) and radiation use efficiency (RUE) (Equation 2.2). To be able to explain the differences of agronomic performance among genotypes or between defoliation treatments, it is necessary to understand how temperature and solar radiation affect these yield forming processes. Therefore, Chapters 6 and 7 were constructed to examine R/R_0 and RUE in relation to environmental factors.

In Chapter 6, the differences in shoot yield among DF treatments or among genotypes were explained by differences in the amount of radiation intercepted. The lower shoot yield in DF28 crops was mainly attributed a lower amount of radiation intercepted (Figure 6.4 a, b, c). Similarly, the greater autumn yield or the lower spring growth of the FD10 genotype were also explained by the higher/lower amounts of radiation intercepted by this genotype, relative to the other two. The differences in the pattern of radiation interception among genotypes or among DF regimes suggests that either the area of green canopy (LAI) and/or the efficiency of interception per unit of leaf area (canopy architecture) changed during these regrowth seasons. The canopy architecture, was quantified by the extinction coefficient (k) which defined the efficiency of interception per unit of leaf area (Hay and Porter, 2006). In this study, a single k value of 0.83 was found for all crops (Figure 6.3). This high and stable k for all crops indicated that canopy structure was unaffected by genotypes and defoliation treatments. This is consistent with previous reports that also found little variation in k among genotypes (Gosse *et al.*,

1988; Thiébeau *et al.*, 2011) or between defoliation treatments (Teixeira *et al.*, 2007b).Therefore, the differences in the amount of radiation intercepted were explained by LAI, rather than canopy architecture. Thus the developmental processes of LAI formation were investigated and quantified through canopy expansion (*i.e.,* LAER) and development (*i.e.,* phyllochron). DF28 crops intercepted less radiation because harvests occurred before canopy closure at the critical leaf area index (LAI_{crit}) of 3.5 (Figure 6.7 a, b, c). This delayed the time to reach 95% radiation interception (Figure 6.6) and subsequently reduced shoot growth rate (Section 5.3.1.3) and yield (Section 5.3.1.1). The lower LAI in DF28 crops was explained predominantly by a lower leaf area expansion rate (LAER). This was 50 and 62% slower during the main spring-summer growth periods than DF42 and DF84 crops, respectively (Figure 6.8 a, b, c). Specifically, the development of the individual leaf area explained the differences in LAER (Figure 6.10). Crops defoliated at 28 day intervals had the smallest individual leaf area which was 50 and 65% smaller than DF42 and DF84 crops.

The components of canopy development were quantified to give insight into the mechanisms responsible for the differences in LAER. These included; leaf appearance and branching, leaf senescence and shoot population across FD ratings and DF treatments. Primary leaf appearance, quantified by phyllochron, was consistent at ≤30°Cd/primary leaf for all crops that experienced an increasing Pp (Figure 6.13). This suggests temperature was the main driver of primary leaf appearance during the spring-summer. This is illustrated in Figure 6.12 which showed no differences in phyllochron among genotypes or between DF regimes during this time. However, phyllochron increased to ≥30°Cd/primary leaf for all crops experiencing a decreasing Pp (Figure 6.13). A longer phyllochron during the autumn period suggests that primary leaf appearance could not be explained solely by photoperiod and potentially the supply of carbon to shoot growth is limited to meet potential demand for forming new basal leaves (Brown *et al.*, 2005b). This is because the biomass demand from crown and taproot organs imposes strong competition for assimilate during the autumn period (Teixeira *et al.*, 2007c) which limits C and N supply to shoots (Avice *et al.*, 1997b). This is demonstrated in Figure 7.2 (Chapter 7) whereby crops with the shortest regrowth cycles (DF28) had limited root storage (sink). This may have reduced new basal bud initiation and therefore increased the phyllochron for all DF28 crops at a rate of 3.8°Cd/h for each 1 hour decrease in photoperiod (Figure 6.13 c). Other components of LAI including branching, shoot population and leaf senescence, were consistent for all crops. These values could be used as constants in the development of crop simulation models.

With regards to FD ratings, the higher autumn shoot yield of the FD10 genotype came from a faster stem elongation rate (Figure 6.16) and greater individual leaf area (Figure 6.10). This allowed more radiation to be intercepted (Figure 6.4). This strategy of elongating shoot length resulted in higher shoot yield (Section 5.3.1.1) but also produced a higher un-palatable proportion (Section 5.3.2.1) because of increased lignification to support the extra height (Christian *et al.*, 1970). Lower spring yield

observed in FD10 under the DF28 regime was mainly due to the reduction in shoot per plant which was unable to maintain 700 stems/m^2 as an optimum population to maximise yield.

