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LUPIN

Growth & Development

This book describes the growth and development of the lupin plant from germination to seed filling.

The environmental factors and management actions that influence each growth stage are also discussed.

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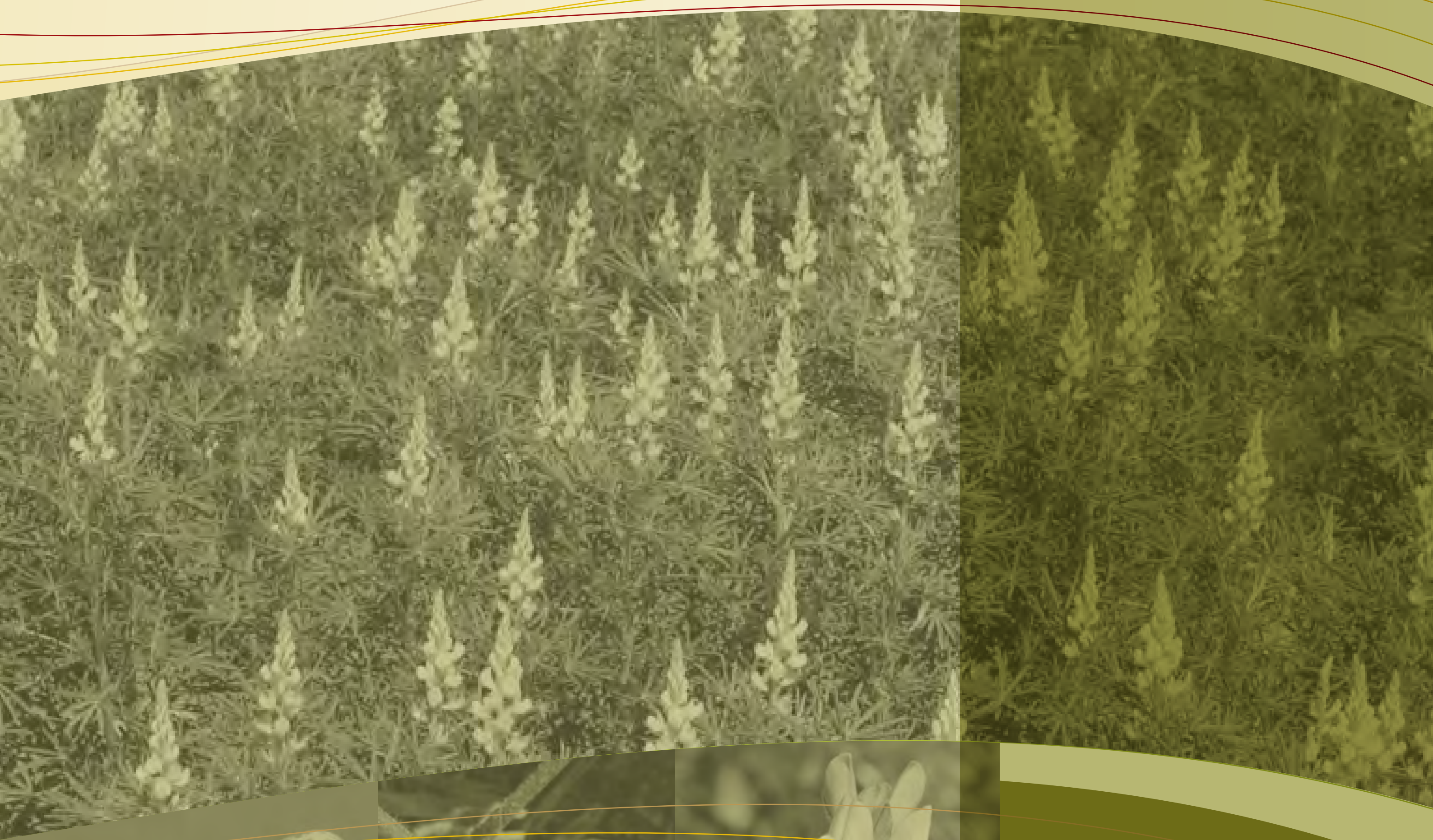
Lupin growth & development



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Contents

Preface

This book describes the growth and development of the lupin plant from germination to seed filling. The environmental factors and management actions that influence each growth stage are provided as a practical reference for managing crops.

The aim of *Lupin growth and development* is to link plant physiology and crop management. It will help agronomists and farmers to understand the life cycle of the lupin plant and the factors that influence growth and development, and to identify the growth stages of the plant. This knowledge can then be applied to crop management to maximise yield and profit.

There are four chapters in the book covering the progression of key stages in the life cycle of the lupin plant, including growth and management. Included in each chapter are practical exercises to demonstrate how knowledge of plant physiology can be applied in the paddock.

Introduction

by Janet Walker

Growing lupin

There are more than 200 species of ***Lupinus*** across the world. About 90% of these originated in North and South America, over a range extending from Alaska in the north, to Argentina and Chile in the south. The remainder of the species are found in the Mediterranean region and northern Africa. Most of the economically important species come from the Mediterranean region and have large seeds.

Three species of the *Lupinus* genus native to the Mediterranean region are grown around the world. They are the white or albus lupin (*L. albus*), narrow-leafed lupin (*L. angustifolius*) and yellow lupin (*L. luteus*). The sweet pearl lupin (*L. mutabilis*) is native to South America, where it is grown. This book will focus on albus and narrow-leafed lupin, the two main species grown commercially in Australia.

Lupin has three main uses:

- in livestock feeding rations in extensive and intensive production systems
- in human consumption (mainly in the Middle East as snack food and for flour in Europe)
- in crop rotations for its ability to add nitrogen and increase the availability of phosphorus in soils.

Lupin is an important crop in Australia as a disease break in crop rotations. More lupin is grown in Australia than any other pulse crop, and Australia is the world's largest exporter of lupin. The majority of production occurs in Western Australia, although lupin is widely grown in New South Wales, Victoria and South Australia (Figure i).

Lupin
The name commonly used for all species of the genus *Lupinus*. 'Lupin' is derived from the latin word lupus, meaning 'wolf'.

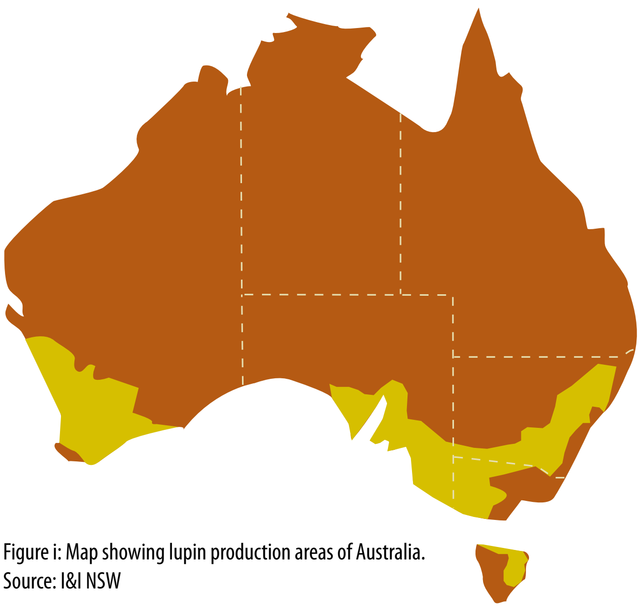

Figure i: Map showing lupin production areas of Australia.
Source: I&I NSW

New South Wales Production

NSW produces an average 75,000 tonnes of lupin annually (Figure ii), with production fluctuating with seasonal conditions. Since the identification of anthracnose in Western Australia in 1999, albus production in NSW has increased (Figure iii). Albus lupin now makes up 50% of the NSW crop, making NSW the largest producer.

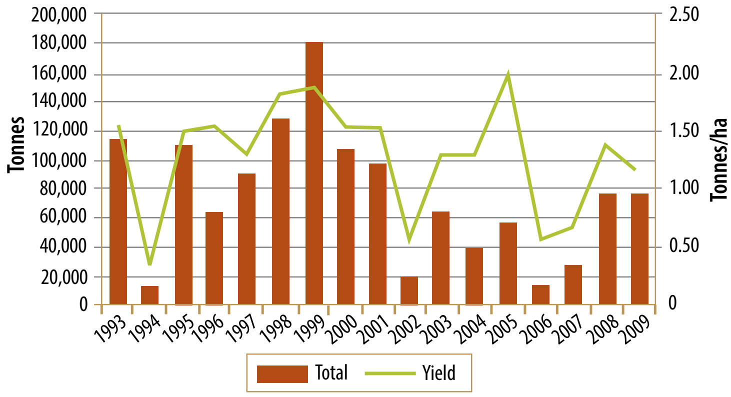

Figure ii: NSW lupin production and yields 1993–2009. Source: I&I NSW (1993–2009)

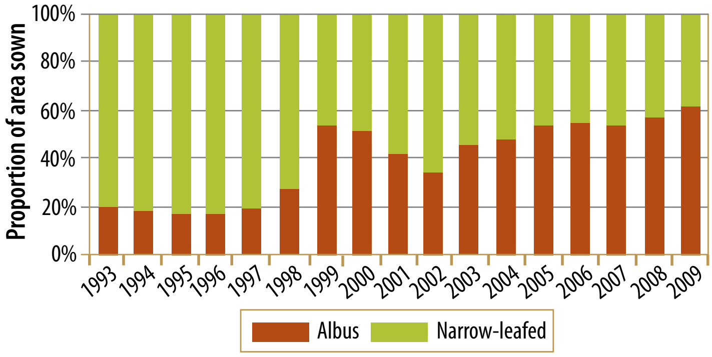

Figure iii: Proportions of narrow-leafed and albus lupin production in NSW. Source: I&I NSW (1993–2009)

The main lupin production area in NSW is in the south-east of the State. A mix of both narrow-leafed and albus lupin is grown. In the north-west, production is predominantly albus lupin; because of their susceptibility to cucumber mosaic virus, very few narrow-leafed crops are grown.

Cultivated lupin types

Narrow-leafed lupin (*Lupinus angustifolius*)

Narrow-leafed lupin (Figure iv) accounts for 80% of the total area sown to lupin in this country. The seed has a protein content of around 35% and is used mainly as stockfeed. Narrow-leafed lupin seed is round and speckled, and slightly smaller than the seed of field pea or soybean.

Narrow-leafed lupin is well suited to light, sandy, acidic soils. It will grow on red clay loams but prefers deep, coarse-textured, free-draining, sandy soils. It grows best in the higher rainfall areas of the central and southern NSW wheat belt.

Figure iv. Narrow-leafed lupin. Photo: Jan Edwards, I&I NSW

Albus lupin (*Lupinus albus*)

The albus or white lupin (Figure v) accounts for 20% of the area sown to lupin in Australia. It is traditionally grown in the Mediterranean region and along the Nile Valley, where it has been grown for several thousand years. The wild populations of this species are all bitter seeded, with an indeterminate growth habit.

Sweet-seeded varieties have been bred for human consumption; excess production is used in the stockfeed industry. Albus lupin has a higher protein content (around 46%) than narrow-leafed lupin. Albus lupin produces a flat, squarish seed that is larger than the seed of the narrow-leafed lupin (Table i).

Albus lupin prefers more fertile, heavier textured and less acidic soils than narrow-leafed lupin. It can achieve higher yields but is more sensitive to frost and waterlogging than narrow-leafed lupin.

Albus lupin has a similar growth habit to narrow-leafed lupin, but with a thicker stem, broader leaflets and larger flowers.

Yellow lupin (*Lupinus luteus*)

Sweet-seeded varieties of yellow lupin were developed in Germany in the 1950s and are grown widely in Eastern Europe for animal feed. The yellow lupin seed has a protein content of up to 48%, similar to that of the albus lupin. Yellow lupin seed also contains very little oil and more fibre. It has a round, beige or brown-speckled seed that is smaller and lighter than that of narrow-leafed lupin.

The yellow lupin is suited to highly acidic soils in low-rainfall agricultural areas but is not widely grown in Australia. Yellow lupin has several advantages over narrow-leafed lupin, including greater tolerance of aluminium, greater ability to scavenge soil for phosphorus, and better waterlogging tolerance. It also has true resistance to the diseases brown leaf spot and *Pleiochaeta* root rot and immunity to cucumber mosaic virus.

Figure v. Albus lupin. Photo: Raymond Cowley, I&I NSW

Yellow lupin is not grown commercially, because the currently available varieties have considerably lower yield potential than the best narrow-leafed lupin varieties. It is also more sensitive to frost and more susceptible to the disease anthracnose.

Pearl lupin (*Lupinus mutabilis*)

The pearl lupin originated in the Andean highlands of South America, where it has been grown for centuries by the indigenous people of Ecuador, Peru and Bolivia. There is no commercial mechanised production of the pearl lupin anywhere in the world.

The high seed protein and oil contents of the pearl lupin are similar to those of soybean (protein 45% and oil up to 18%). However, to grow pearl lupin commercially, high-yielding, low-alkaloid, earlier flowering varieties need to be developed. The pearl lupin tends to flower late and branch readily. This results in low yields under commercial production. Pearl lupin, like albus lupin, requires more fertile soil than narrow-leafed lupin. It is more tolerant of low soil pH and waterlogging than albus lupin but still prefers well-drained soil.

Life cycle

The growth and development of the lupin plant are complex and overlapping (Figure vi).

Growth is the increase in the size and number of leaves, stems and roots, which produce biomass. Because growth is fuelled by photosynthesis it is directly related to water use and light interception. Growth is discussed in detail in Chapter 2.

Table i. Comparison of albus and narrow-leafed lupin characteristics.

SPECIES	PLANT HEIGHT (CM)	FLOWER COLOUR	SEED WEIGHT (MG)
Narrow-leafed lupin (*L. angustifolius*)	20–100	Blue, occasionally pink, white in domesticated forms	30–240
Albus lupin (*L. albus*)	40–150	White, pale pink, light blue, blue	120–870

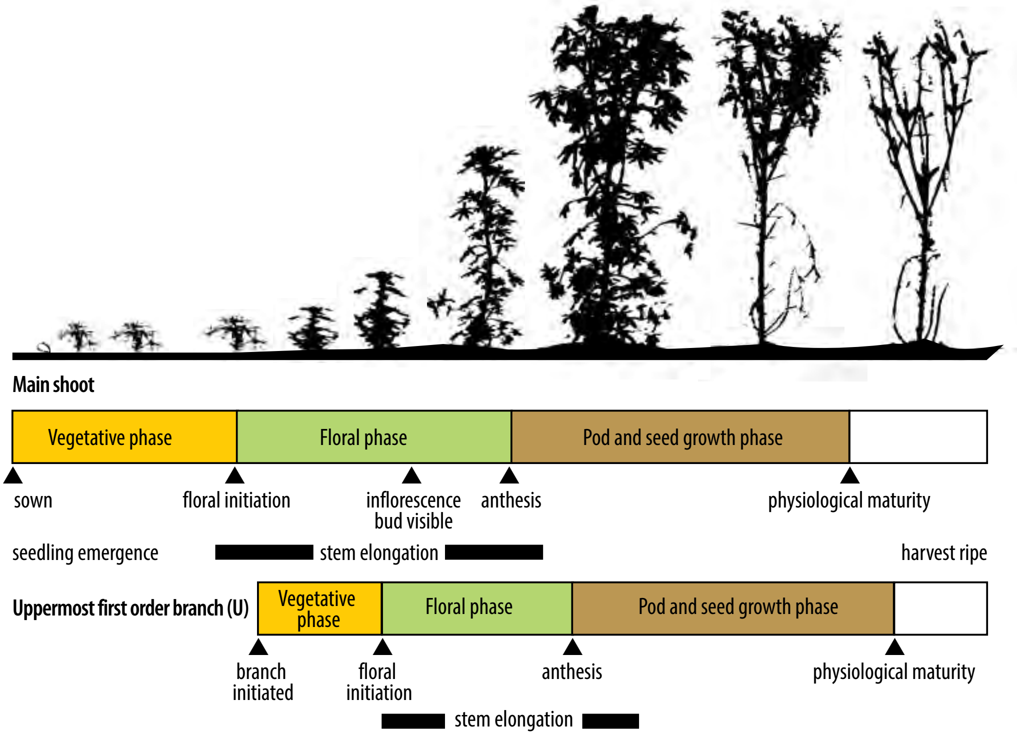

Figure vi. Life cycle of the lupin plant. Source: I&I NSW

Development is the process by which the plant moves from one growth stage to another. The rate and timing of plant development are determined by variety, photoperiod and temperature. Development is discussed in detail in Chapter 3.

Decimal growth scale

Effective crop management depends on correctly identifying the growth stage of the crop. This is important for herbicide applications and harvest timing. A growth scale provides a common reference for describing these growth stages.

The scale (Table ii) is similar to the Zadoks code for wheat. It is designed for assessing the development of the main shoot of individual plants. When assessing flower, pod and seed development, the lowest (most advanced) node of the main shoot inflorescence (flower spike) is used.

There are six stages: germination, leaf emergence, stem elongation, flowering, pod ripening and seed ripening. Each stage is subdivided into 10 units: for example, 0 to 0.9 covers germination and seedling emergence through to 5.0 to 5.9 for seed ripening. Some of the stages overlap, because vegetative and reproductive development occurs simultaneously.

Where appropriate, throughout this book, a growth stage reference is provided for the development stage under discussion.

The lupin plant

In Australia, lupin is grown as a winter pulse crop sown in mid autumn and maturing in late spring. The lupin species currently grown in Australia originated from a Mediterranean environment characterised by cool wet winters, followed by a rapid and sometimes early finish to the growing season brought about by low soil moisture levels and high temperatures. Early flowering is an advantage for Australian grain producers.

Lupin is an annual legume (or pulse crop) that grows to between 20 and 150 cm high. Narrow-leafed lupin can grow to over 100 cm tall, but it normally reaches a height of 50 to 80 cm. Albus lupin may grow up to 150 cm.

The main structures of the lupin plant are the leaves, inflorescence (flower spike), branches, stem (Figure vii), roots, pods and seeds.

Table ii. Lupin growth stages and the numeral system.

STAGE	DECIMAL SCORE
GERMINATION AND SEEDLING EMERGENCE	**0**
Dry seed	0.0
Start of imbibition (water absorption)	0.1
Radicle (root) protruding through the testa (seed coat)	0.3
Radicle 5 mm long (germination)	0.5
Hypocotyl protruding through the seed coat	0.7
Part of the seeding protruding through the soil	0.9
LEAF EMERGENCE	**1**
First pair of leaves protruding beyond upright cotyledons	1.0
1 leaf emerged from bud	1.1
2 leaves emerged from bud	1.2
3 leaves emerged from bud	1.3
4 leaves emerged from bud	1.4
5 leaves emerged from bud	1.5
7 leaves emerged from bud	1.7
10 leaves emerged from bud	1.10
STEM ELONGATION	**2**
Little separation between bases of leaves	2.1
Bases of some basal leaves clearly separated	2.3
Bases of several leaves clearly separated from each other	2.5
Flower spike (inflorescence) bud clearly visible	2.7
Flower spike bud clearly separated from the base of the highest leaf	2.9
FLOWERING	***3***
Bracts completely hiding corolla	3.0
Pointed bud stage	3.1
Hooded bud stage	3.2
Diverging standard petal stage (anthesis)	3.3
Open flower stage	3.4
Coloured corolla stage	3.5
Senescent corolla stage	3.7
Floret abscised	3.8
Pod set	3.9
POD RIPENING	**4**
Young green pod. No septa between seeds, seeds abutting	4.0
Seeds separated	4.1
Green pod, septa between seeds, slight bulging of walls, seeds filling 50% of the space between the septa	4.2
Seeds filling 75% of the space between the septa	4.3
Green pod, clear seed bulges in pod walls, seeds filling all space between septa	4.4
Green pod, septa split	4.5
Pod turning khaki-coloured	4.7
Pod pale reddish-brown and wrinkled	4.9
SEED RIPENING	**5**
Seed small, dark green with watery contents	5.0
Seed medium, dark green with watery contents	5.1
Seed large, dark green with watery contents	5.2
Seed large and soft, light green coat, no watery contents, green cotyledons	5.4
Seed light green to pale greyish-blue coat, green cotyledons	5.5
Green to yellow cotyledons	5.6
Pale fawn coat, yellow to golden orange cotyledons (physiological maturity)	5.7
Seed hard but dentable, mottling of pale fawn coat	5.8
Seeds hard and harvest ripe	5.9

Source: Modified from Dracup and Kirby (1996)

Leaves

Lupin has a palmate leaf structure with leaflets radiating from a central point. Slender, tapered stipules are located on either side of the petiole where it attaches to the stem (Figure vii).

Lupin leaves are made up of leaflets. The leaflets are broad and rounded in albus lupin. Narrow-leafed lupin has narrow, pointed leaflets (Figure viii). The number of leaflets per leaf increases in number up the plant. The initial leaves contain five leaflets per leaf, whereas the top leaves can have between nine and 12 leaflets. The exact number of leaves on the main stem varies according to variety, location and sowing date.

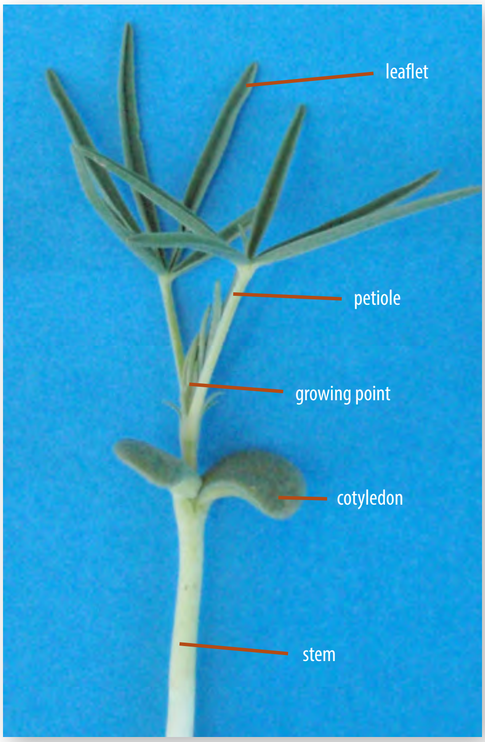

Figure vii: Parts of a narrow-leafed lupin seedling. Photo: Lowan Turton

The lupin plant is heliotropic (Figure ix). This means that the leaves turn throughout the day to follow the sun to maximise light interception. During the night the leaves turn so that they are facing the rising sun in the morning. This continues until flowering commences.

Indeterminate growth
Ability of a plant to produce more branches or flower spikes after the plant has reached the reproductive phase. If conditions (water, nutrients and sunlight) remain favourable the plant will produce flowers over an extended period of time and multiple stages of reproductive development will occur on the plant at the same time, all competing for limited resources.

Determinate growth
Growth that stops (terminates) once a genetically predetermined structure (e.g. a flower) has been produced. Crops that have determinate growth patterns will stop growing and will begin to dry off after seed is produced. Crops with indeterminate growth patterns will continue to produce further shoots and seeds until desiccated.

Stem and branches

Lupin has an **indeterminate growth** habit, meaning that it can continue to initiate new lateral branches with flower spikes after it reaches the reproductive phase. This can occur when the plant has access to adequate moisture, nutrients and sunlight.

Each branch is **determinate** and has a terminal inflorescence (flower spike). The pods on the branch all mature at approximately the same time. The main stem is the first to develop. The lateral branches form orders from the main stem (Figure x). The first order is the branch arising from the main stem below the primary flower spike (see Chapter 2

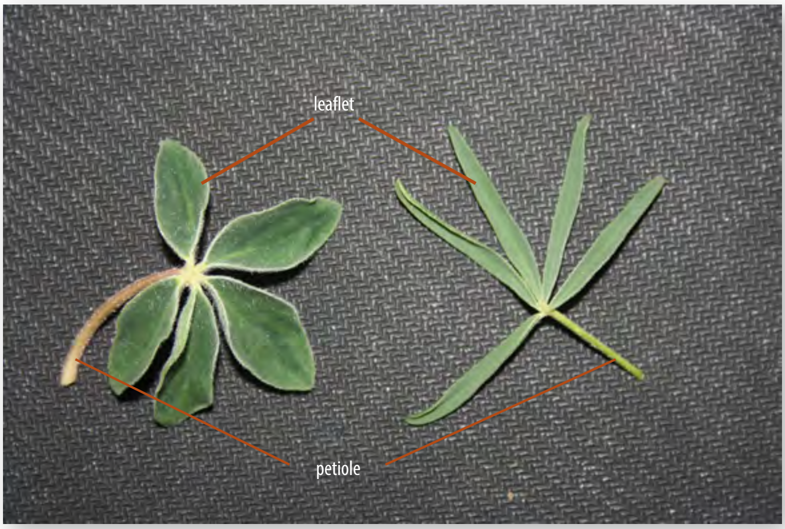

Figure viii. Left: Albus leaf. Right: narrow-leafed lupin leaf. Photo: J Walker


Figure ix. Heliotropism in albus lupin seedlings with all leaves facing the sun. Photo: J Walker

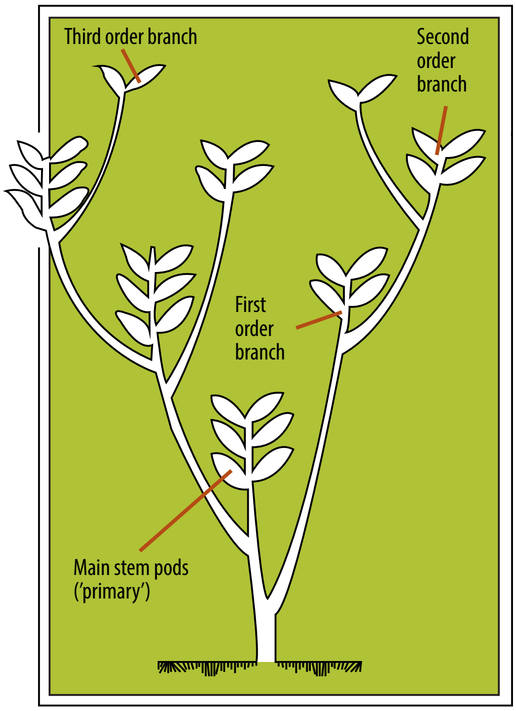

Figure x. The lupin plant, showing branch orders and flowering. Source: I&I NSW

Vegetative growth). The lupin plant can have three or four orders of lateral branches in a good season, although in drier environments more than two orders is uncommon.

To increase harvest index and yield, varieties have been bred to reduce internode length and therefore overall plant height. This reduces lodging and allows easier harvest. Breeding also aims to produce plants with short branches and earlier maturity, allowing the whole canopy to mature together.

Roots

Lupin has a strong taproot system, which is the primary root system. Lateral roots grow out from the taproot and form the secondary root system. The pattern and extent of lateral root growth depend on the species of lupin. Albus lupin species also develop proteoid roots (see Chapter 2 *Vegetative growth*) that help them to take up phosphorus in acidic soils.

Lupin is a pulse crop that can tolerate fairly acidic conditions, down to a pH_{Ca} of 4.5. In acid soils, the level of soil extractable aluminium is a better indicator of lupin yields than pH alone.

Like all legumes, lupin forms nodules (Figure xi) containing rhizobial bacteria, which fix nitrogen in the soil (see Chapter 2 *Vegetative growth*).

Figure xi. Root system of albus lupin seedling, showing taproot and secondary root systems with nodules. Photo: Lowan Turton

Flower spike

Lupin produces a flower spike (raceme) on the end of each branch; this is referred to as a terminal flower spike (Figure xii). Each flower spike is made up of many individual flowers. Each flower has five petals, like all the flowers in the Fabaceae family. Flowering starts at the base of the flower spike and continues up the stem. A lupin plant will flower for 4 to 8 weeks, but an individual raceme usually flowers for only 10 to 14 days.

Narrow-leafed lupin is self-pollinated, with very little cross-pollination. Albus lupin is also self-pollinating but has a higher proportion of cross-pollination (see 'Seed quality' in Chapter 1 and Chapter 3 *Reproductive development*).

Branch order (e.g. first order, second order)

Lateral branches grow from the main stem. The first-order branches grow from the main stem below the primary flower spike (inflorescence). The second-order branches develop below the first-order branch, and so on. Up to four orders of lateral branches develop in a good season.

Cotyledons
The food stores for the germinating plant and the largest part of the seed. They form the seed leaves directly from the embryo. Lupin and all broad-leafed plants are known as dicots, because they have two cotyledons.

Figure xii. Top: flowers of albus lupin. Photo: Janet Walker. Bottom: flowers of narrow-leafed lupin. Photo: Jan Edwards

The pod

Each pod contains between two and seven seeds. The walls of the pod thicken and act as an energy store for the seed as it grows. The pod walls of narrow-leafed lupin are thinner than those of albus lupin and dry faster at harvest. In lupin, the outside of the pod makes up a greater proportion of the total pod weight at maturity than in other legumes such as soybean.

The seed

The lupin seed (Figures xiii and xiv) is made up of several parts. The seed is surrounded by a seed coat called the testa or hull. The seed coat comprises about 25% of the seed weight in narrow-leafed lupin and 15% in albus lupin. This is higher than in most domesticated grain species.

There are several layers in the testa, which surrounds the embryo. The embryo has two main parts, the embryo shoot, which grows up to form the plant, and the radicle, which grows down to form the root system. Each seed has two **cotyledons**, which nourish the embryo during germination and emergence.

Lupin seeds have two distinct marks on the outside. The hilum is the scar left when the seed separates from the seed stalk in the pod. The small bump below this is the radicle bump; the radicle will emerge from this bump at germination.

Lupin seed is valued because of its high protein, high digestibility and low starch levels (Tables iii and iv). The amount of protein depends on the species and variety and where it is grown. See also Chapter 4 *Pod and seed development*.

The high protein level makes lupin seed highly desirable for animal rations. Narrow-leafed lupin is particularly suited as feed for ruminants and single-stomached animals such as pigs and horses, and as a feed in aquaculture. Albus lupin is more suited to feeding ruminants than single-stomached animals because of its high seed manganese levels, which limit the growth of single-stomached animals.

Wild lupin seeds contain high levels of quinolizidine alkaloids. These alkaloids are part of a natural defence mechanism against insects and other herbivores. They are also thought to give some stress tolerance. However, alkaloids produce a bitter taste and are highly toxic. Alkaloids have been bred out of most commercial varieties of lupin, except the lupini bean, which is grown specifically for its bitter seed. Narrow-leafed lupin is free of bitter seed. However, seed from older albus lupin varieties can contain up to 3% quinolizidine alkaloids. See *Bitterness in albus lupin* and *In the paddock* in Chapter 1 for details of how to investigate the proportion of bitter seed.

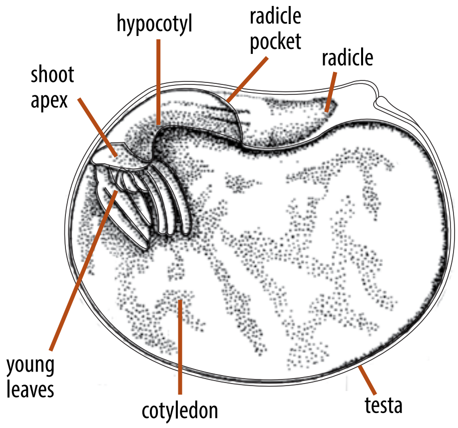

Figure xiii. Seed of narrow-leafed lupin.

Figure xiv. Lupin seeds. Left: narrow-leafed lupin. Right: albus lupin. Photo: Jan Edwards

Table iii. Attributes of lupin seed

	NARROW-LEAFED LUPIN	ALBUS LUPIN
Seed coat	24%	18%
Crude protein (%)	27%–37%	30%–40%
Starch (carbohydrate) (%)	6%	–
Oil (%)	4%–7%	7%–11%
Megajoules of energy (MJ) sheep	12.2	12.5
Megajoules of energy (MJ) cattle	12.0	11.9
Megajoules of energy (MJ) pigs	14.6	16.9
Acid detergent fibre (%)	17%–25%	12%–16%
Minerals (Ash)	2%	3%

Source: I&I NSW; Hawthorne (2006); and Gladstones et al. (1998)

Table iv. Mineral (ash) content of lupin seed

Phosphorus (g/kg)	3.0–3.6
Calcium (mg/g)	15–29
Magnesium (mg/g)	11–20
Sodium (mg/g)	3–11
Potassium (mg/g)	66–90
Iron (mg/kg)	31–150
Zinc (mg/kg)	24–45
Copper (mg/kg)	2.5–6.8

Source: I&I NSW; Gladstones et al. (1998)

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1. Germination and emergence

by Janet Walker and Jan Edwards

Chapter Snapshot

Introduction

Under the right temperature and moisture conditions the lupin seed swells and the first root and the first shoot emerge from the seed. Once the first leaves emerge and the seedling is established it is able to photosynthesise.

Chapter 1 explains the processes of germination and emergence.

Learning Outcomes

At the end of this chapter, you will be able to:

- identify the development stages in germination and emergence
- describe epigeal emergence and its implications for sowing lupin
- describe the climatic and physical factors that affect germination
- calculate germination percentage and seed weight and use these to calculate sowing rate.

Germination
Growth stages 0–0.7

Germination begins when the seed absorbs water and ends with the appearance of the radicle (the first root). Germination has three phases:

- water absorption
- activation
- visible germination.

Germination can take from 5 to 15 days, depending on soil temperature, moisture and depth of sowing. Variety has no effect on the length of this phase.

Phase 1 Water absorption
Growth stage 0.1

For a seed to grow it needs to absorb moisture. Lupin seeds at harvest contain about 13% moisture (see Chapter 4). Germination occurs when the water content reaches about 60% of the imbibed seed weight.

Lupin seeds are low in moisture. This means that the seed is capable of drawing water from soils that are very dry. As a result, the seeds can germinate in relatively dry soils. However, unlike in cereal crops such as oats, once germination starts in lupin it will not stop during moisture stress and then restart when the moisture returns.

Phase 2 Activation

Once the seed has swollen it produces hormones that stimulate enzyme activity, and metabolism begins.

The enzymes break down the starch into sugars. Lupin seedlings rely on sugar and oil from the cotyledons as the main energy source at this first stage of growth.

The storage proteins in the cotyledons are broken down to form the nitrogen and carbon (sugar) sources needed for initial development of the seedling.

Phase 3 Visible germination
Growth stages 0.3–0.7

The emergence of the radicle is the first visible sign of germination. When the radicle emerges it ruptures the testa near the hilum (Figure 1–1). The radicle is the first root and will grow down to anchor the plant in the soil. It then starts to absorb water and nutrients.

The next process is extension of the hypocotyl away from the radicle towards the soil surface. The hypocotyl is the long, white length of stem that connects the cotyledons to the root system.

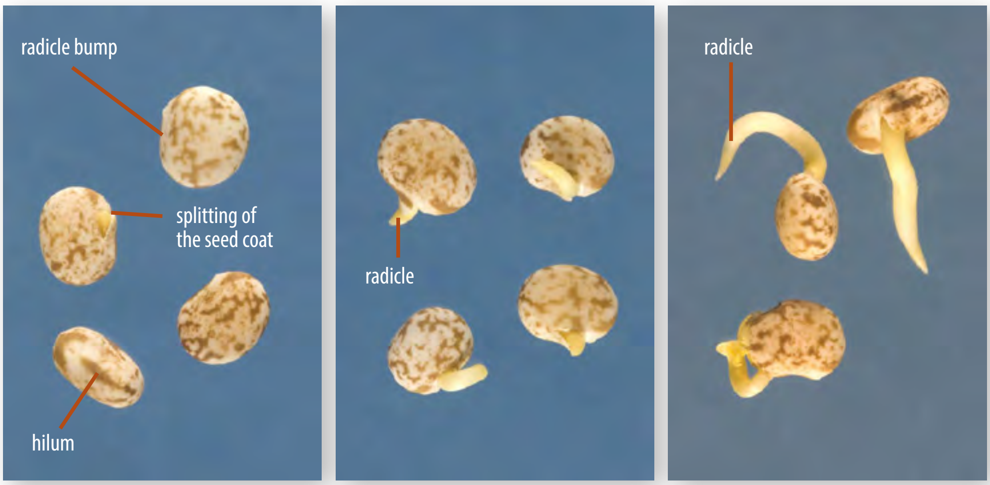


Figure 1–1. Signs of visible germination in narrow-leafed lupin: swelling of the seed, splitting of the seed coat and emergence of the radicle. Photos: L Turton

Emergence
Growth stage 0.9

Lupin has what is called 'epigeal' emergence (Figure 1–2). An epigeal seedling develops with its cotyledons above the ground. This contrasts with many other legumes, such as field pea, chickpea and faba bean, which have hypogeal emergence.

While it is still below ground, the apex of the hypocotyl is bent over to form a hook (Figure 1–3). This hook protects the meristem (or growing point) and eases its passage through the soil.

As the hypocotyl grows towards the soil surface, it pulls the cotyledons with it. They are pointed downwards and so protected. Often the seed coat is dragged to the surface as well.

Obstruction of seedling growth (e.g. by surface crusting) keeps the hook closed and promotes lateral stem expansion to strengthen the emerging shoot (Figure 1–3).

The hypocotyl is the first part to emerge from the ground, followed by the cotyledons. While the seedling is below the soil surface it remains pale or nearly white and the cotyledons do not expand. When the hypocotyl reaches the light it stops lengthening, chlorophyll synthesis is stimulated and the cotyledons expand.

After emergence the cotyledons turn green and the first leaf grows out from between them. At the same time, further root formation occurs from branching of the radicle.

Establishment

The plant is established once it has roots and a shoot (Figure 1–4). It is no longer relying on reserves in the seed, as it is producing its own energy. The leaves are now able to photosynthesise and the roots are able to take up water and nutrients.

A crop is said to be established when 50% of seeds have germinated and emerged and are developing with strong seedling vigour.

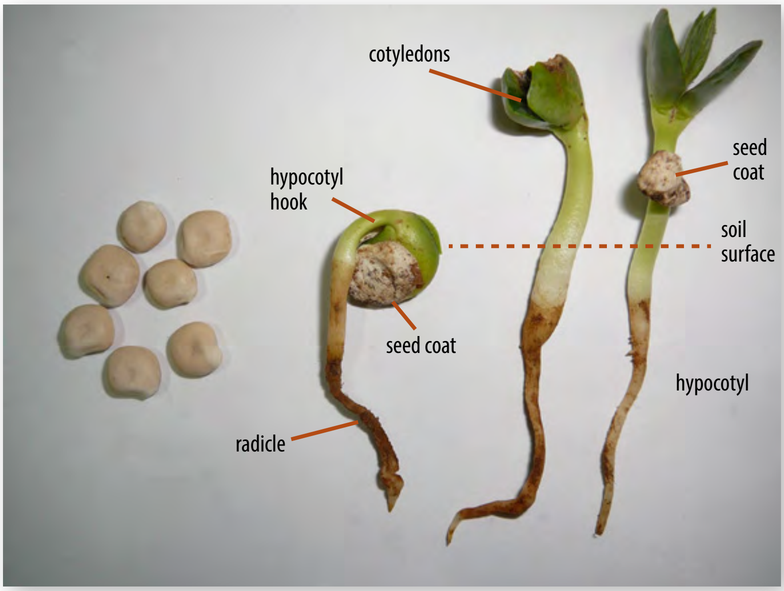


Figure 1–2. In epigeal emergence the cotyledons are carried above the ground. The length of the hypocotyl indicates the sowing depth. Photo Janet Walker

Figure 1–3. Left: Emerging albus lupin. Note thickening of shoot from pressure of surface crusting. Right: Emerging albus lupin seedling with seed coat. Photo: Janet Walker

Figure 1-4. Established albus lupin. Photo: Jan Edwards

Factors affecting germination, emergence and establishment

Successful crop establishment depends on a number of factors, including soil moisture, temperature, aeration, soil crusting, disease or seed quality. It is important to get the correct conditions for good crop establishment. Delayed emergence increases the risk of pathogen attack, predation and low seedling vigour.

Moisture

Moisture is vital for lupin establishment, as it influences how many days it takes for a plant to emerge. Emergence is more sensitive than germination to soil moisture levels (Figure 1–5).

Low soil moisture reduces the extension of the hypocotyl and increases the growth of the radicle. This increases the supply of moisture to the seedling but restricts emergence.

A lupin seed that has partly imbibed and then dried out will have reduced viability. This has implications when sowing into soils with marginal moisture.

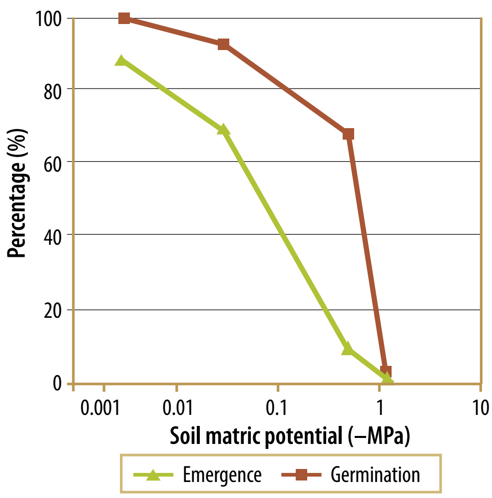
Sowing into hardsetting or crusting soils that dry out after sowing may result in poor emergence. The hard soil, which has high strength, makes it difficult for the hypocotyl to push through the surface.

Too much water can inhibit germination and early root growth. Oxygen is essential for seed germination. When soils become waterlogged, the oxygen supply in the soil solution rapidly decreases. Lupin will not germinate in waterlogged soils, and seed survival may be reduced to zero after as few as 4 days. Waterlogged soils also severely restrict the growth of the main and secondary root systems. Soil moisture at 50% of field capacity gives the best main root growth at establishment.

Temperature

Germination

Germination depends on temperature. The optimum temperature for the germination of lupin is 20°C. The speed of germination depends on the accumulated temperature, which is measured as degree-days. Degree-days are the sum of the average daily temperatures over consecutive days. For further information see Chapters 2 and 3.



- The ability of seed to take up water (imbibition) decreases as the soil gets drier.
- Emergence is more sensitive than germination to soil matric potentials.
- Germination occurs when the seed weight reaches 250% of the original oven-dry weight.
- At low moisture contents, seedlings can germinate but fail to emerge. The shoots are more sensitive to dry soil than the roots, owing to lack of hypocotyl extension.
- Extension of hypocotyls is more sensitive than radicle extension.

Figure 1–5. Effect of moisture on the final germination and emergence percentage of narrow-leafed lupin. A matric potential of about 1 MPa is essentially air dry, whereas 0.001 MPa is saturated. Source: Modified from Dracup et al. (1993)

The rate of germination increases linearly to 20°C, then declines. At 20°C, germination takes between 24 and 36 hours (1 to 1.5 days). This equates to about 27 degree-days. At temperatures greater than 23°C, germination can be highly variable. At temperatures above 30°C germination is very low (Figure 1–6). Germination is unlikely at temperatures greater than 33°C.

Emergence

Plant emergence and establishment are the starting points for crop growth. Maximum emergence occurs between 10 and 20°C. At 20°C, for example, narrow-leafed lupin takes 4 to 4.5 days to emerge from a depth of 4 cm. This equates to 75 degree-days. For every millimetre deeper the seed is planted, emergence will take about 2 degree-days longer.

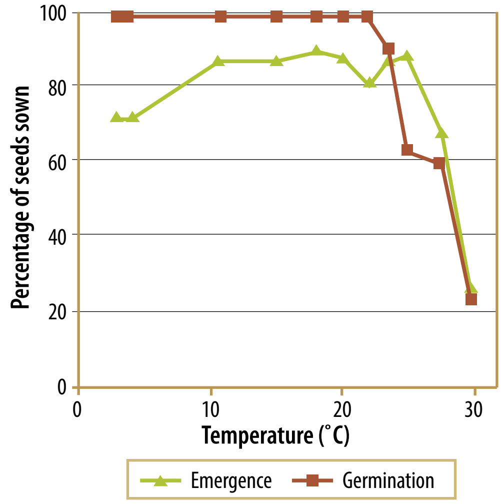
High temperatures during establishment can cause seedling death, reducing the number of plants that establish. At temperatures between 20°C and 25°C, seedlings generally fail to emerge, because splits or breakages occur in the radicle or hypocotyl. Above 27°C, emergence failure occurs mainly because of problems with seed rotting and disease.

In hot environments, the maximum temperature in the top few centimetres of the soil can be 10°C to 15°C higher than the maximum air temperature, especially with a dry, bare soil surface and high radiation intensity. Under these conditions, soil temperatures can reach 30°C, seriously affecting seedling emergence.

Figure 1–7 shows the probabilities that the 9 am soil temperature at a depth of 10 cm at Cowra, NSW, will be greater than 20°C and that the daily maximum air temperature will be greater than 30°C.

Seed quality

Seed quality is important for good establishment. Early seedling growth relies on stored energy reserves in the seed. Good seedling establishment is more likely if the seed is undamaged, stored correctly and from a plant that has had adequate nutrition.



- Germination was close to 100% at < 22°C. At 30°C, germination fell to only 27%.
- This suggests a ceiling temperature of 33°C.
- Emergence was best between 10°C and 20°C.
- At 30°C emergence was less than 40%.