In Chapter 7, radiation use efficiency was also quantified because biomass accumulation depends on the amount of radiation intercepted by the canopy (MJ/m^2) and the efficiency of conversion of the intercepted radiation into biomass (g DM/MJ). As expected, crops created with different defoliation frequencies had different RUE_{shoot}. The lowest RUE_{shoot} values were observed for DF28 crops (Figure 7.3) which contributed to their lower shoot yield. The lower RUE_{shoot} observed in the 28 day defoliation regime was also associated with lower amounts of perennial reserves in DF28 crops (Figure 7.2 c), possibly due to reduced N reserves. This is because frequent defoliation has been shown to diminish the endogenous N in taproots (Graber *et al.*, 1927; Reynolds and Smith, 1962). Post defoliation, a lack of endogenous N in perennial reserves can limit the supply of N to shoots in the early stages of leaf initiation and therefore reduce RUE_{shoot} (Avice *et al.*, 1997a). The short regrowth cycles created in this study caused major reductions in the amounts and levels of root reserves, which reduced DM_{root} by 40 ~ 60% in relation to the longer 42 and 84 day regrowth cycles (Figure 7.2). It can be expected that the amounts of N reserves in DF28 crops were also lower than other DF regimes. The lower DM_{root} in DF28 crops was caused by changes in RUE_{total} and DM partitioning in roots (P_{root}). These changes were related to air temperature (T_{air}) and photoperiod at the start of each regrowth period (Pp). RUE_{total} and P_{root} were poorly associated with T_{air} and Pp in DF28 crops (Figures 7.4 c, 7.5 c and 7.6 c). This indicates that this DF regime altered the response of P_{root} to temperature and photoperiod. Under the 28 day regime, the crop had insufficient time to respond to the environmental changes, possibly because it did not complete its growing cycle (Section 6.3.4; Figure 6.26). This was illustrated in Figure 6.26 in Section 6.3.4, DF28 crops did not have a minimum 10 nodes before these crops can flowering. This interrupted the allocation of DM into roots, particularly when the crop grew in a decreasing temperature or shortening photoperiod environment (Figures 7.5 c and 7.6 c). This limited the availability of reserves for roots to respire through winter and remobilise in early spring growth. The ongoing expectation is that this crop will collapse as a productive stand (Harvey *et al.*, 2014).

With regards to FD ratings, there were clear genotype differences in the seasonal pattern of DM partitioning. Specifically, with an increasing Pp, P_{root} of FD2 decreased from 0.70 at 10 h to 0.15 at 16 h. As Pp declined, P_{root} of FD2 increased from 0.15 at 16 h to 0.80 at 10 h. In contrast, at the same increasing Pp, the FD10 genotype did not partition DM to roots until the Pp was longer than 12 h. In a decreasing Pp, P_{root} of FD10 increased from 0.08 at 16 h to 0.39 at 13h, when the Pp was shorter than 13h, its P_{root} declined towards to 0.0 at 16h. This suggests that the physiological mechanisms responsible for partitioning of different genotypes, was possibly due to different in base photoperiod of the genotypes. The FD2 genotype had a lower base photoperiod, therefore this dormant genotype achieved sufficient biomass into root reserves at all times of year (Figure 7.2). In contrast, the winter-

active (FD10) genotype had a higher base photoperiod. Therefore, the FD10 had less time to recharge root reserves compared with the FD2 genotype. This explains the faster decline at 2.4 kg DM/ha/day in root reserves for FD10 growing into a shortening photoperiod environment, under the 28 day defoliation regime (Figure 7.6 c). Consequently, the root reverses of the FD10 genotype declined over time to 1.5 t DM/ha by the end of the experiment on January 2017.

8.4 Limitations and future work

The use of three DF regimes effectively created differences in the amounts of perennial reserves among genotypes (Section 7.3.2). Increased frequent defoliations reduced the amounts and levels of root reserves (DM_{root}) by 40～60% in the DF42 and DF84 regimes. The smaller root reserves in DF28 crops were caused by a decline in the fractional DM partitioning in roots (P_{root}). Therefore post defoliation, a lack of root reserves reduced RUE_{shoot} (Section 7.3.3), and consequently reduced biomass accumulation for DF28 crops. Specifically, under extreme pressure, the FD10 genotype did not partition DM into roots when the photoperiod was getting shorter (Figure 7.6 c). This was manifest as a faster decline at 2.4 kg DM/ha/day in root reserves for FD10 growing under the 28 day defoliation regime. Consequently, the FD10 genotype reduced its root reserves over time to 1.5 t DM/ha by the end of the experiment on January 2017. It is likely that this reduction in root reserves is associated with reported decreases in persistence of the FD10 genotype over time (Harvey *et al.*, 2014). Ongoing monitoring of this experiment will be needed to confirm this hypothesis. Historically, it is well known that frequent defoliation diminishes the endogenous N in taproots (Graber *et al.*, 1927; Reynolds and Smith, 1962). Lower root reserves reduces yield because they are readily to mobilised to support shoot regrowth after defoliation (Teixeira *et al.*, 2007c). The ongoing expectation is that the amounts of N reserves in DF28 crops were also lower than in the other DF regimes.