Figure 1–6. Effect of temperature on final germination and emergence percentage of narrow-leafed lupin. Source: Modified from Dracup et al. (1993)

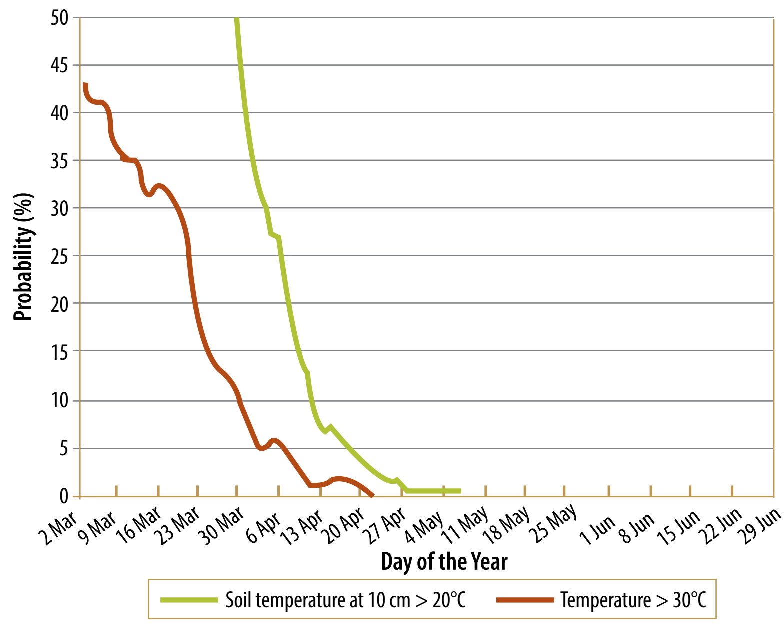


Figure 1–7. Probability that the 9 am soil temperature at a depth of 10 cm is greater than 20°C and the daily maximum air temperature is greater than 30°C; Cowra, NSW (1960–2009).
Source: Data from Bureau of Meteorology and Department of Environment, Climate Change and Water

Endosperm
A nutritive tissue within the seed that surrounds the embryo and provides energy for germination.

A number of factors in producing lupin seed can greatly affect germination. They include seed size, seed handling and harvest timing.

Seed size

The larger the seed, the larger the **endosperm** and starch reserves. Although seed size does not alter germination, larger seeds emerge earlier and faster than medium and small seeds. This is because larger seeds germinate more rapidly and their roots are longer than those of smaller seeds. With adequate moisture, medium-sized seeds will emerge in 5 or 6 days.

Seed size is usually measured by weighing 100 seeds. The result is known as the 100-seed weight. The 100-seed weight varies among varieties and from season to season. Therefore, sowing rates should be altered according to seed weight to achieve the desired plant population. Narrow-leafed lupin has a 100-seed weight of about 13 g, whereas albus lupin has a 100-seed weight of about 35 g (Table 1–1).

Table 1–1. Examples of lupin seed sizes.

	VARIETY	100-SEED WEIGHT (G)
Narrow-leafed lupin	Jindalee	13
	Mandalup	14
	Quilinock	16
Albus lupin	Kiev Mutant	35
	Luxor	35
	Rosetta	35

Source: I&I NSW

Seed grading is a good way to separate good-quality seed of uniform size from small or damaged seeds and other impurities such as weed seeds. Grading is important when sowing into soils with marginal moisture or when sowing depth is uneven.

Seed size and vigour are particularly important following drought years, when there is more small seed. Not only does seed size affect seedling vigour, it can also affect sowing rate. Sowing small lupin seeds at common sowing rates can result in the establishment of very high plant populations per square metre. High plant populations use more soil moisture during vegetative growth, leaving less for grain filling, resulting in small seed and low yields at harvest. It is important to determine the 100-seed weight to determine appropriate sowing rates (see *In the paddock* at the end of this chapter).

Harvest timing

Using a desiccant to bring a lupin crop in for harvest can also affect germination. Using desiccants on lupin dries the plant very fast. If the desiccant is not used at the right time, seed development can be stopped, resulting in unripe seeds with reduced germination ability. See Chapter 4.

Bitterness in albus lupin

Since 2005, the sowing threshold for bitterness contamination has been 0%. This aims to:

- keep the NSW albus lupin crop below the receival and export standard
- ensure that the level of bitter seed contamination does not increase in commercial seed crops
- reduce the chance of the newly released sweet albus lupin varieties becoming contaminated by bitter seed.

Even at a low level of contamination, the overall alkaloid level of the crop can exceed the threshold. There are two standards:

- The current Food Standard sets a threshold of 200 mg/kg of lupin alkaloids.
- Pulse Australia's Receival and Export Standards specify that bitter contaminants must be no more than 2 seeds per 200 g.

Any crops sown from potentially contaminated seed or lupini bean (a large-seeded, bitter albus lupin) must be grown at least 2 km away from other albus crops.

For further information see *The seed* in the Introduction.

Seed storage and handling

The aim of storage is to preserve the viability of the seed for future sowing and maintain its quality for market. Lupin seed stores well, being more resistant to weevil and insect attack than cereal grains. The conditions during storage can have a major impact on crop germination and establishment, so seed needs to be stored and handled correctly.

Temperature and moisture

At physiological maturity the lupin seed contains about 60% water. The seed then dries down to a moisture content of 15% by harvest time. Lupin seed stores best at a moisture content of between 13% and 14%.

Seed stored at 13% to 14% moisture at 20°C has little quality loss. However, above 30°C, quality loss is considerable at these moisture levels. If high temperatures are unavoidable, storing seed at a lower moisture content (e.g. 10%) slows seed quality deterioration.

Aeration

Aeration is important for high-moisture seed such as lupin seed, as it reduces temperature and provides a more uniform and stable storage temperature. Lower temperatures and aeration of silos reduce the chance of pest infestation of stored seed. Closed bulk storages can cause damage, as localised moisture leads to mould and patchy moisture damage.

Seed handling

Avoid excessive handling, as lupin seed is easily damaged. Damage can occur during harvest, grading and sowing. Handling after seed has dried below 15% moisture greatly increases cracking, which reduces germination. Table 1–2 shows the results of germination tests on farm-stored seed. Also see Chapter 4.

Seed dormancy

Wild lupin species have adapted to drought by producing seeds with coats that are impermeable to water (i.e. hard-seeded). This prevents germination of a large proportion of seed in any given year and makes sure that the species will survive when seed production fails, such

Table 1–2. Results of germination tests of lupin samples harvested in the Young district in 1993 and 1994 and tested after 4 months of storage.

	1993 (17 SAMPLES)			1994 (9 SAMPLES)		
	MAX	AVERAGE	MIN	MAX	AVERAGE	MIN
Normal seedlings (%)	93	53	13	90	76	36
Abnormal seedlings (%)	76	45	6	62	21	9
Dead seeds (%)	11	2	0	2	1	0
Hard seeds (%)	0	0	0	11	2	0
Broken seeds (%)	51	21	0	28	4	0

Source: Paul Parker, I&I NSW

- Samples were from Merrit, Gungurru and Ultra.
- Abnormal seedlings are unlikely to develop into plants after sowing.
- Broken seeds indicate severe damage; the seedlings will not germinate when the seed is sown under field conditions.

as after a drought. These hard-seeded species need temperature changes or scarifying to crack the seed coat before germination can begin. The seed of some wild species of lupin also contains inhibitors that must be leached out by water before germination will occur. This also prevents germination without adequate soil moisture.

Domesticated lupin varieties are bred to contain a particular gene (called 'mollis') that makes the seed coat permeable to water, ensuring good germination.

Soil pH

Lupin grows best in neutral to acidic soils. Narrow-leafed lupin is adapted to soils with a pH_{CaCl_2} of between 4.2 and 6.0 and will tolerate up to 20% exchangeable aluminium. Albus lupin grows best in soils with a pH_{CaCl_2} of 4.6 to 7.0 and is tolerant of only moderate acidity (up to 8% exchangeable aluminium).

Sowing lupin on calcareous soil can reduce germination and result in seedling death and crop failure. Root growth of narrow-leafed lupin is more sensitive than that of albus lupin to high soil pH and free calcium carbonate. Root elongation of narrow-leafed lupin slows when the pH increases from 5.5 to 6.0. At a pH_{CaCl_2} greater than 6.0 the root surface can be damaged. Surface cells are peeled off and root hair formation slows. Shoot growth is also reduced in alkaline soils but is less sensitive than root growth.

High soil pH also impairs symbiosis with *Bradyrhizobium rhizobia* and reduces the number of nodules. Nodulation in albus lupin is more sensitive to high pH and free calcium carbonate than is nodulation in narrow-leafed lupin.

Sowing

Seedbed

Seeds need good soil contact for germination. Because lupin (particularly albus) has large cotyledons that are pushed above the ground during germination, they have difficulty emerging through the soil if it is compacted or if they are sown too deep. Therefore, seed placement is very important for good establishment. This can be helped by using press wheels. High stubble loads can also reduce seed–soil contact, causing uneven or poor establishment.

Sowing depth

Sowing depth is the key to uniform, fast emergence and establishment. Despite the large seed size, shallow sowing results in better establishment. Under optimum moisture levels a depth of 1 cm will give the most even emergence. However, this depth is not ideal for root development or for emergence under variable moisture conditions. Root development is improved when the sowing depth is 2 cm. To allow good establishment and let the cotyledons emerge, sowing depth should not be more than 5 cm (Figure 1–8).

Plant population

Unlike cereals, lupin does not tiller, so it is important to establish an appropriate plant population. Plant population is determined by seeding rate and establishment percentage. The current recommendation for NSW ranges from 35 to 45 plants per square metre, depending on location and sowing time. For early sowing, a plant population of 35 plants per square metre is best. In the higher rainfall zones or with later sowing, optimum yield comes from establishing at least 45 plants per square metre.

Figure 1–8. Emerging albus lupin sown with disc seeder at an ideal depth of 2 to 4 cm. Photo: J Walker

There is no yield increase with higher plant populations. A plant density higher than 65 per square metre reduces lateral branching and can cause problems at seed fill if there is not enough moisture.

Sowing time

Sowing time affects the timing of flowering and the length of the seed filling period (See Chapter 3). Sowing should be done early enough to allow a long seed-filling period before soil moisture and high temperatures become limiting, but late enough to reduce the risk of frost damage.

Early sowing is also important to ensure adequate growth before winter, as the growth rate of lupin is very slow in winter. However, early sowing in high rainfall environments can produce large amounts of vegetative growth. This increases water use and the crop's susceptibility to spring moisture stress.

The sowing time recommendations for lupins are not based on the variety. This is because there is a narrow range of maturities in commercial lupin varieties. Figure 1–9 shows the suggested sowing times for lupin in NSW. Up-to-date tables are published in the I&I NSW *Winter crop variety sowing guide* each year.

Variety selection is still important for maximum yield, because temperature can influence the time of flowering differently in each variety – see Chapter 3 for more detail. The effect of sowing time on flowering date can be modelled. Figure 1–10 shows the variation in the number of

	APRIL				MAY			
WEEK	1	2	3	4	1	2	3	4
Low rainfall			Preferred	Preferred	Later	Later		
High rainfall				Preferred	Preferred	Preferred (first half); Later (second half)	Later (first half)	

Preferred sowing time | Later than recommended: yield reduction likely depending on spring conditions

Figure 1–9. Suggested sowing times for narrow-leafed and albus lupin in NSW. Source: McRae et al. (2010)

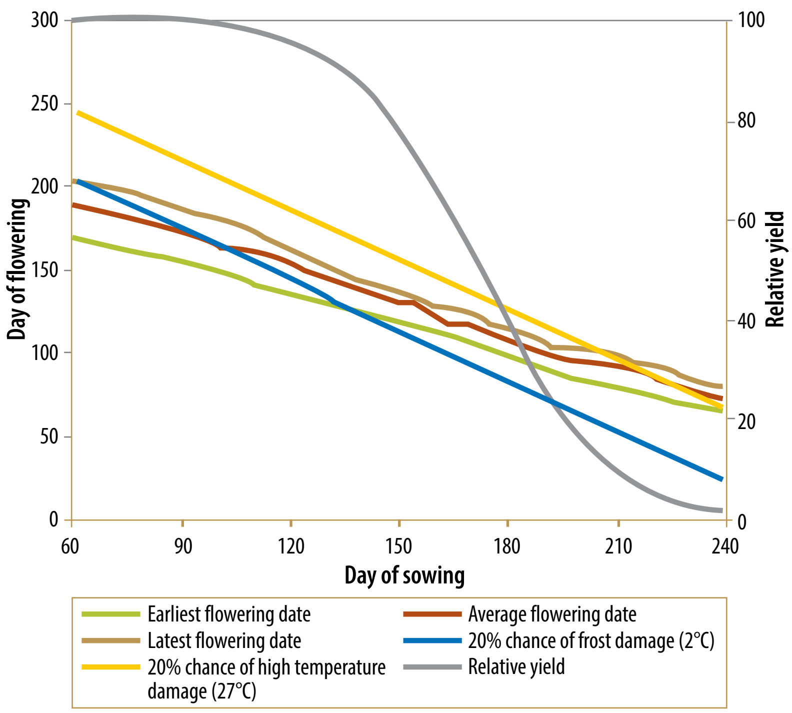


Figure 1–10. Effect of sowing day on flowering day and average yield of lupin at Wagga Wagga. Source: Modified from Liu et al. (2001)

- Lupins were planted in Wagga Wagga on 1 April, the time to flowering varied between 157 and 188 days after sowing.
- When sowing was delayed to 30 July the time to flowering was between 100 and 116 days after sowing.
- The relative yield curve shows that delaying sowing after 10 June reduces the yield by 8% per week.

days to flowering. When the crop was sown on 1 April, the time to flowering varied between 157 and 188 days after sowing, whereas sowing on 30 July reduced the time to flowering between 100 and 116 days. For every week of delay after 10 June the yield will be reduced by 8%.

Row spacing

Yield response to row spacing depends on stored soil moisture, soil type, spring rainfall, and weed control. In low-rainfall environments the yield rarely drops when the row spacing is increased to 60 cm (Figure 1–11). However, in high-yielding high-rainfall environments, or in very wet spring conditions, increasing the row spacing from even 15 cm to 30 cm can reduce the yield.

Inoculation

Lupin seed should be inoculated with Group G rhizobia before sowing. Lupin requires a specific rhizobium that is not found naturally in NSW soils. The rhizobium will form active root nodules (See Chapter 2) that will fix nitrogen. The rhizobium can persist in the soil for up to 5 years once established, but its survival is reduced with increasing soil acidity.

Nutrition

Nutrition is covered in detail in Chapter 2, but there are some nutritional requirements that need to be considered at sowing.

Nitrogen

Lupin is a legume and can fix its own nitrogen. Fixed nitrogen is available to the plant 5 or 6 weeks after emergence. See Chapter 2 on nodulation. On infertile soils, nitrogen deficiency can develop early in crop development, before enough nitrogen has been fixed. In some cases, using starter nitrogen can improve early plant vigour.

Phosphorus

Phosphorus is an essential part of the enzymes that fix light energy during photosynthesis and is needed for cell division and expansion. Nitrogen fixation has a high phosphorus demand.

Many NSW soils are phosphorus deficient. Compared with nitrogen, phosphorus is relatively immobile in the soil. Lupin is very effective at obtaining phosphorus from the soil, and deficiency is rare in albus lupin (see 'Proteoid roots' in Chapter 2).

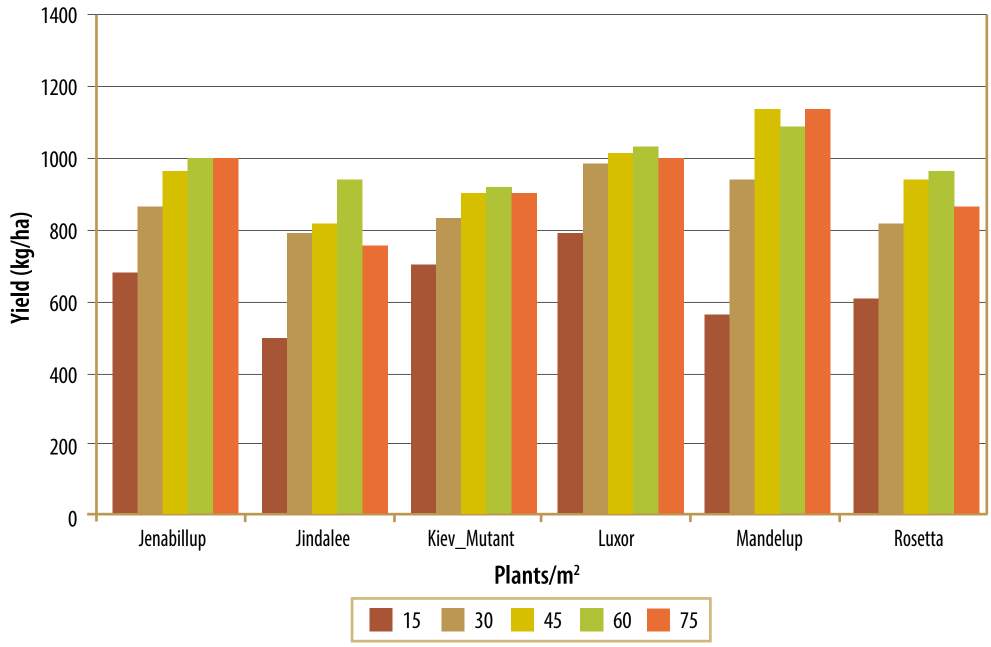


Figure 1–11. Results of the I&I NSW VSAP (Variety Specific Agronomy Packages) trials, showing row spacing versus yield for different lupin varieties at Brocklesby (near Albury) in 2008.

In all lupin species, phosphorus deficiency is seen as poor growth of roots and shoots. In narrow-leafed lupin, phosphorus deficiency is seen when the leaves die back from the tips, followed by plant drooping. In albus lupin the leaves become a mottled yellow before dying from the tips.

Placing fertiliser with the seed at sowing at levels greater than 15 to 20 kg P/ha can reduce crop emergence. Damage will be greater in drier soils. Banding phosphorus below the seed can reduce damage without reducing availability to the plant. Generally, banding fertiliser below the seed gives higher yields than placing it with the seed. Research on red-brown earths in southern NSW showed a slight increase in yield when the fertiliser was banded below the seed (Figure 1–12).

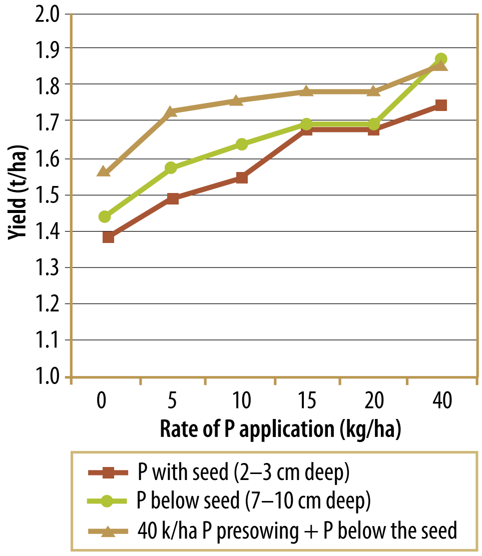


Figure 1–12. Yield response of lupin to fertiliser placed with the seed, below the seed, or below the seed with 40 kg/ha surface-incorporated before sowing. Data are averaged across two sites and 2 years. Source: Modified from Scott et al. (2003)

- Placement of the fertiliser below the seed increased yield slightly.
- The benefit decreased at higher rates of fertiliser.
- The higher rates of P application with the seed had a small negative effect on plant density.

Molybdenum

Molybdenum is a trace element that is essential for the rhizobia to fix nitrogen and as part of the enzyme that converts nitrate to nitrite in cells. Lupin is grown in acid soils, which are often low in molybdenum. Molybdenum is strongly retained by soils at low pH (below pH_{CaCl_2} 5.0) and is usually deficient only is these low pH soils. Deficiency can be counteracted by using seed with a known high level of molybdenum; raising the pH of the soil; coating the seed with molybdenum fertiliser; using a fertiliser containing molybdenum; or applying molybdenum with herbicide. Proteoid roots can also increase the availability of molybdenum in albus lupin (see Chapter 2).

Weeds

Germination and early growth of lupin can be affected by the **allelopathic** effects of camel melon residue (Figure 1–13), so melon control in the summer before growing lupin is essential.

Figure 1–13. Trials of lupin affected by the allelopathic effects of camel melons that were breaking down. Photo: Barry Haskins

Allelopathy
The release by one plant species of chemicals that affect other species in its vicinity. The effect is usually negative, reducing germination rates, root and shoot extension, and growth and development.

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IN THE PADDOCK

by Peter Matthews

The following are some activities that can be done in the shed or paddock to illustrate the main learning outcomes that have been discussed.

Calculating 100-seed weight

Aim: to determine the 100-seed weight of a seed lot.

1. Take a representative sample of your seed lot. If it is ungraded, weigh out 50 to 100 g and remove damaged and split seed that would normally be discarded by grading.
2. Count out 200 seeds from each seed lot to be planted.
3. Weigh 200 seeds on scales accurate to 0.1 g.
4. Divide the weight by 2 to calculate the 100-seed weight.
5. Repeat four times from your sample.

COUNT	SEED LOT 1		SEED LOT 2		SEED LOT 3	
	SAMPLE ID		SAMPLE ID		SAMPLE ID	
1						
2						
3						
4						
5						
Average						
Divide average by 2						
Average 100-seed weight						

Seed sample fractions in graded versus ungraded seed

Aim: To compare a graded seed lot with a sample off the header.

1. Use a cup measure to randomly subsample the seed lots being compared.
2. From each subsample of both the graded and ungraded samples weigh out 200 g. Remember to label the subsamples and their origin to avoid confusion.
3. For each 200 g sample separate out the whole undamaged seed from the cracked, split or shelled seed and the inert trash.

   (Hint: Be sure to identify seed with fine cracks in the seed coat.)
4. Weigh each portion (whole undamaged seed from the cracked, split or shelled seed and the inert trash) and record the results for comparison.

IN THE PADDOCK

COUNT	SEED LOT 1		SEED LOT 2	
	SAMPLE ID		SAMPLE ID	
Total sample weight				
Whole seed				
Cracked seed				
Split seed				
Inert trash				

Calculating bitter seed percentage in albus lupin seed-lots (optional)

Aim: To identify bitter seeds in albus lupin seed lots.

1. Collect a random sample from a 1 kg seed lot either off the header or graded.
2. Using a ultraviolet lamp, screen the sample for the presence of fluorescing (pink) seeds.
3. Count seeds that are pink or purple.
4. Determine the bitter seed level (%).
5. Discuss options for the seed lot in relation to Primefact 682 (see *References and Further Reading* in this chapter).

COUNT	EXAMPLE NO. OF BITTER SEEDS PER KG	SEED LOT 1		SEED LOT 2	
		SAMPLE ID		SAMPLE ID	
1	9				
2	10				
3	6				
4	1				
5	4				
Average	6				
100-seed weight (see the 100-seed weight activity above)	35				
Seed weight (100-seed weight divided by 100)	0.35				
Weight of bitter seed (g) (seed weight x average count)	2.1				
Total sample weight (g)	1000				
Bitter seed % (bitter seed/total sample weight) x 100	0.21				

IN THE PADDOCK

Assessing normal and abnormal seedlings

Aim: To identify normal and abnormal seedlings from a germination test (using prepared germinated samples).

1. Identify abnormal and normal seedlings from the test samples.
2. Separate the abnormal seedlings into groups of similar defect and categorise them (e.g. damaged seed, discoloured seed coat).
3. Discuss the possible reasons for each type of abnormality.

	TYPE	TYPE	TYPE
Count			
Category of defect and suggested reason for abnormality			

Calculating germination percentage

Aim: To calculate the germination percentage of a seed lot.

1. Using a graded seed lot, count out 100 seeds from each lot to be planted, including the damaged seeds.
2. Use a flat tray about 30 cm square and 5 cm deep (a nursery seedling raising tray is ideal). Place a single sheet of paper towel in the bottom to cover the drainage holes and fill with clean sand, potting mix or freely draining soil.

   (Hint: If you don't have a tray the test can be done in any sort of self-draining container or in a cool part of the home garden.)
3. Take the 100 seeds (including the damaged ones) and sow 10 rows of 10 seeds (the rows make it easier to count the seedlings). Seeds should be sown at a normal seeding depth of 2 to 3 cm.

   (Hint: Place the seeds on top of the sand or soil and push them in with a piece of dowel or a pencil and cover with more sand.)
4. Water gently(!) with a spray bottle. Keep moist (not wet). Overwatering will result in fungal growth on the seeds and may cause seed rot and affect normal germination.
5. Count the seedlings after 7 to 10 days, when the majority of seedlings are up. Do not wait until the late ones emerge. (These ones are damaged or have low vigour.)
6. Only normal seedlings should be counted.
7. Calculate your germination percentage (e.g. if you count 83 normal seedlings, then your germination percentage is 83%).
8. Repeat four times.

IN THE PADDOCK

COUNT	SEED LOT 1		SEED LOT 2		SEED LOT 3	
	SAMPLE ID		SAMPLE ID		SAMPLE ID	
1						
2						
3						
4						
5						
Average						

Calculating seeding rate

Aim: Calculate a seeding rate based on a target plant population.

1. Decide on a target plant density
2. Calculate the 100-seed weight (see first activity above)
3. Calculate the germination percentage of the seed lot (see the preceding activity)
   Determine the establishment percentage. A realistic estimate of establishment is 80%. Take into account the likely field conditions (temperature, moisture, soil type, sowing depth, insects and disease).
4. Use the following formula to calculate seeding rate:

$$\text{Seed rate (kg/ha)} = \frac{(\text{target plant density (plants/m}^2) \times \text{100-seed weight (g)} \times 1000)}{(\text{germination \%} \times \text{establishment \%})}$$

	EXAMPLE	SAMPLE 1	SAMPLE 2	SAMPLE 3
	JINDALEE	SAMPLE ID	SAMPLE ID	SAMPLE ID
Step 1: Target plant density (plants/m^2)	35			
Step 2: 100-seed weight (g)	14			
Step 3: Germination (%)	95			
Step 4: Establishment (%)	80			
Seed rate (kg/ha)	65			

IN THE PADDOCK

Examining sowing depth

Aim: To measure sowing depth.

1. Select 10 lupin seedlings in an average row of the crop.
2. Cut each of the seedlings off at ground level.
3. Carefully dig up the plants in the row, including the roots.
4. Wash the plant stumps carefully in a bucket of water.
5. Measure the length from the cut end down to the bottom of the hypocotyl (root–shoot junction) and record the lengths in the table below.
6. Repeat four times across the paddock.

COUNT	SOWING DEPTH (CM)				
	SITE 1	SITE 2	SITE 3	SITE 4	SITE 5
1					
2					
3					
4					
5					
6					
7					
8					
9					
10					
Average					
Paddock average					

Sowing implement and seed placement

Aim: To use hypocotyl measurements to compare the sowing depths of different tillage implements.

1. Conduct this sowing depth activity in paddocks that have been prepared in different ways or sown with different types of implements, or in different soil types.
2. Discuss soil throw in zero till and implications for emergence.
3. Discuss the effects of seed bounce from air seeders, as well as airflow rates and sowing speed.

IN THE PADDOCK

Evaluating the effects of seed treatment on hypocotyl length

Aim: To use hypocotyl length measurements to compare treated and untreated seed.

1. Carefully dig up 10 plants (including the roots) along a row in each of two paddocks with different seed-treatment histories.
2. Wash the plants carefully in a bucket of water.
3. Measure the length from the base of the cotyledons to the bottom of the hypocotyl (root–shoot junction) and record in the table below.
4. Repeat four times across each paddock.

COUNT	HYPOCOTYL LENGTH (CM)									
	TREATED PADDOCK					UNTREATED PADDOCK				
	1	2	3	4	5	1	2	3	4	5
1										
2										
3										
4										
5										
6										
7										
8										
9										
10										
Average										
Paddock average										

IN THE PADDOCK

Calculating plant population

Aim: To determine the plant population in a paddock.

There are two methods for calculating the plant population: one uses a quadrat to count an area and the other counts plants along a linear row.

Method 1: using a 0.25 m² quadrat

This method is best for narrow rows.

1. Randomly place the 0.25 m² quadrat in the crop. (A quadrat is a square of metal, wood or plastic.)
2. Count the plants in the quadrat at 10 locations in the paddock and enter the numbers in the table below.
3. Multiply the average count by 4 to give the number of plants per square metre.
4. Repeat in a different paddock and record the results for both.

Method 2: counting a 1 m row

This method is better for wider rows.

1. Count the plants along 1 m of row randomly selected at 10 locations within the paddock and enter the numbers in the table.
2. Measure and record the row spacing.
3. Multiply average row counts by the row spacing factors below to give the number of plants/m².

Row spacing (cm)	Conversion factor
17.5	5.71
20	5.00
22.5	4.44
25	4.00
27.5	3.36
30	3.33
33	3.03
36	2.77
40	2.50
50	2.00
60	1.66

4. Repeat in a different paddock and record the results for both.

IN THE PADDOCK

PLANT COUNT METHOD USED	PADDOCK 1		PADDOCK 2	
	0.25 m^2 QUADRAT	1 M ROW COUNT	0.25 m^2 QUADRAT	1 M ROW COUNT
	YES/NO	YES/NO	YES/NO	YES/NO
Count				
1				
2				
3				
4				
5				
6				
7				
8				
9				
10				
Average count				
Conversion factor				
Plants/m^2				

Calculating establishment percentage

Aim: To assess the establishment percentage of a paddock.

1. Record the plant population of the paddock (from the preceding activity), in the table below.
2. From the activities described above, record the 100-seed weight, seed lot germination percentage, target plant population and actual seed rate in the table below.
3. Using the equation below:

$$\text{Establishment \%} = \frac{(\text{target plant density (plants/m}^2)) \times \text{100-seed weight (g)} \times 1000)}{\text{germination \%} \times \text{seed rate (kg/ha)}}$$

	EXAMPLE	
Target plant density (plants/m^2)	35	
100-seed weight (grams)	16	
Germination percentage (%)	97	
Seed rate (kg/ha)	70	
Establishment percentage (%)	84	

2. Vegetative growth

by Kathi Hertel

Chapter Snapshot

Introduction

Once the plant is established, it begins vegetative growth. Lupin plants develop a main stem and a series of lateral branches. The root system also develops and begins to form nodules.

Chapter 2 explains the vegetative growth stages and the factors that affect the growth of the plant, such as temperature, light absorption, soil moisture and nutrition.

Learning Outcomes

At the end of this chapter, you will be able to:

- identify the difference between growth and development
- describe how the root system grows
- describe how proteoid roots function
- assess the health of a root nodule
- identify different branch orders of development
- understand the effects of photoperiod and thermal time on the development of plants
- describe the role of plant nutrition during vegetative growth.

Arbuscular mycorrhizae

Arbuscular mycorrhizae (AM) are fungi that occur naturally in soil and help make soil nutrients available to a plant by acting as an extension of the plant's root system. AM increase the volume of soil so that the roots can explore and improve the uptake of nutrients, particularly phosphorus and zinc. AM are particularly important in northern New South Wales.

Vegetative growth

During the vegetative growth stage the roots, leaves, main stem and branches grow simultaneously and the plant begins storing nutrients for the rest of its life cycle. This is a period of high nutrient uptake, and its progression is influenced by moisture and temperature.

The life cycle of lupin can be divided into a number of stages (See Introduction). This chapter focuses on leaf emergence, branch development and stem elongation, as well as root development. The progress of the various stages is continuous: for example, stem elongation continues during the vegetative and reproductive phases.

Root growth

Lupin has a deep root system that consists of a dominant taproot with lateral roots branching from it.

The depth to which lupin roots grow varies with the soil type. The roots of narrow-leafed lupin can grow up to 2.5 cm a day and reach lengths of up to 2.5 metres – deeper than those of peas and barley.

The root system of lupin is much sparser than that of wheat, but lupin tends to have a greater proportion of the root system below 20 cm. Even though the root system of lupin is much sparser than that of wheat, lupin can take up more water than wheat. The root hairs in lupin have less resistance to water flow than do the hairs of cereal roots.

Soil factors – including temperature, moisture, nutrients and structure – all affect root growth. Root growth occurs best at soil temperatures of 18 to 22°C. Early-sown crops are likely to have more extensive root systems than later sown crops, simply because of the extra time available for growth.

Root growth uses about one-third of the products of photosynthesis. Roots can make up to 24% of total crop biomass and contain about 13% of the total crop nitrogen. Albus and narrow-leafed lupin have very different rooting patterns. Although both have deep taproot systems, narrow-leafed lupin is better adapted to extract water from deep in the soil profile, whereas the roots of albus lupin are better adapted to shallower, finer-textured soils.

The root system absorbs nutrients and water for plant growth. Healthy roots, unrestricted by soil constraints or disease, are essential to maximise yield. Lupin does not form associations with mycorrhizal fungi such as **arbuscular mycorrhizae**.

Primary (tap) root system

The radicle is the first root to appear at germination. It becomes established in the soil and can draw up water and nutrients soon after emergence. The radicle develops into the tap root. If unobstructed, it grows straight down into the soil. If taproot growth is restricted, there may not be enough lower roots to meet the moisture and nutrient requirements of the plant.

Secondary (lateral) root system

Lateral roots are produced on the taproot. They extend horizontally and diagonally from the main taproot, branching into second- and third-order laterals.

About 2 weeks after sowing, first-order lateral roots appear about 10 cm from the root tip. Lateral roots continue to appear regularly, alternating from either side of the taproot about every 5 mm. They first grow horizontally and then downwards through the soil profile.

Finer second- and third-order laterals develop off the first order laterals over time, increasing the root surface area and therefore the water and nutrient uptake.

Albus and narrow-leafed lupin differ in their lateral root development. Narrow-leafed lupin has a less extensive root system with a large number of first-order lateral roots in the upper soil layers and few second-order lateral roots. Albus lupin has a more extensive lateral root system. Albus lupin lateral roots are thinner and more evenly distributed with increasing soil depth. This increases the overall contact between root and soil and increases the efficiency of nutrient uptake. This is why albus lupin performs better on fine-textured soils or soil where overall rooting depth is limited.

Proteoid (cluster) roots

Albus lupin is one of a small number of *Lupinus* species that develop specialised root structures known as proteoid roots (Figure 2–1). They are specialised lateral roots. Narrow-leafed lupin does not develop proteoid roots.

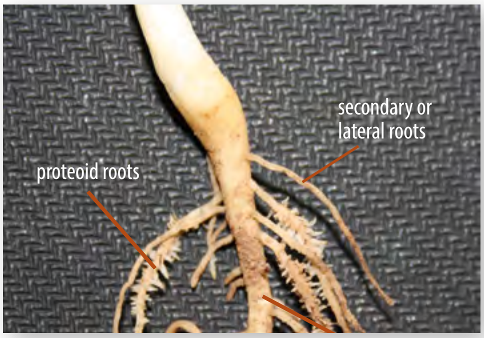


Figure 2–1. Albus lupin seedling, showing proteoid roots developing on the secondary roots. Photo: J Walker

Proteoid roots are short, lateral roots that develop when plant phosphorus levels are low. Proteoid roots release organic acids, mobilising not only phosphorus, but also iron, manganese and zinc in the **rhizosphere** and increasing their rates of uptake. They do not develop in soils with high levels of phosphorus.

Clusters of proteoid roots develop along the primary lateral roots from 8 days after emergence. Their emergence and elongation can take around 4 days, and they emerge simultaneously on all the primary lateral roots.

Mature proteoid roots can increase the root surface area to 14 to 22 times that of equal-length lateral roots without proteoid roots.

Proteoid roots secrete **root exudates** called organic acid phosphatases. These compounds increase the levels of phosphorus available for plant uptake in the rhizosphere.

Released root exudates and mobilised plant nutrients provide food for soil micro-organisms. This creates a complex environment where the concentration of organisms in the rhizosphere greatly exceeds that in the rest of the soil.

Nodulation and nitrogen fixation

Lupin forms symbiotic relationships with *Bradyrhizobium lupini* bacteria to fix nitrogen. The *Bradyrhizobium* bacteria penetrate the roots, causing an infection that becomes a nodule. The bacteria produce an enzyme (nitrogenase) that converts atmospheric nitrogen to ammonium-nitrogen. Nitrogenase requires a low-oxygen environment within the nodule to function. The level of oxygen in the nodule is controlled by leghaemoglobin. When the nodule is functioning, the leghaemoglobin gives the nodules their pink or red colour inside (Figure 2–2). A green or brown colour indicates that no nitrogen fixation is occurring.

In lupin, the process of nodule initiation, infection, and development of a functioning nodule is different from that in other legumes. In other legume species, nodules form after the rhizobia enter the plant root through a deformed root hair, forming an infection thread.

Rhizosphere
The area of soil immediately around the plant roots.

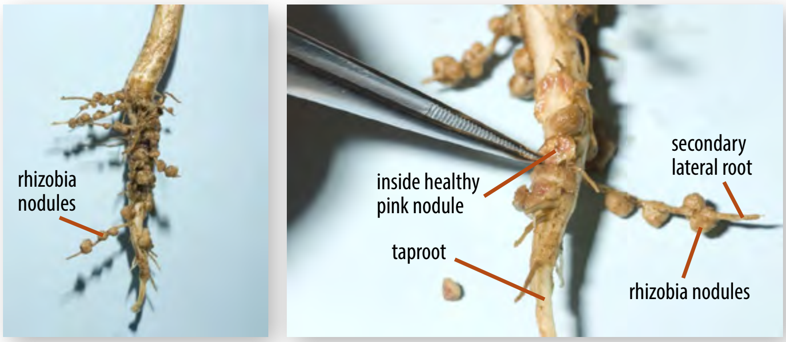


Figure 2–2. Root system of lupin plant (left), showing nodules (right). The functioning nodules are a healthy pink/red inside. Photos: Lowan Turton

In lupin, the *Bradyrhizobium* bacteria penetrate the cells at the junction between the root hair base and an adjacent epidermal cell. There are no obvious signs of infection. The newly infected cells divide repeatedly 5 or 6 days after inoculation to form the central infected zone of the young nodule.

Root exudates
Organic acid phosphatases, like citrate and malate, that are secreted from the roots. Citrate accounts for 80% to 90% of the organic acids produced by proteoid roots. Citrate is very effective at mobilising phosphorus from aluminium-phosphorus and iron-phosphorus forms of phosphorus found in acidic soils. This gives the lupin plant an advantage in the acid sandy soils it commonly grows in.

Degree-days
The unit of thermal time (accumulated temperature), i.e. degree-days (°Cd). It is used to explain the relationship between plant development and temperature.

Thermal time
Thermal time is a way of expressing accumulated temperature. It helps to explain the relationship between plant development and temperature. It is calculated as the mean daily temperature minus a base temperature and is given in degree-days (°Cd). The base temperature used to calculate thermal time is 3°C for albus lupin and 0°C for narrow-leafed lupin.

Nitrogen fixation does not start until 4 or 5 weeks after germination. Nitrogen does not accumulate in the shoots for a further 2 weeks. At this time all main-stem leaves have been initiated and five or six leaves are fully emerged.

If phosphorus supplies are low, nodules grow mainly on the lateral roots in or near the proteoid root clusters of albus lupin. Mild phosphorus deficiency will result in an increased number of nodules, but the nodules will generally be smaller.

Leaf growth
Growth stage 1.1 +

Within the seed, there are five or six leaf primordia (early leaf buds) that have already formed. After the seedling has emerged, these form the first true leaves (Figure 2–3).

Figure 2–3. Cotyledons (rounded) and the emerging true leaves (pointed) of narrow-leafed lupin. Photo: Jan Edwards

The first four leaves to emerge are arranged in pairs. The next leaves emerge singly in a spiral arrangement. Each leaf forms on the stem at 137° to the previous leaf in albus lupin and 146° in narrow-leafed lupin. This forms a spiral pattern that minimises leaf-shading effects and maximises ground coverage.

A leaf has emerged when it has separated from the terminal bud and the leaflets have separated from each other. There are a number of emerged leaves expanding at any one time, and several folded leaves are visible in the bud.

Leaves are bigger at the top of the stem because the leaflet and petioles there are longer. They are also larger on the main stem than on the other branches.

Leaves expand at the rate of about 0.02 to 0.06 cm^2 per degree-day on the main stem (Figure 2–4). A similar pattern and rate of expansion occur along the first-order branches. Expansion continues on the main stem for 380 **degree-days**, on the first-order and second-order branches for 500 degree-days, and on the third-order branches for 240 degree-days.

The number of leaves on a plant varies with the:

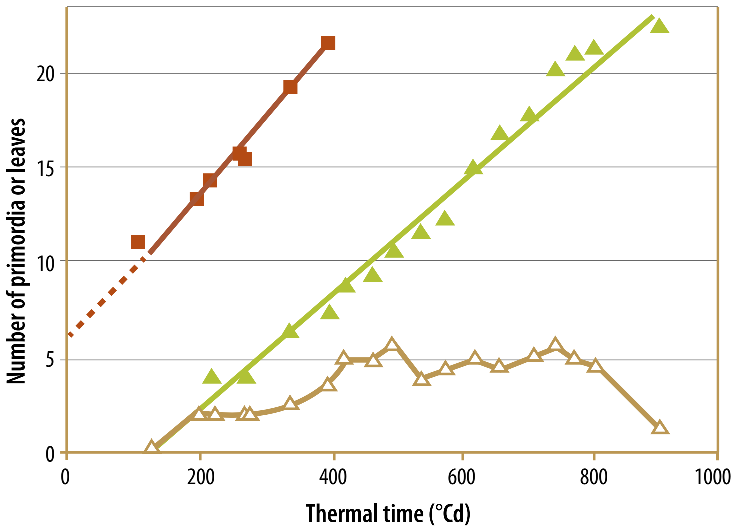
- variety
- temperature (i.e. the accumulated **thermal time** at the apex of the main stem)
- daylength
- position of the branch on the main stem.

In narrow-leafed lupin each leaf takes about 34.5 degree-days to emerge, about twice as fast as in albus lupin.

Lupin leaves can track the daily movement of the sun (see Figure ix in Introduction). This ability is important when the plant is under moisture stress. If the leaves are parallel to the sun's rays, then transpiration and direct temperature effects are minimised. This increases water-use efficiency, especially when combined with folding of the leaflets along the midrib when the plant is under moisture stress.

The end of the phase of leaf initiation on the main stem coincides with the start of reproductive initiation, when about eight leaves are fully emerged.

Once there are about 11 main-stem leaves, initiation of leaves on the first-order branches begins. There are usually more leaves on the first-order branches than on the second-order or third-order branches.



- The slopes of the lines in the graph show the rates of development.
- Leaf primordia are initiated every 25.6 degree-days.
- Leaves emerge every 34.5 degree-days.

Figure 2–4. Initiation of leaf bud primordia (■), emergence of leaves (▲), and number of expanding leaves (△) on the main stem of narrow-leafed lupin. Source: Dracup and Kirby (1993).

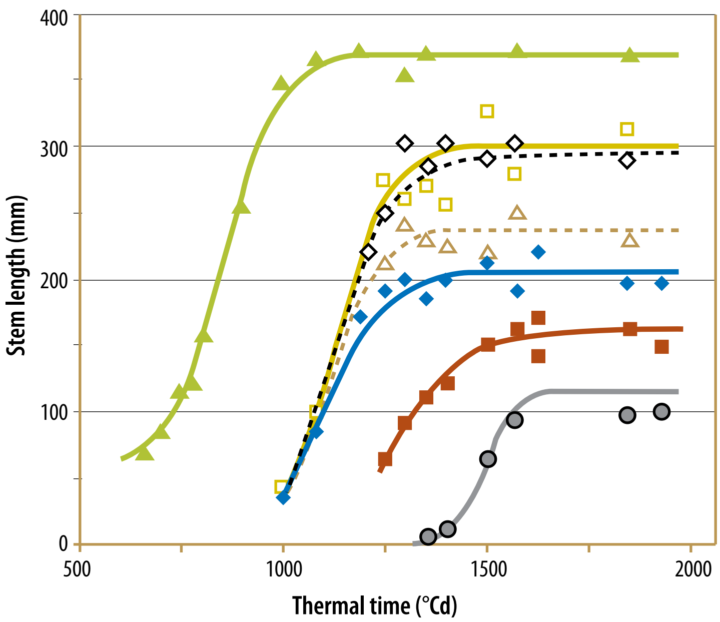
Main stem growth
Growth stages 1.13, 2.5

After emergence, the shoot apex (growing point) is above the ground and therefore vulnerable to damage. By contrast, the wheat shoot apex remains below the ground until stem elongation starts.

Main stem elongation is controlled largely by accumulated temperature (thermal time). During the vegetative phase (in early winter), growth of the main stem is slow.

The main stem elongates because of the initiation and development of internodes. Internodes elongate at 0.1 to 0.2 mm per degree-day, depending on their location on the stem. All stem internodes begin and end their growth in sequence, from the stem base to the top of the plant (apex).

At any time, up to 10 internodes are elongating. The main stem reaches its maximum length at about 1050 degree-days (Figure 2–5). This is equivalent to 25 or 30 degree-days between each internode. Earlier flowering lupin genotypes have fewer leaf nodes than later flowering genotypes.



- Internodes elongate at rates between 0.1 and 0.2 mm per °C, depending on their location.
- The main stem (and final internode) reaches its maximum length at about 1050 degree-days; this is equivalent to 25 to 30 degree-days between each internode.

Figure 2–5. Elongation of the main stem, first-order branches and uppermost second- and third-order branches. ▲ main stem; ◆, △, ◇, □, first-order branches; ■ uppermost second-order branches; ● uppermost third-order branches. Source: Dracup and Kirby (1993).

Branch growth

Branches are produced from the leaf axils (the points where the leaves join the stem). Like the main stem, the branches produce leaves and flowers.

The branches that develop on the main stem are called first-order branches. The branches that develop on the first-order branches are called second-order branches (Figure 2–6). Under very good growing conditions, a lupin plant can produce fifth-order apical branches. However, in most commercial crops, moisture is limiting and branching stops at the third-order branches. The signal that stops the branching is not yet known.