The physiological mechanisms responsible for partitioning of different genotypes, was possibly due to different in base photoperiod response. The FD2 genotype showed the most response to Pp direction, suggesting this genotype has a low base photoperiod response. This strategy ensured this dormant genotype achieved sufficient biomass into root reserves at all times of year when it grown under a changing Pp environment such as New Zealand or North America and therefore high persistence. In contrast, the higher FD ratings showed less photoperiod responses. This indicates the winter-active (FD10) genotype has a higher base photoperiod. This may explain why it has poor survival throughout winter when grown in these regions at mid-range latitude. Traditionally, these higher FD ratings are grown in warmer regions at lower latitude such as South America. These regions are characterised by only small changes in the photoperiod environment. There, the higher FD ratings could grow more total biomass because of a small overall response of genotypes to the smaller changes in photoperiod.

Future studies are required to determine how these genotypes respond under different photoperiod conditions and to confirm if a difference in their base photoperiod is the genetic basis of FD ratings.

Physiological relationships are the basis of crop simulation models and have previously been integrated into APSIM–lucerne (Teixeira *et al.*, 2009; Moot *et al.*, 2015). The model was successfully used to estimate yield production of "Kaituna" lucerne, a semi-dormant (FD5) genotype. The collective results of this growth and development study suggest some similarities but also important differences among different FD ratings with implications for lucerne models. Leaf appearance was consistent among FD ratings. The phyllochron was ≤30°Cd/primary leaf for all genotypes as Pp increased but this was ≥ 30°Cd/primary leaf as Pp decreased (Section 6.3.3). Other LAI components including branching, shoot population and leaf senescence, were consistent for all genotypes. These values could be used as constants in the development of crop simulation models. However, the autumn growth advantage of the winter-active genotype came from a faster stem elongation rate and greater individual leaf area. Thus, these values should be used when modelling with different genotypes during the autumn period. Furthermore, the fractional partitioning of DM to roots of different FD ratings appears related to different base photoperiod. Therefore, these physiological mechanisms responsible for partitioning of different genotypes should be considered to develop more mechanistic and universally applicable lucerne models.

8.5 Conclusions

This research investigated the growth and development of different FD ratings in response to defoliation frequency regimes. These results indicate that;

- Growth differed among FD ratings. The winter-active genotype (FD10) produced more yield and herbage quality in the first year but this advantage did not persist and actually decreased by year 3 with increased defoliation frequency.

- Quality did not affected by FD ratings and explained by the leaf stem ratio, associated with changes in shoot DM.

- Phenological development (phyllochron, branching, canopy structure and leaf senescence) and reproductive development were conservative among FD ratings. In contrast, vegetative growth (leaf area expansion and stem elongation) was most closely correlated with fall dormancy ratings, particular in atumn period.

The main findings in each chapter is summarised in the Table 8.1.