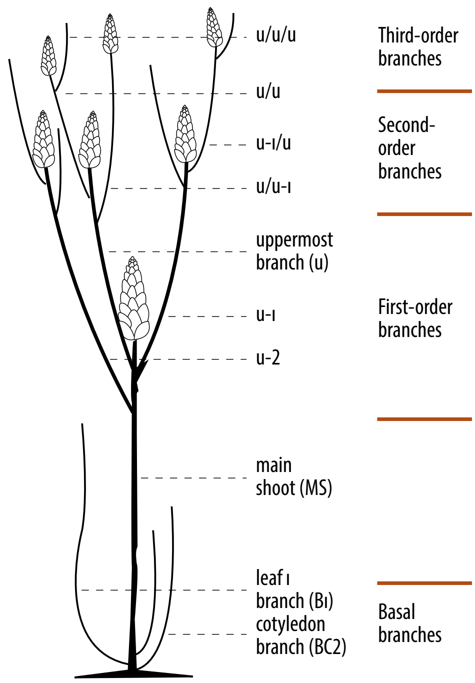


Figure 2–6. Naming of lupin branches. Modified from Dracup and Kirby (1996a, b)

Emergence of branches within an order occurs almost simultaneously. Each branch order is determinate, carrying a terminal flower spike. Branches are also divided into three types: apical (upper), mid and basal (lower).

Apical branches grow from the axils of the uppermost leaves. They produce most of the plant's yield. The apical branches form second-order branches, which themselves may produce third-order branches. Mid branches grow from the axils between the basal and upper branches. They are small, producing only a few small leaves and, rarely, a flower cluster. Basal branches occur only in narrow-leafed lupin. They grow from the axils of the cotyledons and leaves 1 to 4 and contribute little to overall plant yield.

The sequence of development of branches is related to thermal time. All the branches in an order reach their maximum length at the same time, despite differences in the numbers of internodes. In seasons when seed production on the main stem fails, branch growth is very important to seed yield.

Factors affecting vegetative growth

The indeterminate growth habit of lupin means that there is a period when the vegetative growth and reproductive development phases overlap. This creates competition within the plant for moisture and nutrients. The competition can delay seed fill and reduce productivity. At the same time, rapid vegetative growth late in the season means that there is poor light distribution in the canopy when soil water levels are often frequently declining. This further reduces photosynthesis and resources for seed fill.

Photosynthesis and respiration

Plants get their energy to grow from sunlight captured by the leaves. Photosynthesis (Figure 2–7) is the process by which plants use this energy to convert carbon dioxide to sugars. The sugars are converted to cell-wall-forming substances that make up the leaves, stems, roots and other plant parts. Excess sugars are stored as water-soluble carbohydrates.

When energy cannot be obtained from sunlight, such as at night, the plant draws on its reserves of starch and sucrose. This process is called respiration (Figure 2–8).

The rate at which the plant grows is closely linked to the amount of sunlight being captured by the leaves. Temperature influences the rate at which the chemical reactions of photosynthesis occur.

Lupin has high rates of photosynthesis when there is abundant soil water. Lupin leaves photosynthesise 65% to 80% faster than wheat leaves, but the rate of photosynthesis declines dramatically when the leaf water potential falls.

Rates of photosynthesis (and transpiration) are controlled by abscisic acid produced in the roots. The roots are sensitive to mild water deficits and respond by rapidly closing the leaf stomata, although photosynthesis continues at a low rate. This allows plants to continue to develop, even under conditions of severe water shortage.

Transpiration

Transpiration is the loss of water by evaporation in terrestrial plants. It takes place through the stomata. During transpiration, evaporating water moves into the leaf airspaces and out through the leaf stomata.

Transpiration and photosynthesis are related. Leaf stomata need to be open to allow water vapour to move out and to allow carbon dioxide for photosynthesis to move in. When plants are transpiring, water is drawn up from the soil all the way to the leaves to replace the water lost to the atmosphere.

During the vegetative growth stages the transpiration rates of lupin are high. When soil water levels are high, lupin leaves can transpire at twice the rate of wheat leaves. However, transpiration rates in lupin are more sensitive to decreasing water potential. This has a direct impact on photosynthetic rate.

Photosynthesis

$$6CO_2 + 6H_2O \rightarrow C_6H_{12}O_6 + 6O_2$$

carbon dioxide + water → carbohydrate + oxygen

Figure 2–7. Photosynthesis.

Respiration

$$C_6H_{12}O_6 + 6O_2 \rightarrow 6CO_2 + 6H_2O + \text{energy}$$

carbohydrate + oxygen → carbon dioxide + water + energy

Figure 2–8. Respiration.

Temperature

Lupin will grow in temperatures between 0°C and 40°C. The optimum temperature for photosynthesis is between 10 and 22°C (see Table 2–1). Above 22°C, photosynthesis, and therefore growth rates, tend to slow.

Cold temperatures reduce growth. Fewer leaves form on the main stem at 10°C than at 18°C.

Temperatures below 7°C restrict nodulation and nodule development and hence plant growth.

Table 2–1. Temperature ranges for the development and photosynthesis of lupin.

	MINIMUM	OPTIMUM	MAXIMUM
Phenology	0°C	20°C	30°C
Photosynthesis	0°C	10–22°C	40°C

Source: Dracup et al. 1993

Heat stress

Heat stress alone does not appear to affect the rate of photosynthesis or leaf drop (abscission). However, heat stress does affect pod development, seed number and seed weight (see Chapter 4 *Pod and seed development*).

Cold and freezing

Lupin can be damaged by frost during vegetative growth, although the leaves enclosing the meristem give some protection to the vegetative shoot tips.

For frost injury to occur, ice must form between or inside the cells. Water surrounding the plant cells will freeze at 0°C, but water inside the cells needs to be colder to freeze. In growth chamber experiments conducted on albus lupin, damage to leaf cells started at –6°C. Cells in the stems were destroyed when temperatures reached –10°C.

Lupin grown in the paddock acclimatises to low temperatures by exposure to cold over several days. Cold-hardened plants may then suffer injury at slightly colder temperatures. The length of time the plant is exposed to cold also has an important influence on the level of damage.

Table 2–2. Approximate degree-days for the main development stages.

DEVELOPMENT STAGE	THERMAL TIME (DEGREE-DAYS)
Crop emergence	20°Cd
Appearance of each main stem node	40°Cd
Emergence to end of juvenile phase	360–375°Cd
End of juvenile phase to floral initiation*	560–665°Cd
Floral initiation to flowering	135–140°Cd
Emergence to flowering	495–1160°Cd
Flowering to start of grain filling	500°Cd
Start of grain filling to maturity	500°Cd
Emergence to maturity	2260°Cd

* For daylength equal to, or shorter than, 10.8 h
Source: Dracup et al. (1993); Dracup and Kirby (1996a, b); Farre et al. 2004

The roots of albus lupin growing 10 cm below the soil surface can survive temperatures as low as –3.5°C.

Thermal time

Thermal time is a way of expressing accumulated temperature. It is calculated as the mean daily temperature minus a base temperature and is recorded as degree-days (°Cd). The base temperature is the minimum temperature at which the plant grows, and this varies for each crop. Thermal time varies from year to year in the same location.

Thermal time is the main influence on the timing of development. For example, first-order branches flower 164 to 244 degree-days later than those on the main stem (i.e. 11 to 16 days later at 15°C). The total number of degree-days required to reach a specific growth stage can be calculated (Table 2–2).

Daylength (Photoperiod)

Photoperiod or day length is the duration (number of hours) of exposure to daylight. Lupin (like wheat) is a long-day plant, meaning that it responds to increasing photoperiod. Increasing daylength provides a signal for the start of reproductive development.

When lupin is grown with increased daylength, the time from sowing to flowering is shorter (Figure 2–9). There is also an interaction with temperature.

- The number of days to flowering was less with the longer daylength. At 10°C, the number of days to flowering was 32 days less with the longer daylength than with the shorter one.
- The number of days to flowering was also less at the higher temperatures. The number of days to flowering was 23 to 53 days less at 16°C than at 10°C.

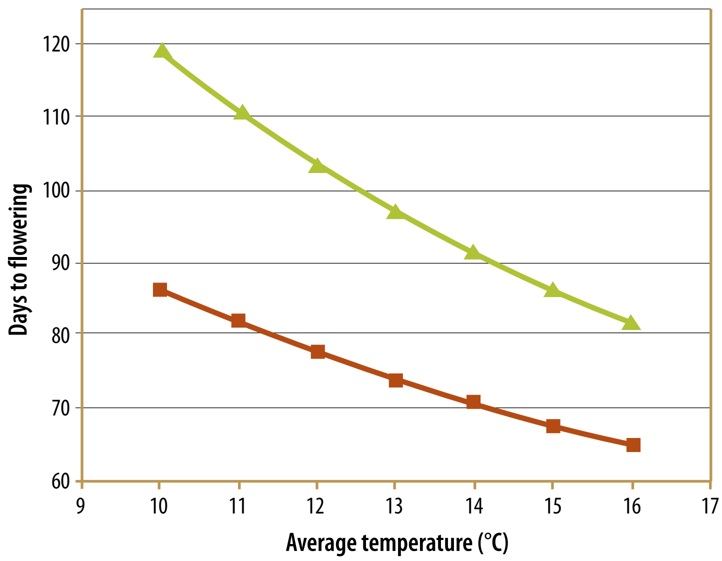


Figure 2–9. Predicted days to flowering for lupin variety Gungurru grown under different temperatures and two different daylengths (▲ 11.1 hours and ■ 12.2 hours).
Source: Reader et al. (1995)

Increasing daylength also increases the rate of leaf area expansion, increases dry matter production and increases stem height. There is no impact on the number of leaves or branches on the main stem with increasing daylength.

Light intensity

Light intensity can also affect plant growth. Reduced light intensity during cloudy weather can reduce photosynthesis. This can outweigh the effects of daylength (photoperiod) and can increase the time taken for lupin to flower.

Moisture

Waterlogging

Lupin is more sensitive than other pulse crops to waterlogging, and albus lupin is more sensitive than narrow-leafed lupin.

Waterlogging causes low soil oxygen concentrations, which limit root function and survival. Waterlogging also affects shoot growth by reducing the plant's respiration rate.

In general, young vegetative plants (growth stages 1.2 to 1.10; 28 to 42 days after sowing) are more sensitive to waterlogging than are plants during reproductive development (growth stages 2.6 to 3.3; 56 to 70 days after sowing).

Nitrogen fixation needs large amounts of oxygen. Prolonged conditions of low oxygen, as occur during waterlogging, will cause nodules to stop functioning and die.

Moisture stress

Lupin is less able to make osmotic adjustments than wheat and other pulse crops such as chickpeas and lentils. This makes lupin less able to keep metabolising when there is a severe plant tissue water deficit.

As a water deficit develops, branch growth slows and carbohydrates (assimilates) are diverted from vegetative growth to reproductive development. The deep roots of lupin allow it to access soil water from deep within the soil profile.

The lupin plant can reduce the rate of water loss in a number of ways. One of these ways is to close the stomata (leaf pores). In narrow-leafed lupin there are about twice as many stomata on the top surface of the leaf than on the bottom.

When there is plenty of soil water the lupin leaves track the sun. If water deficits begin to develop, the leaves roll to minimise the interception of radiation. Wilting can also occur, but at a higher water potential than in wheat.

If moisture stress occurs, growth rates can recover fully if the plant later receives enough moisture.

Dry matter accumulation and leaf area

The number of leaves produced before flower initiation has a major influence on leaf area and hence the ability of the plant to photosynthesise.

The growth rate of the crop is closely related to the amount of solar radiation captured by the leaves. The leaf area index is a measure of the upper surface area of leaves per unit of ground surface. A leaf area index of 4 means that there is 4 m^2 of leaf surface area per square metre of ground surface.

A leaf area index of about 4 is required for the crop canopy to intercept about 90% of the incoming solar radiation. The larger the leaf area the crop can expose to the sun, the more dry matter the crop can produce per day.

Differences in leaf area reflect differences in a combination of the maximum leaf expansion rate and the timing of that expansion at individual positions on the plant.

Temperature, water supply and nutrition (especially nitrogen) affect leaf size. The timing of any stress is critical. Stresses that occur before leaf initiation are more likely to affect the numbers of leaf cells, whereas later stresses affect mainly leaf cell size.

Towards the end of the growing season there is a rapid decline in transpiration when the leaves senesce (grow old).

Competition

Competition exists between the branches for nutrients. The apical branches take priority; therefore, the leaves of the later (lower-order) branches are smaller. There are also fewer leaves on the lower-order branches. The decrease in the number and size of leaves also reduces the plant's capacity to supply nutrients to pods developing higher up in the canopy. This situation is exacerbated by declining root length, root activity, nitrogen fixation and water availability.

Nutrition

Nitrogen (N)

Nitrogen influences nearly all components of growth. Nitrogen is required for leaf and root growth, nodule formation and chlorophyll production. The rate of leaf expansion is sensitive to early nitrogen levels. Even temporary fluctuations in levels of available nitrogen can slow the rate of leaf emergence and reduce leaf size. A subsequent increase in the supply of nitrogen will not compensate.

In the early stages of growth, fertiliser planted with the seed and nitrate-nitrogen mineralised from the soil supply the plant until nitrogen-fixation begins. Early sowing and warm soil temperatures promote root growth and speed up the start of nitrogen fixation. Too much fertiliser- or soil-nitrogen tends to reduce or delay nodulation and slow down nitrogen fixation by the root nodules. Short periods of waterlogging can also reduce nodulation and cause nitrogen deficiency.

Using ammonium-based fertiliser can reduce nodule formation and growth. Ammonium has a greater effect than nitrate. Delaying or separating ammonium application increases nodule numbers by improving infection by *Bradyrhizobium lupini* bacteria.

Potassium (K)

Potassium is used in many plant processes (e.g. photosynthesis, sugar transport and enzyme activation). It is particularly important in regulating leaf stomata. Plants that have adequate levels of potassium are better able to tolerate drought and waterlogging than plants deficient in potassium.

Lupin takes up less potassium than wheat and canola but uses it more effectively. No potassium deficiency has been reported in lupin crops in NSW.

Sulfur (S)

Sulfur is needed for seed production and to form chlorophyll and protein. It also helps in nodule formation and is essential for nitrogen fixation.

Leaf symptoms of sulfur deficiency are generally not distinct enough to be detected in the paddock. When sulfur is deficient, protein synthesis is inhibited and plants become pale, with symptoms similar to those of N deficiency in legumes.

Most soils in NSW have adequate levels of sulfur for lupin production. The only soils where critical levels have been recorded are the deep sands and sandy soils on the alluvial coastal plains of Western Australia. If sulfur deficiency is suspected, then a tissue test is the best way to confirm the deficiency.

Micronutrients

Zinc (Zn). Zinc is involved in the enzyme systems of plants. It is needed for protein synthesis, hormone production, carbohydrate metabolism and membrane stability. Zinc is taken up from the soil solution as water-soluble zinc. Lupin is less efficient than other winter crops at accessing zinc from the soil. Lupin is grown mainly on acid soils where zinc deficiency is rare. Zinc deficiency is more common in high-pH soils and those with high carbonate content. Albus lupin is more sensitive than narrow-leafed lupin to zinc deficiency.

Leaf symptoms of zinc deficiency are generally not distinct enough to be detected in the paddock. Plants with mild zinc deficiency produce new leaves that are slightly paler than non-deficient plants. Severe zinc deficiency causes irregular, dark-brown blotches on the tips and margins of older leaves and the crown. It can also delay flowering. Other symptoms are a reduction in stem length and increased branching of lateral roots.

Iron (Fe). Iron is needed for effective nitrogen fixation, so the nodule initiation phase is the most sensitive to low soil iron levels. Plants with iron deficiency produce bright yellow young leaves. Iron deficiency is rare on acid soils. On alkaline and calcareous soils, narrow-leafed lupin is more sensitive than albus lupin to iron deficiency. Waterlogged alkaline soils can also induce a temporary deficiency that dissipates when the soil dries out.

Cobalt (Co). Cobalt is needed by the rhizobial bacteria to fix nitrogen. Therefore, cobalt deficiency reduces the nitrogen concentrations in the shoots. Narrow-leafed lupin is more sensitive than albus lupin to cobalt deficiency. The cobalt level in lupin seeds needs to exceed 0.13 mg/kg to ensure that cobalt deficiency does not affect the rhizobia.

Manganese (Mn). Manganese is needed for many metabolic processes in the plant, including chlorophyll production. It is relatively immobile in the plant. The vegetative phase is usually not affected, as deficiency symptoms occur mostly during pod fill (see Chapter 4).

Molybdenum (Mo). Molybdenum is a constituent of the enzyme nitrate reductase, which converts nitrate-nitrogen (the form taken up from the soil) to nitrite-nitrogen (the form used by plants. It is also essential for nitrogen fixation.

Disease

Several diseases can infect lupin during the late vegetative and early reproductive stages of growth and can cause yield losses.

Sclerotinia

Sclerotinia infection of the stem can cause stem collapse. If infection occurs at the stem base, the plant can die. This disease can infect a wide range of broad-leafed plants, so using appropriate rotations is currently the best means of control. The disease can occur in both albus lupin and narrow-leafed lupin.

Brown leaf spot

Brown leaf spot infection in narrow-leafed lupin (Figure 2–10) can cause premature leaf drop and complete defoliation of seedlings. Infected plants that survive generally have reduced vigour, leaf area and yield. Crop rotation, with at least a 4-year break between lupin crops and separation from last year's lupin paddock is essential for effective control.

Pleiochaeta root rot

Pleiochaeta root rot is the root-attacking form of the brown leaf spot pathogen and infects albus lupin (Figure 2–11). It can kill large numbers of plants within a paddock. Good crop rotation, with at least a 4-year break between lupin crops, is essential for effective control. Luxor is the only resistant variety currently available commercially.

Phytophthora root rot (Sudden Death)

Phytophthora root rot can cause sudden death of lupin plants during flowering and pod filling. It appears to be associated with

Figure 2–10. Brown leaf spot in narrow-leafed lupin. Photo: Raymond Cowley I&I NSW

Figure 2–11. Pleiochaeta root rot on Kiev Mutant seedlings grown in a growth-room disease-screening experiment. Photo: Raymond Cowley I&I NSW

short periods of waterlogging in late winter, often caused by soil hardpans . Affected plants occur as scattered single plants or as larger patches of plants within a crop.

*Lupin anthracnose (***Colletotrichum gloeosporioides***)*

Anthracnose is more likely to severely damage albus lupin than narrow-leafed lupin. Anthracnose causes distinct bending and twisting of stems. Dark brown lesions form with distinct pink/orange spore masses, causing the stems and lateral branches to weaken and collapse. Bright pink/orange spore masses also form on developing pods. At this stage the disease is present only in the alpine areas of NSW in populations of naturalised Russell lupin (*L. polyphyllus*).

Anthracnose also occurs in commercial lupin crops throughout Western Australia and South Australia

Root rot from cucumber mosaic virus (CMV)

CMV is a sporadic problem in southern NSW. The virus is spread from plant to plant by aphids. It can also be seed borne. Infected plants will be stunted and bunchy and have few pods. They remain green while other plants are haying off. The prevalence of CMV in northern NSW is one reason why albus lupin, rather than narrow-leafed lupin, is grown in that region. Albus lupin is immune to seed transmission of CMV.

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IN THE PADDOCK

The following are some examples of what can be done in the paddock to demonstrate the physiology of vegetative growth. These are practical exercises to help farmers assess the progress of their crop during the vegetative growth stage.

Examining the root system

Aim: To check the root system of the crop for the presence of hardpans, functioning nodules, proteoid roots (albus lupin only) and signs of disease.

1. Carefully dig up 10 plants
2. Wash the soil from the roots.

Hardpans

3. Are the roots angled sidewards?

Nodulation

4. Are the nodules healthy (see nodulation assessment below).

Proteoid roots

5. Examine the primary lateral roots for the presence of short proteoid roots.
   What is the phosphorus status of the paddock?

Root disease and insect damage

6. Observe the colour of the roots. They should be bright (almost white). Are there any signs of discolouration or evidence of insect chewing?

Assessing nodulation

Aim: To assess the effectiveness of crop nodulation and the health of nodules

1. Carefully dig up 10 plants and soak in bucket of water.
2. Locate nodules.
3. Note their distribution, on the primary root and lateral roots.
4. Slice open a nodule. Check the colour inside the nodule. Is it pink/red or green or brown?
5. Score 10 plants for nodulation and record in the table below.
6. Look at root health and structure.

PLANT	NODULATION SCORE	ROOT HEALTH SCORE	COMMENTS
1			
2			
3			
4			
5			
6			
7			
8			
9			
10			

IN THE PADDOCK

Assessing plant growth stage

Aim: To accurately assess the current crop growth stage.

1. Carefully dig up a plant.
2. Locate the first two pairs of leaves (leaves 1 to 4). Note the very short internodes and the positions of the paired leaves on the stem relative to each other.
3. Count the number of fully emerged leaves on the main stem. Note the pattern of emergence of successive leaves. Refer to the growth stage chart in the Introduction (Figure vi) and the table describing decimal scores (Table ii). Record the growth stage and the decimal score for each plant.
4. If you need to use a herbicide, note the herbicide application options that are suitable for the identified growth stage. These can be found in the post-emergence section of the I&I NSW *Weed Control in Winter Crops* book online.

PLANT	GROWTH STAGE	DECIMAL SCORE	NOTES/COMMENTS
1			
2			
3			
4			
5			
6			
7			
8			
9			
10			

Calculating thermal time

Aim: To calculate the accumulated thermal time for a location.

1. Using records from the nearest meteorological station, calculate the mean temperature for each day, i.e.:

   daily maximum temperature + daily minimum temperature – base temperature. (Albus lupin base temperature = 3°C. Narrow-leafed lupin base temperature = 0°C.)
2. If the answer is equal to, or below, the baseline temperature, record a zero reading.
3. Add the temperatures together to give the accumulated degree-days (thermal time).

IN THE PADDOCK

DAY	MAXIMUM DAILY TEMPERATURE (°C)	MINIMUM DAILY TEMPERATURE (°C)	DAILY THERMAL TIME (°Cd) (MEAN DAILY TEMPERATURE MINUS BASE TEMPERATURE	ACCUMULATED THERMAL TIME (°Cd)
1				
2				
3				
4				
5				
6				
7				
8				
9				
10				
11				
12				
13				
14				
15				
16				
17				
18				
19				
20				
21				
22				
23				
24				
25				
26				
27				
28				
29				
30				
31				
Total				

3. Reproductive development

by Janet Walker and David Luckett

Chapter Snapshot

Introduction

The reproductive phase continues the process of determining final yield. A number of environmental and management factors during both vegetative growth and the early reproductive phase can greatly affect yield potential. In lupin, vegetative growth continues simultaneously after the start of reproductive development. This can have an impact on yield.

Chapter 3 covers the phases of lupin flower development and the effects of different management decisions on yield potential.

Learning Outcomes

At the end of this chapter, you will be able to:

- identify the various reproductive development stages
- recognise the parts of the lupin flower
- describe the impacts of temperature on flowering time and duration
- describe the effects of frost and heat on flower development and fertilisation.

Reproductive development Growth stages 2.7–3.9

The change from vegetative growth to reproductive development starts when the growing point of the main stem stops forming leaves and begins to produce flowers. This is called floral initiation. The phase continues until the flowers are pollinated and pod development begins.

This is a complex phase. Lupin has an indeterminate growth habit, meaning that plant development is continuous and overlapping (Figure 3–1). After the main stem has switched to reproductive development, branches in the uppermost leaf axils of the main stem are formed and are still in the vegetative phase.

The timing of this stage is determined by factors such as species, variety, temperature and daylength. Location and sowing date also have a significant impact on flowering time.

Floral initiation

Floral initiation marks the point when the growing point stops forming leaves and starts producing flowers.

This can be seen only under a microscope. The shoot tip changes shape from a dome in the vegetative phase to become more conical in shape. Initially, the floral primordia form a compact bump joined to a ridge. This ridge eventually forms the bract (the modified leaf structure that covers the flower) (Figure 3–2).

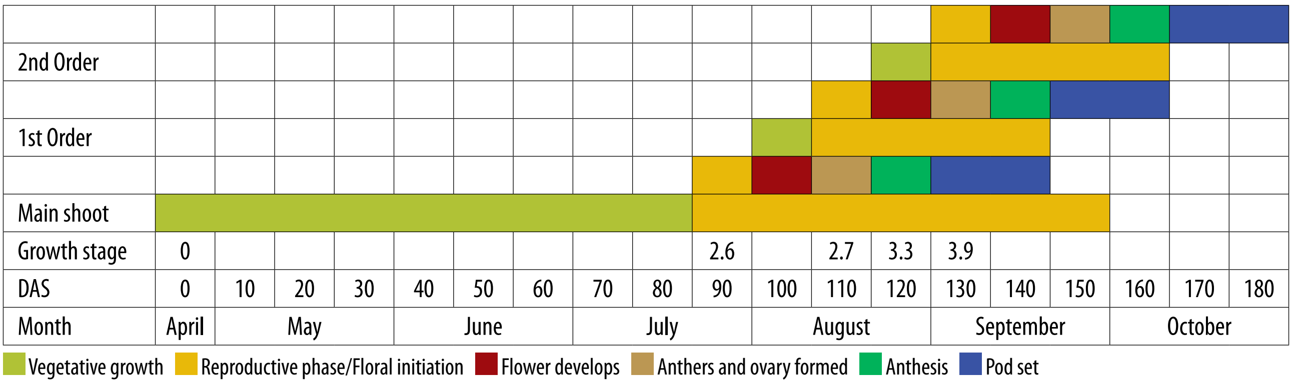


Figure 3–1. Reproductive phase development in lupin. Source: Janet Walker, I&I NSW

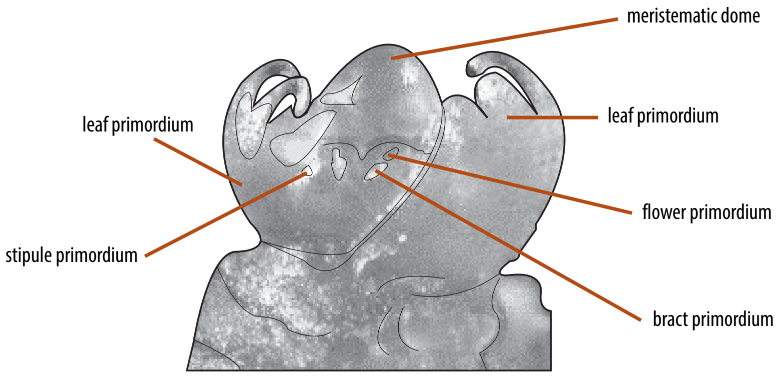


Figure 3–2. Shoot apex at floral initiation in narrow-leafed lupin.

Like the vegetative shoot, the flower has a growing point. The growing point (apical meristem) is determinate – only one flower spike is produced per branch. It ceases activity after all flowers on the flower spike have been initiated.

Flower-spike formation Growth stages 2.7–3.0

After floral initiation, many flowers are initiated in sequence over several days to form a flower spike (also called an inflorescence). A microscope is needed to see this development.

Later, the lower flowers on the flower spike bend outwards from the stem (rachis) and the bract falls off. At this time all the flowers have formed and the apical meristem ceases to grow. Flowers are initiated more rapidly than leaves at this stage, taking around 10 days to initiate, although this again depends on environmental factors and species.

The lupin flower spike is not a single flower but is a raceme made up of many flowers (Figure 3–4). The number of flowers initiated on a flower spike depends on plant size, growth in the vegetative phase, and lupin species.

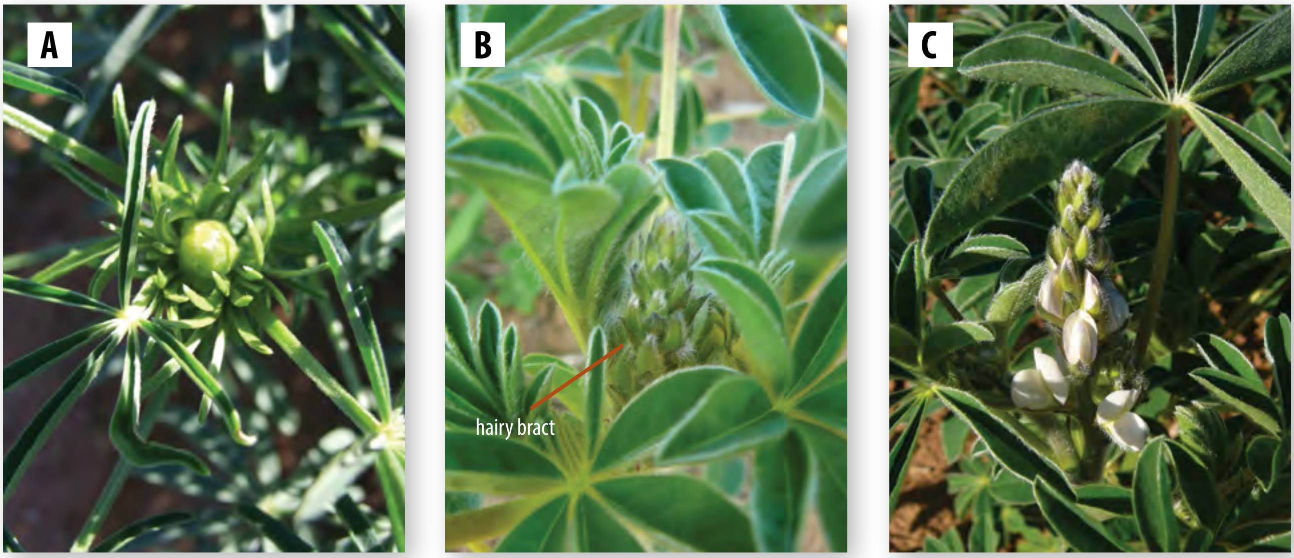


Figure 3–3. Left: Developing flower spike (growth stage 2.7). Photo: Jan Edwards; Middle: Lupin flower spike with covering hairy bracts. Photo: J Walker; Right: Developing lupin flower spike with internodes expanding. Photo: J Walker

The ridge formed beside the initiated flower develops into a hairy bract (specialised leaf) covering the developing flower. As more floral primordia are initiated, the overlapping bracts form the flower spike. The leaves formed in the vegetative phase (before floral initiation) continue to unfold and grow. When all leaves from the terminal bud have unfolded, the flower spike is easily seen and is about 10 mm long (at growth stage 2.7) (Figure 3–3).

The internode under the peduncle (the stem holding the flower spike), as well as the flower spike internodes (Figure 3–3), then starts to grow and lengthen.

Figure 3–4. A flower spike of narrow-leafed lupin (*Lupinus angustifolius*). Photo: J Walker

Lateral flower spikes

While the main stem is forming a flower spike and developing floral organs, the upper first-order branches begin to grow. These can contribute substantially to yield. Each of these primary branches produces a terminal flower spike, and lateral branches are subsequently produced (see Chapter 2 for further details).

The number of branches in an order depends on the growth rate at the beginning of elongation and the number of nodes on the stem. Only a short time (3 or 4 days) elapses between the emergence of a flower spike and the start of growth of the next-order laterals. Each order axis increases the amount of stem tissue and hence the amount of dry matter through the reproductive phase.

Flower development

All flowers follow a similar course of development. The first flower formed remains the most advanced, and the flowers that form later develop in sequence. Flowers at the top of the later-order branches may not reach anthesis (pollen release).

The floral organs develop at varying rates, with the sepals initiated first, followed by the petals, stamens and carpel. The carpel later differentiates to form the ovary, style and stigma, eventually forming the seed once fertilised (Figure 3–5).

It usually takes about 40 days, depending on the environment and the variety, for flower primordia to develop into a mature flower.

Lupin flowers are similar to those of all species in the legume family. The corollas or flowers have five sepals (fused to form the calyx), five petals, two whorls of five stamens and a single carpel (Figure 3–6).

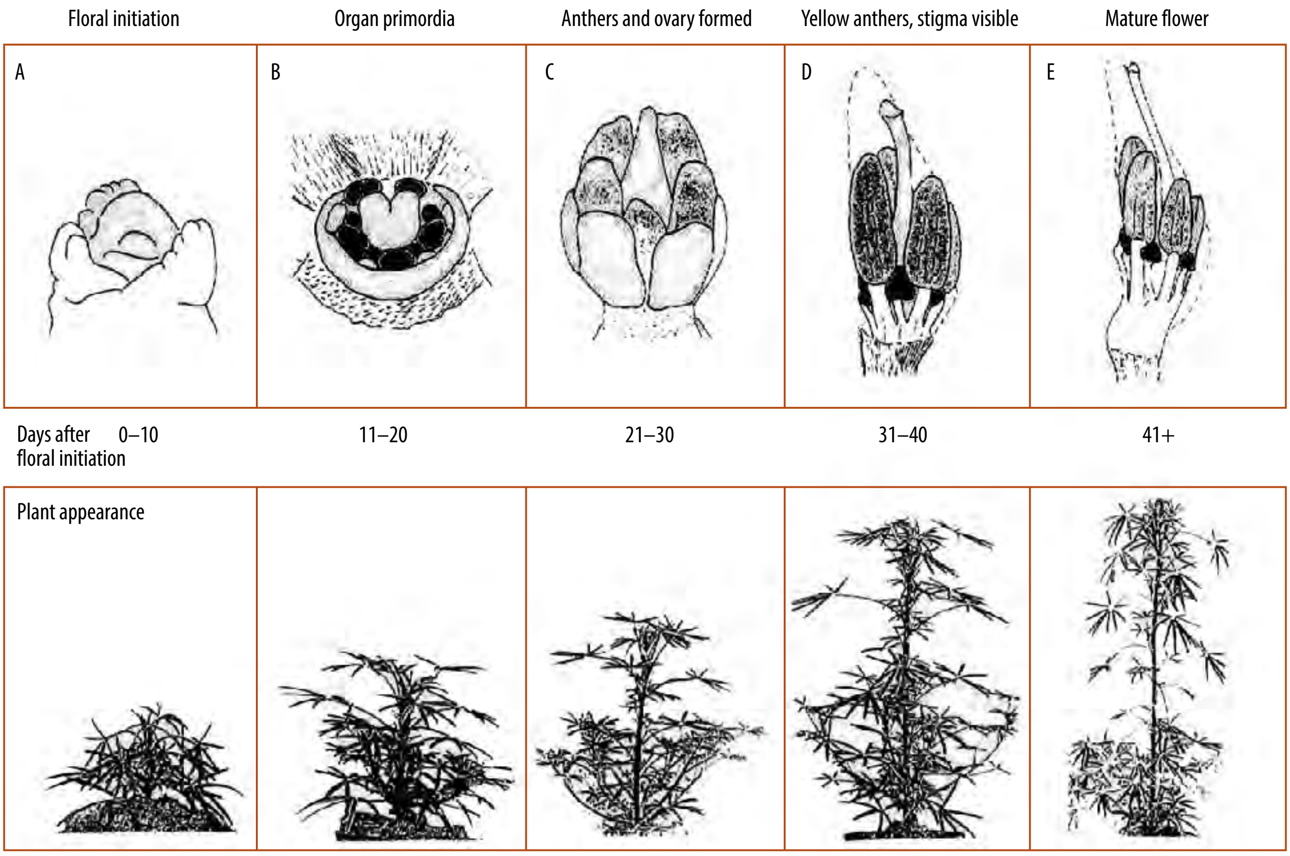


Figure 3–5. Stages of floral development. Source: modified from Dracup and Kirby (1996).

The green outer structure of the flower is made up of sepals fused to form the calyx. In lupin the calyx is very hairy, with a long lower lobe on the bottom and short, pointed lobes on the sides. Of the petals, the standard or vexillum is the large upper petal over the top of the flower. The two wing petals form the sides of the flower and cover the keel (Figure 3–7). The keel at the centre of the flower is made up of two petals. These petals are fused together on the margins, except at the tip.

The keel's structure, with its fused petals, is one mechanism used to restrict the pollinator of the flower. Lupin flowers have a 'tripping' mechanism. This is where the wing and keel petals interlock. The flower is tripped when an insect lands. The insect's weight depresses the wing and keel, exposing the style, stigma and stamens. In the case of lupin, many of the flowers are self-pollinated.

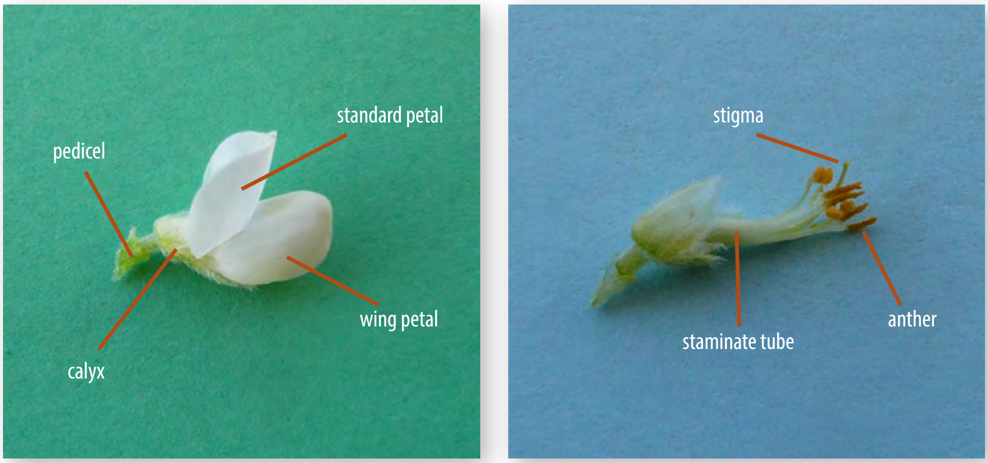


Figure 3–6. Left: A mature lupin flower. Right: Lupin flower without the petals, showing the anthers, stigma and staminate tube.
Photos: Janet Walker

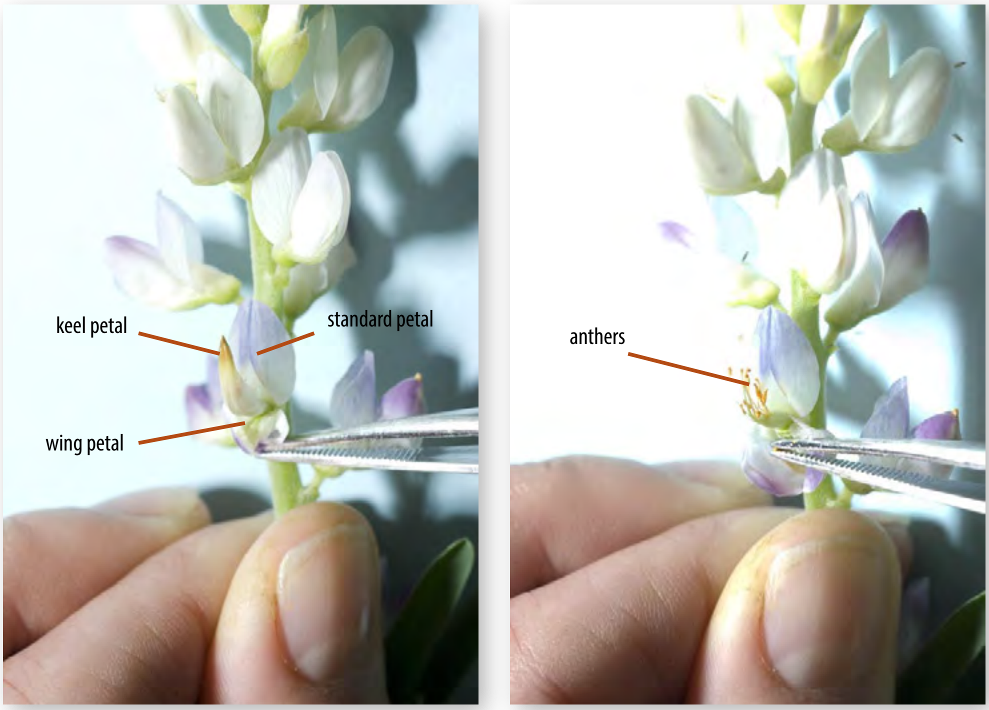


Figure 3–7. Flowers of narrow-leafed lupin, showing (left) the standard, wing and keel petals and (right) the anthers.
Photos: Lowan Turton

On the inside of the flower there are 10 stamens alternating in two circles of five. As the flower develops, the stamens are reoriented into a single whorl. Their filaments become joined together at the base to form a staminate tube, whereas the upper ends and anthers are loose. The anthers of the stamens on the outer circle are much larger, with longer filaments, and are positioned next to the sepals. The anthers of the inner circle are small and next to the petals. The anthers of the five inner stamens develop later than the outer ones. The pollen grains in both sets of anthers are the same size. Initially the stamens are joined together, but later in development one of the stamens from the inner circle becomes isolated from the others.

The single ovary contains two or more ovules and has a curving style ending in a conical stigma surrounded by a fringe of hairs. The stigma is open, and a long channel in the style goes from it into the ovary. In all lupin species stigma maturation occurs during the final stages of flower development.

Flowering Growth stages 3.0–3.8

Once a flower spike emerges, flowers begin to emerge from the bracts. The flowers go through a number of stages, defined by their appearance (Figure 3–8). Flowering of the first-order laterals coincides with the rapid growth of the second-order laterals.

On a single flower spike, the beginning of flowering is defined as the opening of the flower on the bottom of the flower spike. In a crop, it is when half of the plants have open flowers at the base of the flower spike.

Flower opening moves up the flower spike, with one to three flowers opening each day. So, if 30 flowers open on a main shoot, it will take about 20 days. Lateral branches bear fewer flowers and their duration of flowering is shorter. On each flower spike the duration of flowering is about 30 days for the main flower spike (average 29 flowers per flower spike), 21 days for first-order laterals (eight flowers) and 12 days for second-order laterals (four flowers). Pods form on the lower flower nodes while the terminal flowers are still immature.

The duration of flowering is longest in albus lupin and shortest in narrow-leafed lupin.

Pointed and hooded bud stages (Growth stages 3.1 and 3.2)

The longest stage is the pointed bud stage (3 or 4 days). This is followed by the hooded bud stage, which takes less than a day. During this stage the standard petal starts to unfold from the wings and the bract falls off.

Diverging standard petal stage / anthesis (Growth stage 3.3)

Anthesis is the moment when pollen is released from the anthers. The lowest flower on the flower spike is the first to reach anthesis. Anthesis coincides with the divergent standard petal stage (Figure 3–8).

Pollination and fertilisation occur immediately after anthesis and before flower opening. The flower begins to lean away from the stalk and the standard petal begins to unfold and become erect. This stage takes less than a day.

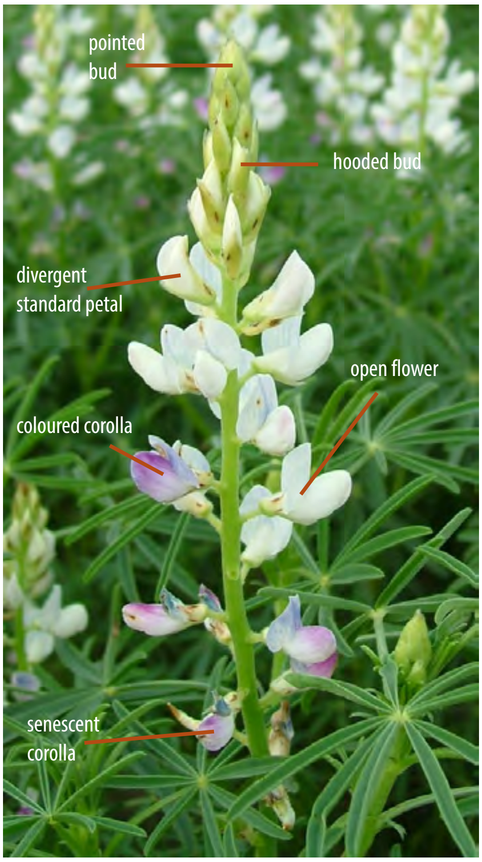


Figure 3–8. Narrow-leafed lupin flower spike, showing the different stages of flower development. Photo: Jan Edwards

Within the flower there are two circles of anthers. At pollen release the anthers of the upper stamens open to shed pollen inwards, forming a plug, or mass, of pollen. At the same time the anthers of the lower circle turn yellow.

The protruding stamen on the inner ring pushes a plug of pollen into the tip of the keel petals, where it surrounds the stigma. These small anthers then shed their pollen.

As a flower approaches pollen release, the stigma, which is well above the long stamens, becomes sticky. In this period the keel is filled with pollen.

The floral phase is finished when all 10 anthers wither.

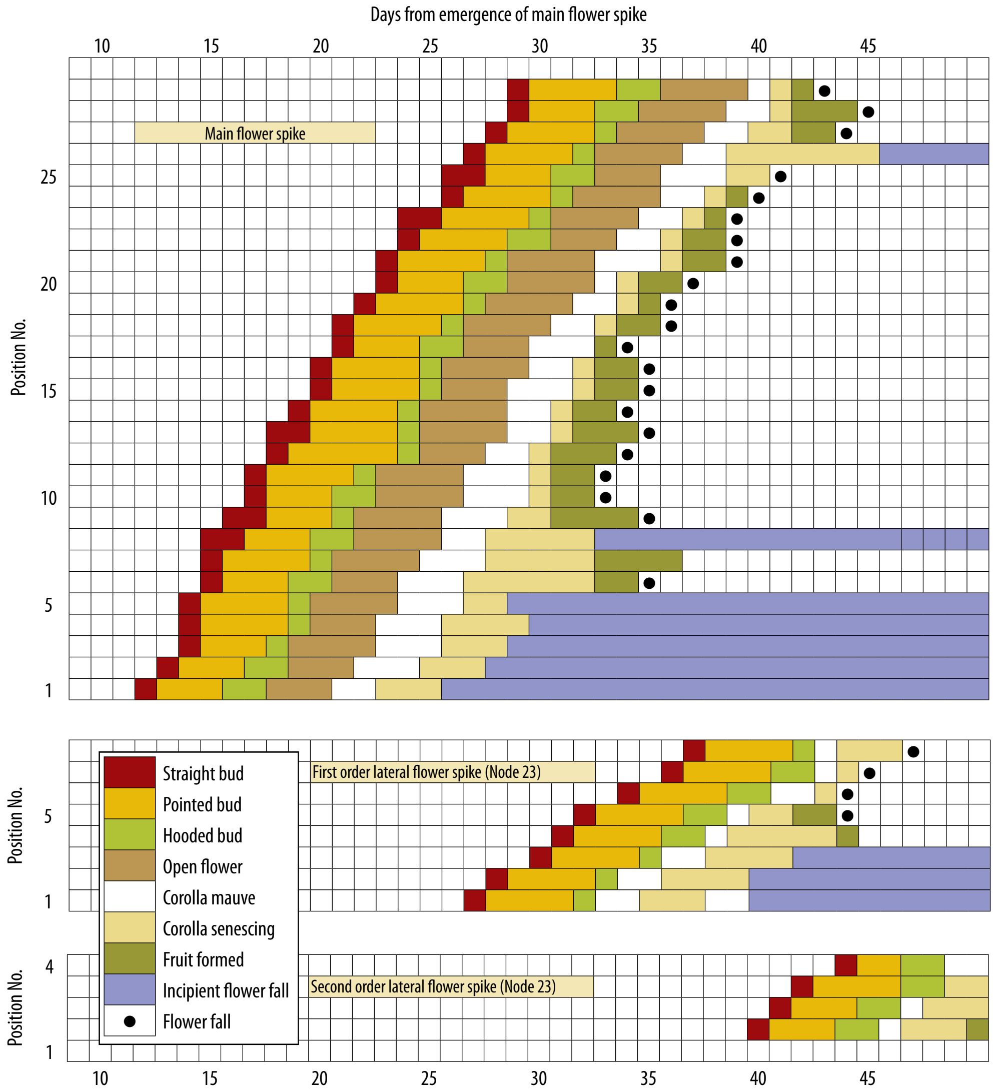
Open flower stage (Growth stage 3.4)

After anthesis comes the open flower stage (Figure 3–9), the length of which depends on the position of the flower on the plant. The open flower stage can last for up to 4 days on the main stem.