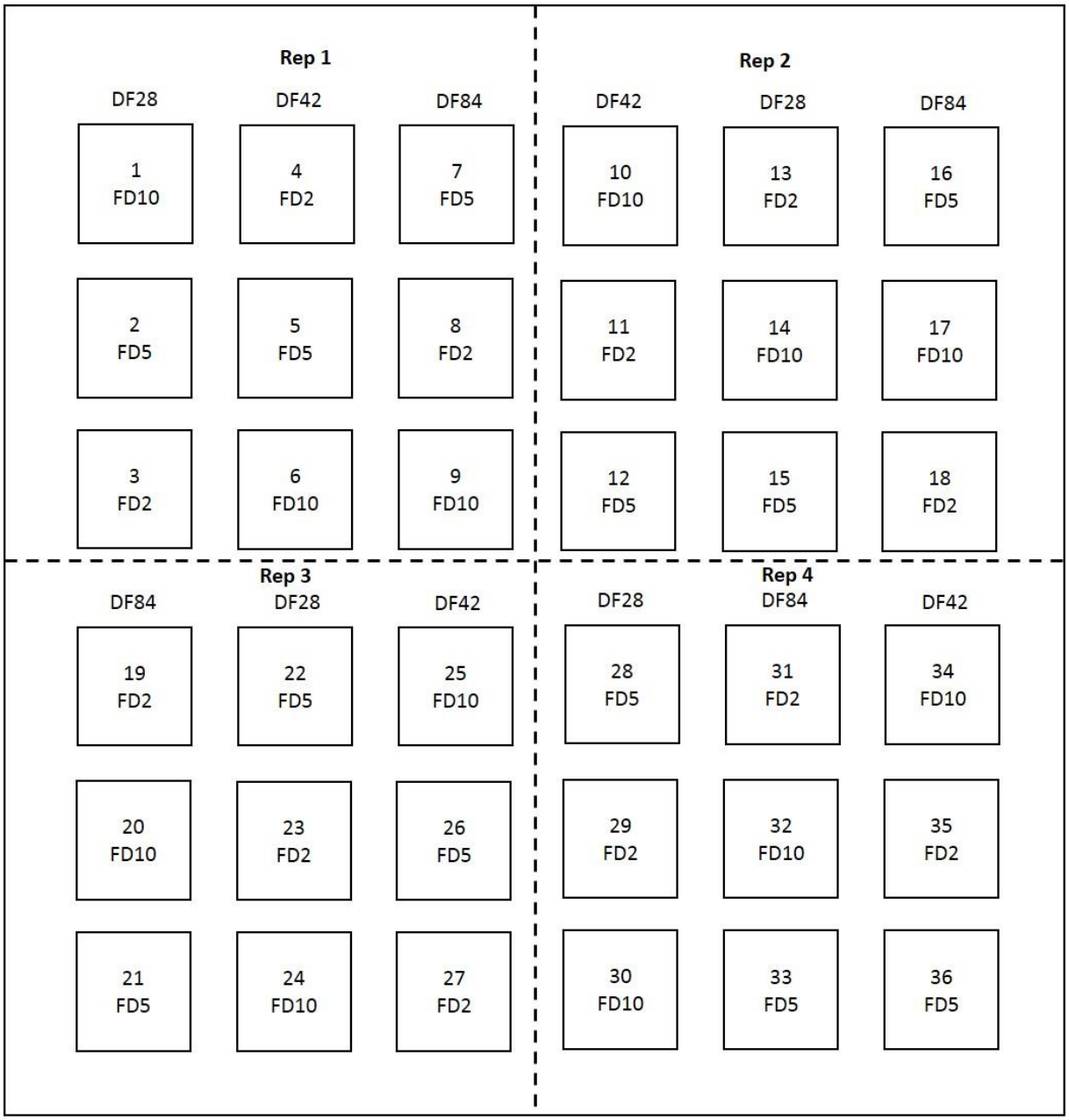
Table 8.1 Growth and development parameters affected by FD rating or DF regime.

Parameters	Defoliation regime (DF)	Fall dormancy (FD)
Shoot yield and quality	√	√
Phyllochron	√	×
Branching	√	×
Senescence	√	×
flowering	√	×
Canopy structure	×	×
LAER	√	√
Individual LA	√	√
Shoot elongation	√	√
Plant population	√	√
RUE_{shoot}	√	√
RUE_{total}	√	√
Partitioning	√	√

Note: symbol √ reprents parameter affected by DF or FD. Symbol × represents paprameter was not affected by DF or FD.

Appendix A

A.1 Experimental plan for Iversen 12



FD2: a dormant genotype

FD5: a semi-dormant genotype

FD10: a non-dormant or winter-active genotype

DF28: defoliation at the 28 day intervals

DF42: defoliation at the 42 day intervals

DF84: defoliation at the 84 day interval

A.2 Canopy expansion and development

Table 0.1: The slope (S), coefficients of determination (R^2) and standard errors of differences of means (SE) for leaf area index (LAI) in relation to accumulated thermal time of three lucerne genotypes with different FD ratings subjected to three contrasting DF grown at Lincoln University, New Zealand.

Regrowth cycle	Defoliation frequency	R^2	S	LAER ($m^2/m^2/°Cd$)			SE
				FD2	FD5	FD10	
	Year: 2015						
1	DF84						
At 42 days		0.96	0.007	0.007	0.006	0.008	0.0008
End of cycle 1		0.70	-0.004	-0.002	-0.003	-0.006	0.0009
2							
At 42 days		0.78	0.008	0.005	0.009	0.01	0.0007
End of cycle 2		1	0.001	-	-	-	-
	DF42						
1		0.96	0.007	0.006	0.007	0.008	0.0008
2		0.99	0.005	0.005	0.005	0.006	0.0004
3		0.73	0.004	0.003	0.004	0.006	0.0005
4		0.98	0.005	0.005	0.005	0.004	0.0005
	DF28						
1		0.97	0.007	0.006	0.007	0.008	0.0005
2		0.99	0.005	0.004	0.005	0.007	0.0004
3		0.70	0.005	0.003	0.004	0.007	0.0008
4		0.97	0.004	0.004	0.003	0.004	0.0008
5		0.90	0.003	0.003	0.002	0.004	0.0008
6		0.80	0.005	0.004	0.005	0.008	0.0017