The flower is at its maximum weight just before the open flower stage.

Coloured corolla stage (Growth stage 3.5)

The flowers on the lateral branches enter the coloured stage, in which the wing petals turn mauve/blue immediately after opening (Figure 3–8 and 3–9).



- Between one and three flowers open each day, starting at the bottom of the flower spike and progressing upwards.
- Lateral branches bear fewer flowers and their duration of flowering is shorter.
- The duration of flowering is about 30 days for the main flower spike (average 29 flowers per flower spike), 21 days for first-order laterals (eight flowers) and 12 days for second-order laterals (four flowers).

Figure 3–9. Lengths of the different floral stages at different positions on the stem. Source: Farrington and Pate (1981)

The flower begins to lose weight from this stage until pod formation (in about 10 days' time). At this time the flower is most vulnerable to stresses that can cause flower fall (abscission). Competition for assimilates between the lateral branches and the flowers on the main stem can increase abscission. There is also competition among flowers on the stem. Assimilates are diverted to pods in the basal positions, causing abscission of the upper flowers on the main stem.

Senescent corolla stage (Growth stage 3.7)

The corolla senescing stage is much shorter for flowers destined to abscise (fall) than for flowers that set a fruit (Figure 3–9). The time elapsing between the straight bud stage and the corolla senescing stage is about 13 to 16 days for flowers on the main flower spike, 10 to 13 days for first-order flowers, and 10 or 11 days for second-order ones.

The times taken for flowers to pass through the various developmental stages are shown in Figure 3–9.

Pollination and fertilisation

Pollination and fertilisation follow pollen release. Pollination is the process in which pollen grains are forced into contact with the stigma. Mature pollen is made up of two cells, the gamete and pollen tube.

Once the pollen grains germinate, the pollen tubes grow down inside the style to the stigma, transferring the male gametes to the ovary (to fertilise the ovary). This transfer is fertilisation.

Most lupin pollination does not depend on the flower being tripped. The pollen comes into contact with the stigma without any pollinating agent. The flowers can be tripped (Figure 3–10) when a large enough insect lands on the flower, causing the style and stigma to protrude from between the wing petals. During the tripping the stigma may be pollinated with either the plant's own pollen or pollen carried on the insect from another flower. Lupin flowers attract insects by their colour, pollen, and scent. The flowers contain large amounts of pollen but do not contain nectar. Lupin pollen is too large to be carried on the wind.

Narrow-leafed lupin is self-pollinating, because pollen release occurs just before flower opening. By the time the flower is open for insects to visit, the stigma is already covered with its own pollen. Although insects still visit the flowers, their visits do not increase the pod set or yield, so the amount of cross pollination is very low. This means it is easier to keep varieties pure.

Albus lupin has a pollination mechanism similar to that of narrow-leafed lupin, but cross-pollination is more frequent. Cross-pollination in albus lupin occurs only at low levels (10% to 15%). Thus newer varieties of albus lupin must be grown separately from the older varieties to prevent cross pollination and maintain their low seed alkaloid levels. The albus lupin industry has set a zero bitter (high alkaloid) contamination level (see Chapter 1 for further details).

Yellow lupin is the most cross-pollinated type of cultivated lupin, with about 40% cross pollination. Other wild types of lupin are cross-pollinated to differing degrees.

Figure 3–10. A bee tripping and pollinating an albus lupin flower. Photo: Lowan Turton

Pod set
Growth stage 3.9

Pod set is the process undergone by a fertilised ovary before it starts to grow rapidly to form a pod. A flower has set a pod when first the style, and later the top of the pod, protrudes beyond the withered petals (Figure 3–11). After fertilisation, the ovary starts to grow rapidly into a pod.

Not all flowers on a flower spike form mature pods, and not all set pods survive to maturity. Natural shedding of flowers and young pods is common in many species of grain legumes.

Two things can occur: flower fall and pod abortion.

Flower fall (floral abscission)

Some flowers do not set pods even if they are fertilised. The first sign that a flower will not reach pod set is a change in the flower stalk (pedicel) from green to yellow. The flowers are shed because of the formation of an abscission layer at the base of the pedicel. Once the abscission layer is fully formed the flower falls off (flower abscission).

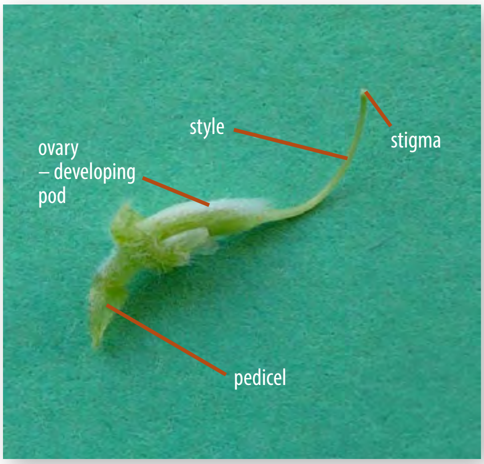


Figure 3–11. Pod set. The fertilised ovary is developing a pod [shown without the petals]. Photo: Janet Walker

Petal senescence (Growth stage 3.7) occurs about 10 days after pollen release. This is also the time at which some of the flowers drop off.

Only some of the flowers on a flower spike form a pod: up to 90% of flowers can be shed and not set pods. Producing many flowers can be an advantage, ensuring adequate pod set in spite of insect damage and poor environmental conditions. The disadvantage is that it can lead to poor harvest index and inconsistent yields.

Current varieties are bred to have higher levels of pod set than older varieties. However, it is still common for high numbers of flowers to be shed because of environmental factors. Under the most favourable conditions, flower fall in lupin usually exceeds 60%. It reaches higher levels under moisture stress and high temperatures.

Abscission of the first flower on a flower spike coincides with the opening of the first flower on the next-order flower spike.

First-formed fruits (pods and seeds) restrict the setting of younger fruits higher up the flower spike. The onset of abscission in the flowers in the mid-regions of the flower spike coincides with rapid growth of fruits at the base of the flower spike.

Once the lateral branches are developing, light penetration to the main stem leaves declines. Light penetration is below 50% by the time flower fall is occurring on the main flower spike. However, even when the main flower spike is placed in full light during flowering, it still forms a similar number of pods as when it was shaded, so there is no direct effect of shading on fruit set. Removing branches, and therefore competition, increases pod set on the primary flower spike.

Factors affecting reproductive development

Plant maturity

The maturity or length of time taken for a variety to reach the start of flowering depends on the thermal time (accumulated temperature) (see Chapter 2*)*, photoperiod (daylength) (see Chapter 2), vernalisation (cold requirement), species and variety.

There are differences in maturity among lupin species and varieties, but they are not as great as among, for example, wheat varieties. Lupin varieties are generally ranked in maturity relative to that of Kiev Mutant, as this is one of the earliest varieties to flower. For example, where Kiev Mutant is the first to flower it is usually followed by Wonga, then Luxor 7 days later, Jindalee 10 days later than Kiev Mutant, and Rosetta 11 to 14 days later.

Vernalisation

Vernalisation is the accumulation of cold that triggers the switch to reproductive development. Plants that are vernalisation responsive will remain in the vegetative phase until they have experienced a certain number of 'cold' hours. Generally, lupin accumulates vernalisation at temperatures between 1°C and about 14°C. The number of cold hours or 'vernalisation response' required depends on variety.

Inadequate vernalisation results in continued leaf production and no flowering at all. It can also create abnormal flowers with odd-shaped wings and petals that are narrower than normal. If vernalisation is delayed, pod fill is likely to occur later in spring when it is hotter and drier.

The vernalisation requirement has been bred out of most narrow-leafed lupin varieties. This has created early flowering varieties adapted to Australian conditions. In these varieties, flowering time depends almost entirely on temperature and daylength. Varieties flower after producing a predetermined number of leaves on the main stem.

Lupin varieties that need vernalisation can be divided into two types: obligate and facultative. Obligates need vernalisation to flower and include varieties such as Jindalee. Facultative types will flower eventually without the cold requirement, but they will flower much faster with vernalisation. Examples are Luxor and Rosetta.

The albus varieties Kiev Mutant and Ultra have the *Brevis* gene for early flowering. Kiev Mutant has no vernalisation requirement, whereas Ultra responds partly to vernalisation.

Sowing time

In Australia, the growing season is rarely long enough to reflect the plant's genetic maturity. Maturity is usually imposed by environmental conditions. Therefore, sowing times are selected that maximise the flowering and pod fill period between the date of the last frost and the time when available soil moisture and high temperatures become limiting.

In NSW, lupin usually flowers 100 days after sowing. However, this can vary by as much as 30 days depending on seasonal conditions. Daylength also has an effect. Lupins flower earlier in northern NSW because temperatures are higher and days longer during winter.

Examples of the relationships between sowing date and flowering time are given in Figures 3–12 and 3–13.

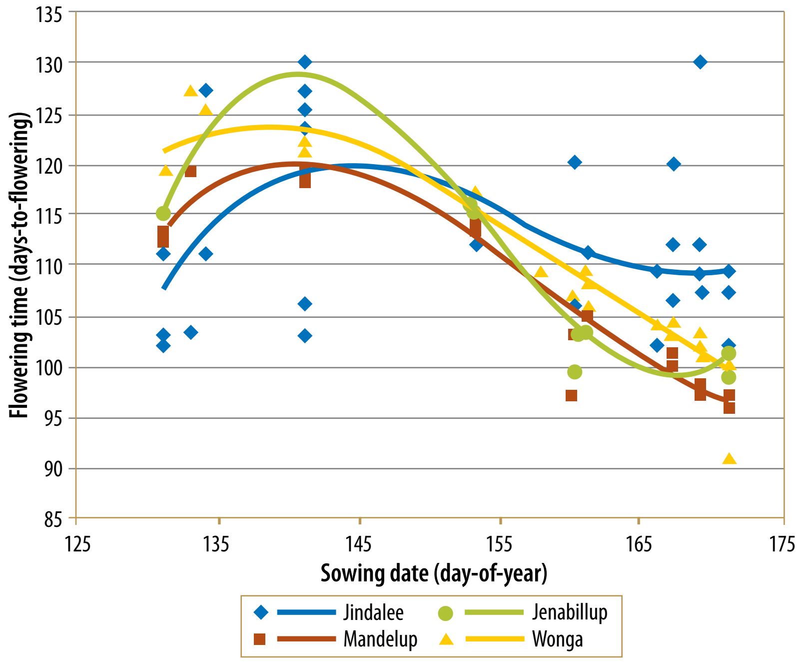
Competition

Competition between the leaves, flowers and fruit (seeds and pods) can increase flower fall and seed abortion. In severe cases it causes flowering to cease early. If carbohydrates are in short supply, the later-formed flowers are more likely to be starved for resources (See Chapter 4 for more information).

Moisture

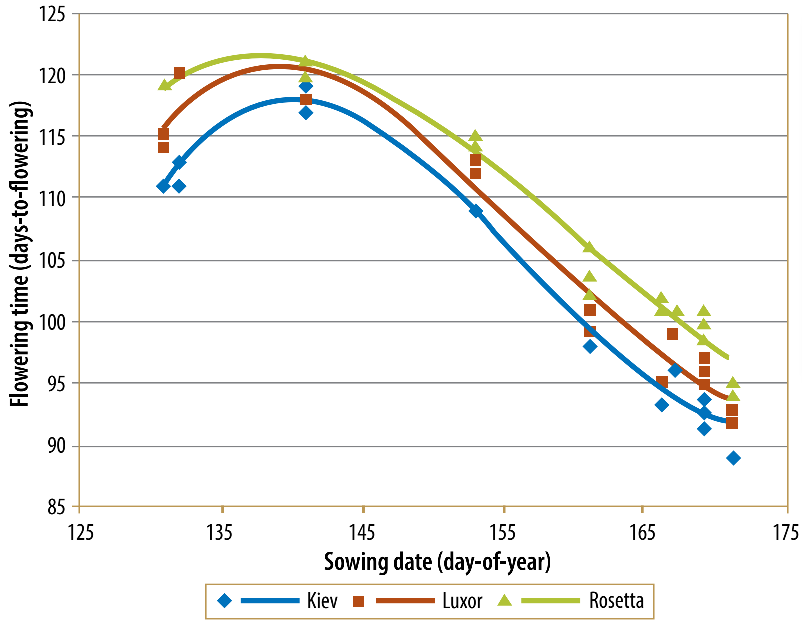
Moisture stress

Moisture stress before flowering (from growth stage 2.5) or during flowering has the largest effect on yield. It causes flower abortion and reduced pod set.



- As the sowing date becomes later in the year, the number of days to flowering decreases.
- If sown on day 135 (15 May), varieties take between 115 and 125 days to flower.
- If sown on day 165 (14 June), varieties take between 100 and 115 days to flower.
- There is less response in Jindalee because it needs vernalisation.

Figure 3–12. Flowering responses of narrow-leafed lupin to sowing date. Source: David Luckett, I&I NSW (unpublished)



- If sown on day 135 (15 May), varieties take between 110 and 120 days to flower.
- If sown on day 165 (14 June) varieties take between 95 and 110 days to flower.
- As the sowing date becomes later in the year, the number of days to flowering decreases.
- The response of flowering time to sowing date is more consistent than in narrow-leafed lupin.

Figure 3–13. Flowering responses of albus lupin to sowing date. Kiev Mutant is consistently the quickest. Source: David Luckett and De Li Lui, I&I NSW (unpublished)

Severe moisture stress will also hasten the onset of flowering, shortening both the flowering and grain-filling periods.

Waterlogging

Lupin is very susceptible to waterlogging. The reduced supply of oxygen in the root zone reduces nitrogen uptake and nitrogen fixation and increases the risk of root diseases.

Roots can adapt to short periods of waterlogging by changes in their metabolism and anatomy. Yellow lupin is better adapted than narrow-leafed lupin, and narrow-leafed lupin is better adapted than albus.

Temperature events

Heat stress

High temperatures at flowering cause greater yield loss than at any other growth stage. Temperatures above 28°C reduce pollen tube growth and can cause sterility. This reduces the number of flowers that are fertilised, which in turn reduces the number of pods set. Temperatures above 33°C cause abortion of flowers and pods. Very high temperatures above 36°C to 40°C will sterilise pollen, preventing fertilisation. Moisture stress makes the effects of temperature worse.

Cold and frost

Actively growing tissues tend to be more sensitive than dormant tissues to low temperatures. For example, pollen tubes are very sensitive to low temperatures. Temperatures below 8°C to 10°C delay pollen grain germination and reduce the rate of pollen tube growth.

In the vegetative phase, lupin has good frost tolerance (see Chapter 2). However, frost during the reproductive phase causes flower abortion. Some compensation is possible because the flowers do not develop at the same time. Extra seed production on the lateral branches may result.

Lupin pods have better frost tolerance than faba beans and fieldpeas.

Nutrition

Phosphorus

Low phosphorus has a greater impact on reproductive development than vegetative growth. Phosphorus deficiency slows the rate of leaf appearance and delays flowering. It also reduces the number of flowers on the flower spike. High phosphorus increases the number of pods set and the yield on lateral branches but has no effect on the number of seeds per pod or on pod size.

Nitrogen

If nitrogen deficiency (through poor nodulation) occurs early in plant growth, the plant is less likely to recover and there will be a greater delay in plant development.

Nitrogen deficiency around the time of floral initiation can delay flowering. It reduces the number of leaves initiated and slows the rate of leaf appearance. This does not affect the time to floral initiation, but it can delay flowering. The delay can be between 68 and 220 degree-days (4 to 14 days), depending on the sowing date.

Nitrogen deficiency also reduces flower numbers and slows branch growth.

Disease

Several diseases can infect lupin during the early reproductive stages and can cause yield losses. Sclerotinia stem rot infection (described in Chapter 2) can reduce yield if humid/wet conditions occur during flowering and early pod fill. Infection can also spread to developing pods. Phytophthora root rot will also become apparent as plants with damaged root systems attempt to flower and fill pods, but die prematurely. Symptoms of lupin anthracnose are most noticeable during the reproductive stages as infected plants appear as patches of distoted plants within a crop, with bright pink/orange spore masses in developing pods.

Insects

Heliothis caterpillars are an annual pest of lupin flowers. They can cause damage from flowering to early pod filling. Small caterpillars (1 to 5 mm) feed inside the flowers.

Aphids can be an intermittent problem at late vegetation, budding and flowering. They reduce pod set.

Thrips are rarely a problem in lupin. Thrips feed on immature flower buds, producing dead, greyish-white buds, bare flower stems and distorted pods. Injured flower buds rot and fall, leaving the bract behind.

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IN THE PADDOCK

Identifying development stage

Aim: To identify plant growth stages through to the reproductive stage.

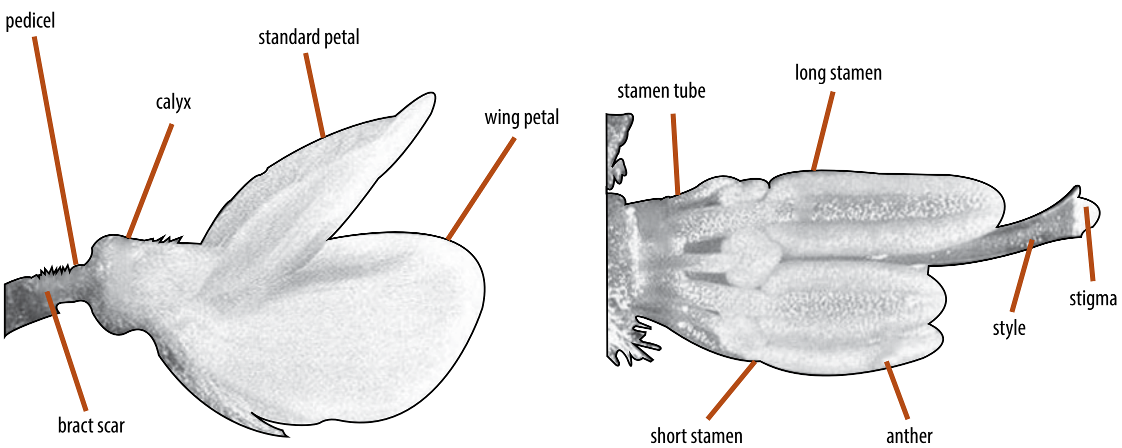
1. Dig up 10 plants.
2. Assess each plant and determine the developmental stage by using the growth stage chart in the Introduction.
3. Record the growth stages of plants in the table below.

PLANT	GROWTH STAGE	COMMENTS
1		
2		
3		
4		
5		
6		
7		
8		
9		
10		

Flowering

Aim: To identify parts of the lupin flower and look at the flower spike to assess the stage of pollination of the flowers.

1. Take a flower and dissect it to reveal the different types of petal. Identify the flower components and label the diagram below.
2. Identify flower stages in the pollination process.
3. Compare the flowers of narrow-leafed lupin and albus lupin for differences in structure in terms of self-pollination and cross-pollination.
4. Identify flowers that are close to pod set.
5. Look at any possible frost damage or flower abortion.



IN THE PADDOCK

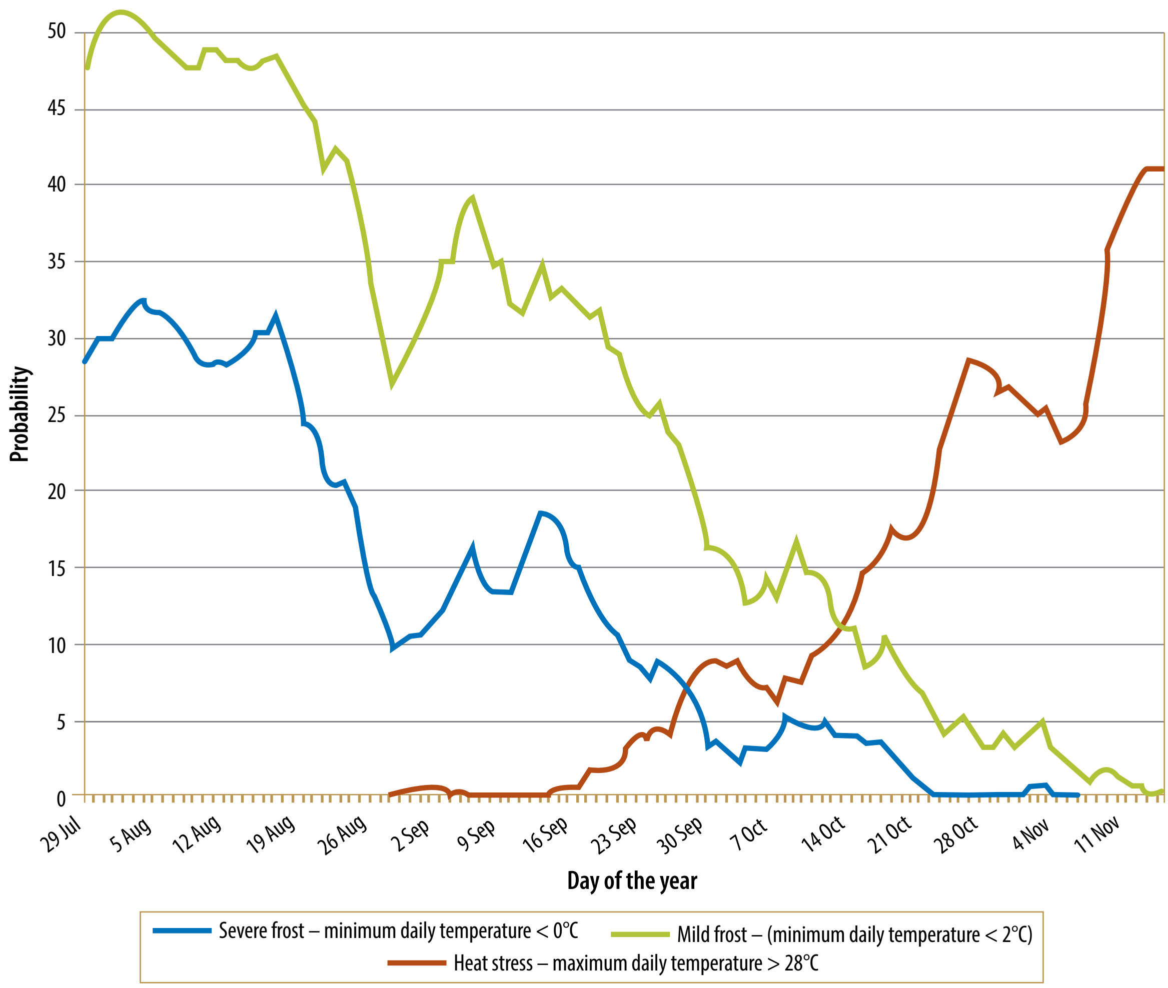
Modelling flowering time

Aim: To determine the risk of frost damage and heat stress at flowering to determine optimum flowering dates.