Regrowth cycle	Defoliation frequency	R^2	S	LAER ($m^2/m^2/°Cd$)			SE
	Year: 2015/16			FD2	FD5	FD10	
1	DF84						
At 42 days		0.96	0.013	0.013	0.011	0.015	0.0020
End of cycle 1		0.46	0.002	0.002	0.007	-0.003	0.0035
2							
At 42 days		0.99	0.015	0.015	0.018	0.012	0.0035
End of cycle 2		0.81	-0.003	-0.003	-0.004	-0.004	0.0020
3							
At 42 days		0.96	0.009	0.007	0.009	0.01	0.0010
End of cycle 3		0.48	-0.0017	-0.0003	-0.002	-0.003	0.0008
	DF42						
1		0.90	0.009	0.01	0.009	0.008	0.0015
2		0.98	0.010	0.010	0.01	0.008	0.0010
3		0.98	0.012	0.012	0.013	0.01	0.0020
4		0.96	0.007	0.007	0.008	0.007	0.0015
5		0.92	0.007	0.006	0.007	0.009	0.0004
6		0.66	0.004	0.002	0.004	0.007	0.0005
	DF28						
1		0.94	0.005	0.005	0.007	0.005	0.0015
2		0.90	0.005	0.006	0.006	0.004	0.0020
3		0.90	0.005	0.006	0.005	0.004	0.0010
4		0.97	0.006	0.006	0.007	0.005	0.0010
5		0.91	0.006	0.007	0.006	0.004	0.0010
6		0.91	0.005	0.007	0.005	0.004	0.0015

Regrowth cycle	Defoliation frequency	R^2	S	LAER ($m^2/m^2/°Cd$)			SE
	Year: 2015/16			FD2	FD5	FD10	
	DF28						
7		0.99	0.004	0.004	0.004	0.003	0.0005
8		0.97	0.003	0.003	0.003	0.004	0.0005
9		0.88	0.003	0.002	0.003	0.004	0.0010
	Year: 2016/17						
	DF84						
0		0.81	0.004	0.003	0.004	0.006	0.0009
1		0.87	0.009	0.009	0.007	0.01	0.0018
2							
At 42 days		0.97	0.019	0.02	0.019	0.018	0.0010
End of cycle 2		0.4	-	-	-	-	-
	DF42						
0		0.73	0.002	0.001	0.001	0.002	0.0005
1		0.95	0.005	0.005	0.005	0.004	0.0010
2		0.93	0.012	0.014	0.011	0.011	0.0015
3		0.98	0.01	0.010	0.009	0.009	0.0025
4		0.98	0.009	0.009	0.01	0.0083	0.0020
	DF28						
2		0.94	0.008	0.009	0.008	0.007	0.0015
3		0.71	0.008	0.012	0.008	0.004	0.0009
4		0.67	0.005	0.007	0.004	0.003	0.0013
5		0.87	0.005	0.006	0.006	0.003	0.0015
6		0.73	0.006	0.009	0.005	0.004	0.0011

Table 0.2: The slope (S), coefficients of determination (R^2) and standard error of the mean (SE) for primary leaf number in relation to accumulated thermal time of lucerne genotypes with FD ratings of FD2, FD5 and FD10 subjected to 28-, 42- and 84 days defoliation frequency (DF) grown at Lincoln University, New Zealand.

Regrowth cycle	Defoliation frequency	R^2	S	Leaf appearance rate (Primary leaf/°Cd)			SE
	Year: 2015			FD2	FD5	FD10	
1	DF84						
At 42 days		0.97	0.026	0.025	0.026	0.026	0.0009
End cycle		0.90	0.013	0.013	0.013	0.014	0.0016
2							
At 42 days		0.8	0.025	0.024	0.025	0.025	0.0010
End cycle		0.16	0.002	0.001	0.002	0.003	0.0005
	DF42						
1		0.98	0.027	0.025	0.026	0.027	0.0008
2		0.98	0.025	0.025	0.025	0.026	0.0009
3		0.97	0.027	0.027	0.026	0.027	0.0008
	DF28						
1		0.99	0.028	0.028	0.028	0.029	0.0007
2		0.98	0.024	0.022	0.024	0.026	0.0005
3		0.99	0.021	0.02	0.021	0.022	0.0008
4		0.98	0.018	0.017	0.018	0.019	0.0008

Regrowth cycle	Defoliation frequency	R^2	S	Leaf appearance rate (Primary leaf/°Cd)			SE
	Year: 2015			FD2	FD5	FD10	
	DF84						
1							
At 42 days		0.94	0.045	0.043	0.043	0.045	0.0017
End cycle		0.99	0.025	0.024	0.025	0.026	0.0008
2							
At 42 days		0.96	0.034	0.034	0.033	0.034	0.0012
End cycle		0.98	0.014	0.013	0.014	0.015	0.0011
3							
At 42 days		0.99	0.029	0.028	0.029	0.029	0.0005
End cycle		0.92	0.018	0.017	0.016	0.02	0.0029
	DF42						
1		0.96	0.039	0.039	0.037	0.040	0.0009
2		0.99	0.038	0.039	0.038	0.038	0.0010
3		0.98	0.04	0.039	0.038	0.043	0.0015
4		0.99	0.026	0.025	0.027	0.027	0.0009
5		0.98	0.028	0.026	0.027	0.029	0.0012
6		0.88	0.03	0.028	0.029	0.038	0.0009

Regrowth cycle	Defoliation frequency	R^2	S	Leaf appearance rate (Primary leaf/°Cd)			SE
	Year: 2015			FD2	FD5	FD10	
	DF28						
1		0.99	0.032	0.030	0.034	0.030	0.0010
2		0.98	0.031	0.031	0.030	0.032	0.0011
3		0.97	0.035	0.035	0.036	0.035	0.0009
4		0.99	0.032	0.030	0.031	0.033	0.0015
5		0.98	0.028	0.028	0.029	0.030	0.0012
6		0.92	0.023	0.023	0.023	0.024	0.0009
7		0.98	0.022	0.022	0.021	0.023	0.0005
8		0.94	0.020	0.019	0.018	0.023	0.0007
9		0.96	0.019	0.017	0.017	0.022	0.0025
	Year:2016/17						
	DF84						
1							
At 42 days		0.98	0.038	0.036	0.036	0.037	0.0012
End cycle		0.86	0.025	0.025	0.024	0.027	0.0020
2							
At 42 days		0.99	0.040	0.042	0.040	0.038	0.0025
End cycle		0.93	0.016	0.017	0.016	0.015	0.0020

Regrowth cycle	Defoliation frequency	R^2	S	Leaf appearance rate (Primary leaf/°Cd)			SE
	Year:2016/17			FD2	FD5	FD10	
	DF42						
2		0.98	0.039	0.040	0.039	0.038	0.0012
3		0.99	0.034	0.035	0.034	0.034	0.0010
4		0.99	0.028	0.028	0.030	0.028	0.0021
	DF28						
2		0.95	0.027	0.029	0.027	0.026	0.0020
3		0.97	0.028	0.029	0.028	0.028	0.0015
4		0.98	0.025	0.026	0.025	0.025	0.0012
5		0.95	0.024	0.025	0.023	0.024	0.0009
6		0.96	0.025	0.025	0.024	0.025	0.0011

Table 0.3: The slope (S), coefficients of determination (R^2) and standard error of the mean (SE) for axillary leaves (branches) on the main-shoot in relation to accumulated thermal time of lucerne genotypes with FD ratings of FD2, FD5 and FD10 subjected to 28-, 42- and 84 days defoliation frequency (DF) grown at Lincoln University, New Zealand.

Regrowth cycle	Defoliation frequency	R^2	S	Branching rate (Axillary leaves/°Cd)			SE
	Year: 2015			FD2	FD5	FD10	
1	DF84						
At 42 days		0.98	0.022	0.021	0.020	0.021	0.0008
End cycle		0.89	0.009	0.007	0.011	0.012	0.0060
2							
At 42 days		0.9	0.0135	0.013	0.014	0.013	0.0013
End cycle		0.12	0.0003				
	DF42						
1		0.99	0.022	0.023	0.021	0.023	0.0009
2		0.95	0.021	0.022	0.020	0.021	0.0009
3		0.84	0.015	0.013	0.015	0.017	0.0010
	DF28						
1		0.99	0.024	0.024	0.024	0.022	0.0030
2		0.82	0.012	0.015	0.009	0.011	0.0040
3		0.86	0.009	0.010	0.009	0.008	0.0018
4		0.5	0.006	0.007	0.004	0.006	0.0038

Regrowth cycle	Defoliation frequency	R^2	S	Branching rate (Axillary leaves/°Cd)			SE
	Year:2015/16			FD2	FD5	FD10	
	DF84						
1							
At 42 days		0.97	0.032	0.032	0.031	0.034	0.0017
End cycle		0.87	0.015	0.015	0.017	0.012	0.0028
2							
At 42 days		0.94	0.020	0.021	0.020	0.019	0.0012
End cycle		0.96	0.007	0.007	0.006	0.007	0.0010
3							
At 42 days		0.97	0.015	0.015	0.014	0.015	0.0015
End cycle		0.78	0.007	0.007	0.006	0.008	0.0022
	DF42						
1		0.85	0.024	0.027	0.019	0.027	0.0029
2		0.95	0.02	0.019	0.020	0.022	0.0010
3		0.96	0.0248	0.025	0.023	0.026	0.0013
4		0.96	0.015	0.016	0.014	0.014	0.0019
5		0.87	0.014	0.013	0.014	0.014	0.0013
6		0.81	0.008	0.006	0.008	0.012	0.0017

Regrowth cycle	Defoliation frequency	R^2	S	Branching rate (Axillary leaves/°Cd)			SE
				FD2	FD5	FD10	
	Year:2015/16						
	DF28						
1		0.9	0.009	0.010	0.009	0.008	0.0012
2		0.98	0.007	0.008	0.008	0.007	0.0014
3		0.88	0.009	0.010	0.010	0.008	0.0019
4		0.79	0.009	0.009	0.010	0.008	0.0017
5		0.98	0.01	0.010	0.011	0.010	0.0013
6		0.95	0.008	0.008	0.008	0.008	0.0017
7		0.58	0.004	0.006	0.002	0.003	0.0045
8		0.88	0.002	0.002	0.001	0.002	0.0017
9		0.35	0.001	0.002	0.001	0.001	0.0015
	Year:2016/17						
	DF84						
1							
At 42 days		0.85	0.013	0.012	0.012	0.015	0.0013
End cycle		0.94	0.033	0.033	0.035	0.031	0.0021
2							
At 42 days		0.95	0.027	0.028	0.029	0.026	0.0022
End cycle		0.65	0.0059	0.006	0.005	0.007	0.0021

Regrowth cycle	Defoliation frequency	R^2	S	Branching rate (Axillary leaves/°Cd)			SE
				FD2	FD5	FD10	
	Year:2016/17						
	DF42						
2		0.92	0.019	0.022	0.021	0.019	0.0013
3		0.93	0.017	0.018	0.016	0.017	0.0014
4		0.91	0.0156	0.016	0.015	0.016	0.0023
	DF28						
2		0.79	0.008	0.008	0.007	0.006	0.0024
3		0.85	0.0106	0.012	0.010	0.009	0.0017
4		0.82	0.011	0.012	0.011	0.010	0.0015
5		0.91	0.017	0.018	0.016	0.013	0.0015
6		0.88	0.016	0.018	0.015	0.016	0.0016

Table 0.4: The slope (S), coefficients of determination (R^2) and standard error of the mean (SE) for plant height in relation to accumulated thermal time of lucerne genotypes with FD ratings of FD2, FD5 and FD10 subjected to 28-, 42- and 84 days defoliation frequency (DF) grown at Lincoln University, New Zealand.

Regrowth cycle	Defoliation frequency	R^2	S	Stem expansion rate (cm/°Cd)			SE
	Year: 2015			FD2	FD5	FD10	
1	DF84						
At 42 days		0.96	0.115	0.105	0.114	0.127	0.0078
End cycle		0.12	0.026	0.014	0.016	0.048	0.0065
2							
At 42 days		0.53	0.042	0.022	0.038	0.079	0.0073
End cycle		0.43	0.002	0.003	0.008	0.019	0.0085
	DF42						
1		0.83	0.109	0.081	0.101	0.146	0.0059
2		0.84	0.066	0.052	0.062	0.084	0.0019
3		0.47	0.032	0.014	0.026	0.056	0.0047
	DF28						
1		0.92	0.117	0.094	0.117	0.141	0.0037
2		0.88	0.098	0.072	0.099	0.120	0.0064
3		0.7	0.055	0.030	0.050	0.090	0.0052
4		0.57	0.036	0.018	0.027	0.064	0.0048

Regrowth cycle	Defoliation frequency	R^2	S	Stem expansion rate (cm/°Cd)			SE
				FD2	FD5	FD10	
	Year:2015/16						
	DF84						
1							
At 42 days		0.94	0.128	0.103	0.140	0.142	0.0079
End cycle		0.72	0.066	0.063	0.065	0.070	0.0048
2							
At 42 days		0.92	0.154	0.132	0.160	0.171	0.0052
End cycle		0.27	0.021	0.020	0.023	0.020	0.0050
3							
At 42 days		0.92	0.122	0.104	0.123	0.140	0.0089
End cycle		0.23	0.034	0.032	0.035	0.036	0.0042
	DF42						
1		0.89	0.102	0.083	0.098	0.124	0.0075
2		0.97	0.144	0.127	0.146	0.158	0.0081
3		0.91	0.178	0.143	0.190	0.201	0.0190
4		0.94	0.136	0.120	0.141	0.149	0.0120
5		0.86	0.089	0.066	0.094	0.110	0.0093
6		0.54	0.066	0.033	0.052	0.113	0.0028

Regrowth cycle	Defoliation frequency	R^2	S	Stem expansion rate (cm/°Cd)			SE
				FD2	FD5	FD10	
	Year:2015/16						
	DF28						
1		0.9	0.051	0.040	0.050	0.063	0.0212
2		0.99	0.087	0.083	0.086	0.092	0.0121
3		0.95	0.107	0.060	0.104	0.121	0.0620
4		0.8	0.061	0.041	0.061	0.080	0.0402
5		0.9	0.097	0.073	0.099	0.119	0.0254
6		0.96	0.100	0.085	0.099	0.117	0.0061
7		0.78	0.050	0.033	0.043	0.065	0.0078
8		0.38	0.031	0.009	0.021	0.063	0.0045
9		0.46	0.030	0.012	0.018	0.055	0.0021
	Year:2016/17						
	DF84						
1							
At 42 days		0.87	0.057	0.043	0.064	0.065	0.0250
End cycle		0.91	0.157	0.146	0.180	0.145	0.0179
2							
At 42 days		0.98	0.161	0.150	0.166	0.167	0.0235
End cycle		0.77	0.055	0.060	0.052	0.053	0.0164

Regrowth cycle	Defoliation frequency	R^2	S	Stem expansion rate (cm/°Cd)			SE
	Year:2016/17			FD2	FD5	FD10	
	DF42						
2		0.91	0.101	0.087	0.103	0.123	0.0321
3			0.111	0.102	0.111	0.122	0.0250
4		0.97	0.13	0.124	0.132	0.136	0.0124
	DF28						
2		0.98	0.052	0.044	0.049	0.061	0.0201
3		0.97	0.08	0.071	0.086	0.083	0.0115
4		0.97	0.089	0.080	0.088	0.099	0.0120
5		0.99	0.076	0.071	0.078	0.077	0.0151
6		0.99	0.106	0.101	0.113	0.110	0.0212

Table 0.5: The slope (S), coefficients of determination (R^2) and standard error of the mean (SE) for leave senescence in relation to accumulated thermal time of lucerne genotypes with FD ratings of FD2, FD5 and FD10 subjected to 28-, 42- and 84 days defoliation frequency (DF) grown at Lincoln University, New Zealand.

Regrowth cycle	Defoliation frequency	R^2	S	Leaf senescence rate (senesced leaf/°Cd)			SE
	Year: 2015			FD2	FD5	FD10	
	DF84						
1		0.96	0.017	0.015	0.016	0.019	0.0015
2		0.84	0.017	0.017	0.018	0.014	0.0060
	DF42						
1		0.96	0.011	0.011	0.010	0.013	0.0042
2		0.99	0.0185	0.018	0.019	0.019	0.0021
3		0.98	0.024	0.022	0.024	0.026	0.0032
	DF28						
1		0.98	0.021	0.021	0.019	0.024	0.0202
2		0.88	0.014	0.010	0.015	0.018	0.0254
3		0.27	0.001	0.001	0.001	0.002	0.0201
4		0.50	0.003	0.004	0.002	0.004	0.0152
	Year:2015/16						
	DF84						
1		0.95	0.016	0.016	0.014	0.018	0.0058
2		0.97	0.016	0.016	0.016	0.017	0.0035

Regrowth cycle	Defoliation frequency	R^2	S	Leaf senescence rate (senesced leaf/°Cd)			SE
	Year:2015/16			FD2	FD5	FD10	
	DF84						
3		0.95	0.021	0.016	0.023	0.024	0.0031
	Year:2015/16						
	DF42						
1		0.89	0.019	0.021	0.018	0.018	0.0059
2		0.93	0.015	0.016	0.016	0.015	0.0036
3		0.96	0.023	0.024	0.021	0.023	0.0067
4		0.93	0.018	0.014	0.015	0.016	0.0026
5		0.9	0.018	0.019	0.017	0.018	0.0074
6		0.76	0.015	0.012	0.012	0.022	0.0043
	DF28						
1		0.96	0.025	0.029	0.025	0.020	0.0087
2		0.98	0.021	0.023	0.022	0.019	0.0049
3		0.97	0.017	0.020	0.017	0.015	0.0053
4		0.94	0.026	0.020	0.028	0.031	0.0097
5		0.97	0.025	0.028	0.026	0.021	0.0098
6		0.95	0.012	0.012	0.009	0.014	0.0028
7		-	-				
8		-	-				

Regrowth cycle	Defoliation frequency	R^2	S	Leaf senescence rate (senesced leaf/°Cd)			SE
	Year:2015/16			FD2	FD5	FD10	
	DF28						
9		-	-				
	Year:2016/17						
	DF84						
1		0.96	0.017	0.016	0.018	0.018	0.0026
2		0.97	0.018	0.018	0.019	0.018	0.0018
	DF42						
2		0.93	0.020	0.024	0.016	0.019	0.0076
3		0.94	0.019	0.018	0.018	0.021	0.0083
4		0.98	0.019	0.019	0.020	0.019	0.0034
	DF28						
2		-	-				
3		-	-				
4		-	-				
5		0.94	0.016	0.020	0.013	0.017	0.0067
6		0.91	0.014	0.014	0.013	0.016	0.0024

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