Look at the climate data for your location and determine the optimum flowering time for avoiding frost and temperatures over 28°C:

1. If sown on 15 May (year day 135), Rosetta will take 125 days to flower and will flower on 17 September. If sown on 14 June (year day 165), varieties take between 100 and 115 days to flower.
2. Using the graph of 5-day rolling averages of temperatures (August to November) supplied below, or a similar graph for your region, calculate and write down the probability of frost for Rosetta planted on 15 May and starting to flower on 16 September.
3. Repeat this process for a planting date of 14 June (sown on day 165) and start of flowering on 6 October.

   Temperatures above 33°C during the day cause abortion of flowers and pods.
   Very high temperatures (above 36°C) will sterilise pollen, preventing fertilisation.
4. Using the graph of 5-day rolling averages of temperatures (August to November) supplied below, or a similar graph for your region, calculate and write down the probability of temperatures above 33°C and 36°C for Rosetta planted on 15 May.
5. Repeat this process for a planting date of 14 June (sown on day 165) and start of flowering on 6 October.
6. Discuss the risks associated with a planting date of 15 May.



Example of 5-day rolling average temperatures (August to November) at Cowra

IN THE PADDOCK

VARIETY	SOWING DATE /DAY OF THE YEAR	FLOWERING DATE /DAY OF THE YEAR	PROBABILITY OF FROST DURING FLOWERING	PROBABILITY OF HEAT EFFECTS AT FLOWERING

Pest/virus identification and monitoring

Aim: To assess the impacts of insects and diseases on lupin at flowering, and the need for control.

1. Identify *Heliothis* caterpillars and *Heliothis* damage of flowers.
2. The threshold levels are one or two larvae less than 5 mm long per square metre for albus lupin for human consumption, and one or two larvae per 10 sweeps for stock feed.
3. Thrips are rarely a problem in the actual flower. The threshold levels are one or two thrips per flower. Inspect buds and flowers and shake the flowers into a white container to dislodge them. Record the number of thrips per bud and flower.
4. Identify thrips and thrips damage of flowers. Thrips are slender-bodied, feathery winged insects 1 to 1.5 mm long.
5. Discuss the need for thrips and *Heliothis* control. Refer to the I&I NSW publication *Insect and Mite Control in Field Crops* (Hertel et al. 2009 in the reference list for this chapter).
6. Check for viruses and diseases in crop (e.g. *Sclerotinia*).

4. Pod and seed development

by Paul Parker and Jan Edwards

Chapter Snapshot

Introduction

Pod and seed development is the period from fertilisation to physiological maturity and is the final stage in the life cycle of the lupin plant.

Final yield is determined during this phase and is influenced not only by current conditions and management decisions, but by everything that has preceded it. Seed quality is greatly affected by the conditions during seed development.

This chapter explains how first the pod and then the seed develops, fills, ripens and reaches physiological maturity. It describes the environmental conditions that influence the progression of this stage. Suggestions are provided for management strategies to maximise yield and quality.

Learning Outcomes

At the end of this chapter, you will be able to:

- recognise the development stages of pods on the primary flower spike and the difference between this and the development of pods on the flower spikes on later-order laterals
- become familiar with the development stages of the pods and the seed
- identify when physiological maturity has been reached
- identify when harvest maturity has been reached.

Pod development Growth stages 4.0–4.9

Pod and seed development actually begins before flowering. The developing flower contains tissues that will eventually be part of the pod and the seed. After pollination and fertilisation the pod begins to grow.

Pod growth Growth stages 4.0–4.9

After pod set a period of rapid pod growth begins. During the initial stages of pod development, the pod wall increases in thickness at the base close to the stem. This extra thickness provides strength to keep the pod attached to the flower spike.

When the developing pod is 8 to 10 mm long, the pod is considered set and is unlikely to abort. Once the pods have reached their maximum length and width they continue to thicken. The pod walls (carpels) reach their maximum length and width before there is any significant development of the seeds within each pod.

The pod walls are storage sites for carbohydrates (sugars), nitrogen and other nutrients. At this stage the seeds are generally less than 5% of their final mass. As the pods reach maximum weight, most of the nutrients are then transferred into the developing seeds.

As the pods approach maturity they begin to dry out and change colour from green through tan to a light reddish brown (Figure 4–1).

Pod development follows a similar sequence to flowering, starting on the primary flower spike, followed by the lateral flower spikes. It also begins at the bottom of the flower spike and proceeds upwards. Flowers on the lower part of the plant are more likely to form pods, as these flowers are earlier and are better positioned to compete for assimilates.

Pod abortion

Even if the flower is fertilised, some pods may fail to develop, in which case they are usually aborted from the flower spike.

Most pods that set survive to maturity, but a few may abort after pod set. A period of pod abortion from fertilised flowers occurs 10 days after pollen release.

The pod retention rate is the number of pods that survive to crop maturity. When pods abort after pod set, they may remain attached to the plant but do not produce viable seed. For pod retention to be maximised, flowering needs to occur at a time that allows an adequate period


Figure 4–1. Pods at growth stages 4.4 (right) and 4.9 (left). Photos: Janet Walker (left) and Jan Edwards (right)

for seed fill before the onset of dry hot conditions. Seeds can also abort. This often occurs in the early stages of their growth.

Some pods can remain and continue to grow but do not develop seeds. The number of pods that develop seeds is highest at the bottom of the flower spike, and the probability of pods being set decreases towards the top. However, environmental stress during flowering or initial pod development can result in gaps between pods along the flower spike.

Seed development
Growth stages 5.0–5.9

During seed development the seeds expand and rapidly accumulate protein and carbohydrate and nutrients. This does not begin until the pods have expanded to their full length and thickness.

Seed enlargement
Growth stages 5.0–5.2

Seed enlargement begins after fertilisation. Five or six seeds develop per pod. The seed rapidly increases in size as the cells divide and expand. During this time, there is little increase in seed weight. The developing seeds are green. Cutting the seed open lengthwise soon after pod set reveals a small embryo and radicle. The space in the embryo sac is filled with endosperm (jelly-like material around the embryo). When squashed, the seed appears to contain only water.

Seed fill
Growth stages 5.3–5.6

Seed growth lasts for 38 to 72 days. Cell division in the cotyledons has stopped, but the cells continue to expand as they take in water and nutrients.

Seed dry weight increases because of rapid but constant accumulation of storage reserves in the developing seed. The rate of dry matter accumulation is constant with time. Pools of sugar and amino acids are established in the first 2 to 6 weeks after anthesis. Polysaccharides, protein and oil are laid down. This process is complete by 12 weeks after anthesis (Figure 4–2). Seeds produced at the top of the canopy contain more oil than seeds produced on the main stem.

During seed fill the seed coat is green. By the end of this phase the cotyledons have become firm and the radicle of the embryo has turned white. This indicates that the seed is approaching physiological maturity (see below).

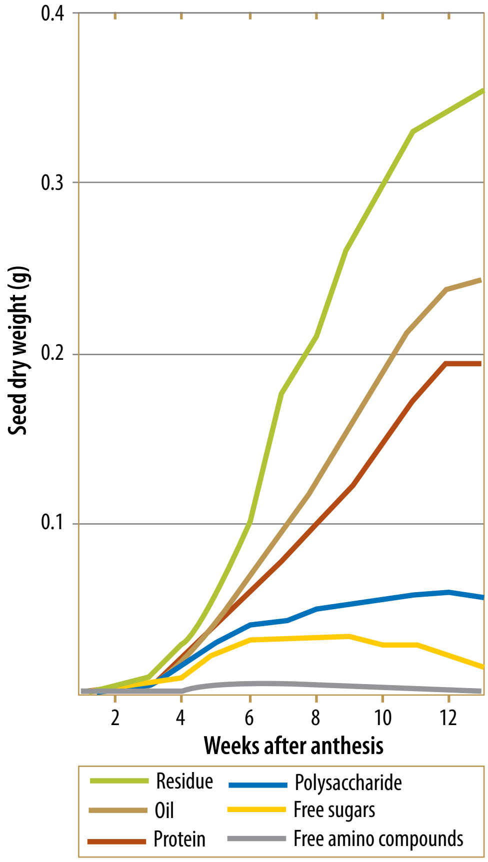


Figure 4–2. Changes in soluble and insoluble components of developing seeds of albus lupin during fruiting. Source: Atkins et al. (1975)

- Pools of sugar and amino acids are established in the first 2 to 6 weeks after anthesis.
- Polysaccharides, protein and oil finish being laid down by 12 weeks after anthesis.

The time taken for individual seeds to fill is related to when pollination of individual flowers took place. Seed filling takes progressively less time as the branch order increases. Seeds from late-developing flowers frequently have shorter development periods and faster seed-filling rates. This affects their final composition and size (Figure 4–3).

Physiological maturity Growth stage 5.7

Finally, the accumulation of nutrients in the seed slows and ultimately stops. The seed no longer has a functioning connection to the carpel, and nutrients cannot be transferred into the seed. The leaves on the main stem and lateral branch orders die off.

Physiological maturity is the stage at which the seed-filling period has ended and the seed has reached its maximum dry weight. The seeds can have a moisture content of 62% (on a dry weight basis). The cotyledons turn from yellow to golden brown. The halves of the pods turn tan to light brown (Figure 4–4).

Each seed has a fully developed plant with a root, two cotyledons, young leaves and a shoot apex. It can germinate and grow into a new plant. It is during this period that the seeds of narrow-leafed lupin develop a speckled coat (Figure 4–5).

Some water-soluble carbohydrates remain in the stem and some nutrients remain in the pod walls and are not transferred to the seed.

Physiological maturity of the whole plant occurs when more than 90% of the pods on the highest order branch have reached maturity.

Harvest maturity Growth stage 5.9

After physiological maturity, the seed dries down further. Seed quality is best when the seed moisture content is between 13% and 14%. At higher moisture contents the seed will require aeration or drying for longer-term storage. Harvesting at or below 10% moisture can increase the

- Because pod and seed filling takes less time as the branch order increases, seed filling occurs at almost the same time on all branch orders.
- Seeds in pods on the uppermost second-order branches tend to be lighter than those in pods on the main shoot.
- Although the seed weight on all branches is similar under irrigation, the seed weight of the second-order branches is much lower under drought stress.

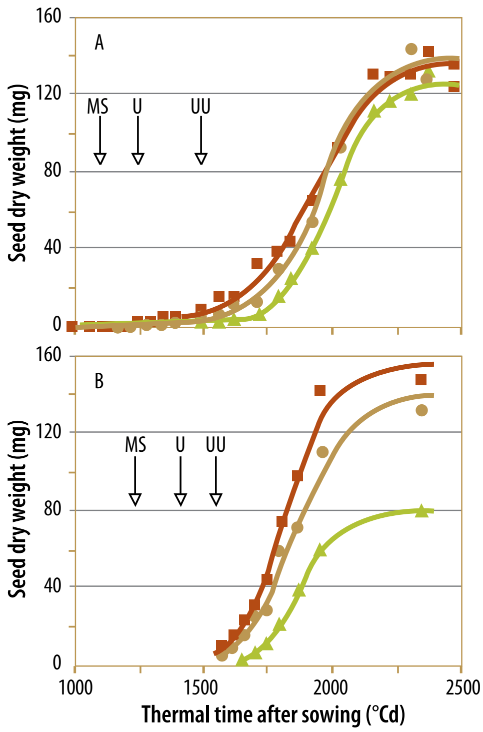


Figure 4–3. Growth of individual seeds of narrow-leafed lupin. Graph A) is under irrigation and B) is under drought stress. The graphs show the dry weights of healthy seeds on the lowest pod on the main shoot (MS: ■), uppermost first-order branch (U: ●), and uppermost second-order branch (UU: ▲) in two experiments. Arrows show the timing of pod set on the various shoots. Source: Modified from Dracup and Kirby (1996b)

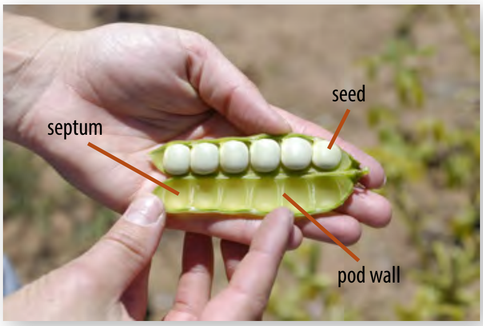


Figure 4–4. Seeds and pod of albus lupin. Photos: Michel Dignand

Figure 4–5. Seeds of narrow-leafed lupin (left) and albus lupin (right). Photo: Lowan Turton, I&I NSW

amount of bruised and cracked seed (Figure 4–6), greatly reducing quality. This will reduce the germination percentage of the seed when it is sown the next year. A seed can be damaged even though the seed coat may appear undamaged (See *In the paddock – Checking seed quality*).

Windrowing and desiccants

Windrowing or the use of desiccants can help to reduce shattering, pod loss and plant lodging during harvest. Once a seed has reached physiological maturity (62% to 65%) it is possible to start windrowing or to use desiccants. At this stage the stem and leaves are light green to yellow and the leaves are beginning to fall from the plant.

In practice, the correct time can be difficult to determine. If windrowing or desiccating is done too early, some of the seeds may not ripen fully and the cotyledon will remain green instead of turning yellow. Figure 4–7 shows the correct stage of maturity at which windrowing should be done. It is a compromise between the earlier and later pods.

Competition between plant parts

The overlap between vegetative growth and reproductive development in the lupin plant means there will be flowers, pods and seeds at different stages of development on the one plant. This results in competition between these plant parts for assimilates. This competition is the main reason cause of pod abortion.

Competition between branches

Flowering on the main stem coincides with lateral branch development. Eight to 10 days after the lateral branches start to grow, their demand for assimilates increases. This reduces the assimilate supply to the pods on the main stem and can reduce the number of pods set.

By comparison, plants bred with restricted branching experience reduced competition between the main stem and lateral branches. As a result, pod set on the main stem is greater.

The main stem does not contribute assimilates to any of the lateral branch orders (See *Main stem growth* in Chapter 2). This results in lower seed weights on the lateral branches compared with the main stem (Figure 4–8).

Competition between pods

All the pods on the plant form at different times, but they reach maturity at a similar time. This means that the earlier-formed pods have a competitive advantage over the later-formed pods.

The later-formed pods (those at the top of the flower spike) have a shorter filling time and often smaller seeds. The later-formed pods on the higher-order branches also have progressively shorter filling periods.

Figure 4–6. Cracking of albus lupin seeds due to handling at the wrong moisture content. Photo: Lowan Turton, I&I NSW

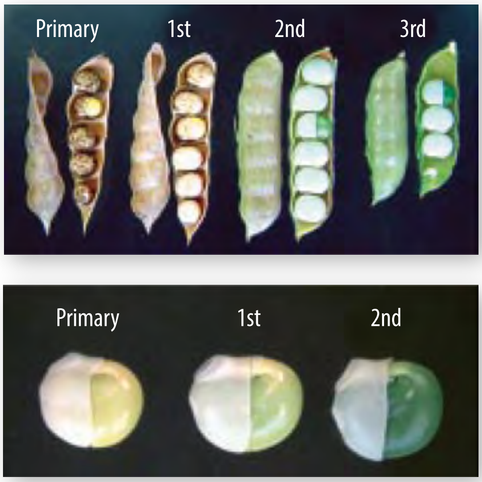
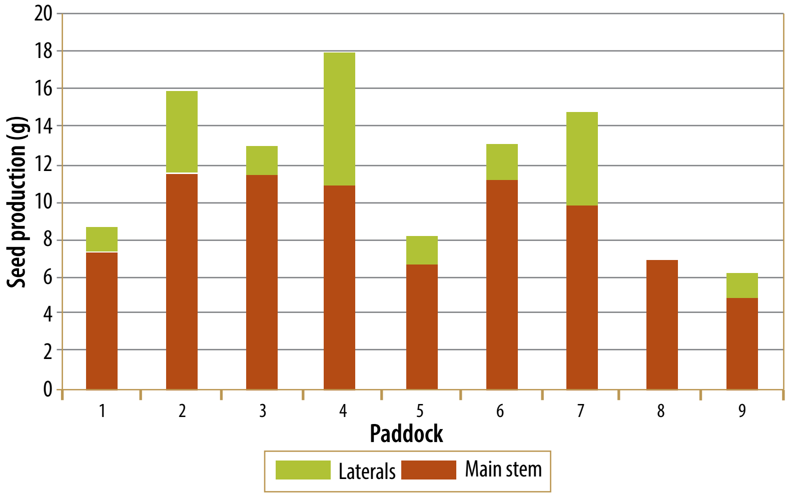


Figure 4–7. Pod wall, seed coat and cotyledon colours of narrow-leafed lupin (left) and albus lupin (right) at the correct stage of maturity to windrow. Pods are from the main stem, first-order lateral, second-order lateral and third-order lateral.
Source: I&I NSW



- In 2006 there was a very late autumn break and a dry spring.
- The average weight of seeds on the main stem is heavier than that of seeds from the lateral branches.
- The average seed weight varies among paddocks.

Figure 4–8. Average seed weights from lupin paddocks at Dubbo in 2006. Source: Kathi Hertel, I&I NSW

Assimilates
Simple sugars (e.g. carbohydrates) that are a product of photosynthesis.

Competition between seeds within a pod

There is also competition for **assimilates** between seeds within a pod. Seed weight and seed survival tend to be highest in the middle part of the pod (Table 4–1).

Sources of assimilates for pod and seed growth

Carbohydrates
A group of compounds that includes sugars, starches and celluloses that serve as major energy sources in plants.

Sources of carbohydrate

There are two sources of carbohydrate available to the developing seed. The first is from photosynthesis during seed fill. The second is from water-soluble **carbohydrates**.

Table 4–1. Seed dry weight and survival at different positions within the pod. 1 = closest to the pedicle.

	SEED POSITION IN POD	1	2	3	4	5
Main stem	Seed weight (mg)	119	122	129	120	105
	Frequency of surviving seed (%)	89	95	95	88	43
Uppermost first-order branch	Seed weight (mg)	128	145	133	124	105
	Frequency of surviving seed (%)	85	94	94	91	60
Uppermost second-order branch	Seed weight (mg)	108	124	130	122	120
	Frequency of surviving seed (%)	58	86	92	96	60

Source: Modified from Dracup and Kirby (1996a,b)

During photosynthesis, carbon dioxide is converted to simple sugars (e.g. sucrose). Most of these sugars are used to form the cell walls of the plant. Excess sugars are stored in the plant as water-soluble carbohydrates.

Photosynthesis during seed fill comes mainly from the pods while they are green, and also from the stem. At this time, most of the leaves have died. The pod is capable of photosynthesis and is an important source of carbohydrates for the developing seeds, especially after the onset of rapid pod growth, as most of the leaf canopy has died off by this time.

Water-soluble carbohydrates are stored in the plant during the vegetative growth stage. During seed-filling, carbohydrates can be redistributed from dying plant parts (mainly leaves) and from the pods. Water-soluble carbohydrates contribute only about 12% to 18% of final seed yield.

Decreased dry matter production decreases the carbohydrate supply and causes increased reliance on reserves.

Seed growth rate is determined by carbohydrate availability during seed filling and by the number of competing seeds. Remobilisation of reserve carbohydrates accumulated during earlier growth stages in the roots, stems, leaves and pod hulls may contribute to seed filling, but the remobilisation rate is only small.

Sources of protein

Protein is synthesised from simple amino acids, which are made up of nitrogen. Nitrogen is an essential component of chlorophyll and the enzymes involved in photosynthesis. During the plant's life, nitrogen is remobilised from old or dying leaves to young growth or the pods.

As seed filling begins, amino acids are translocated to the seed and converted into protein. Protein accumulation occurs 2 to 6 weeks after pollen release and coincides with rapid cell expansion and a rapid increase in embryo weight.

By the time protein accumulation begins, the lupin plant has shed most of its leaves. As a result, the pods supply 23% to 33% of the nitrogen to the seeds.

Lupin has a high protein content (usually 30% to 40%). Most of the protein in the mature seed is found in the cotyledons (Table 4–2).

Table 4–2. Locations of protein in lupin seed.

Cotyledons	76%
Rest of the embryo	17%
Seed coat	7%

Factors affecting seed development

Because production of the final yield occurs just before physiological maturity is reached, any plant and environmental factors that affect yield can only do so before physiological maturity has been reached. Yield losses after this stage are usually a result of weather damage, disease, insect attack or other problems occurring between physiological maturity and harvest.

Moisture

Moisture stress

Because lupin has an indeterminate flowering habit, moisture stress after flowering has a greater impact on later-formed pods.

Water deficit during flowering markedly increases flower abortion and reduces the number of flowering nodes and the subsequent number of pods, because lateral branch development is reduced.

Water deficit during pod set and pod filling has little effect on main-stem dry matter, but it progressively reduces the amount of dry matter accumulated in the higher-order laterals, resulting in reduced seed number and size.

Intermittent periods of water deficit during different stages of the lupin plant's development can also affect yield, depending on when the deficit occurs. Research has shown that whereas a water deficit during the vegetative period of growth does not reduce seed yield, a water deficit during flowering on the main stem and first-order laterals reduces total seed yield by reducing the seed yield of the first-order laterals but not of the main-stem pods.

Lupin does have a way of coping with water stress at flowering. Under water stress at flowering, lupin carbohydrates are stored in the stems and pods. They are later transferred to the developing seed to maximise the development of some seeds under stress conditions.

In albus lupin the duration of pod growth is much longer than in narrow-leafed lupin, so even the best-suited varieties can suffer water stress during pod growth and seed fill.

Temperature

Both low and high temperatures during pod and seed fill can affect seed size and yield in lupin.

Cold and frost

The developing pods are very susceptible to frost (Figure 4–9). Low temperatures are more likely to occur in early spring during flowering and the early stages of pod development. They can cause abortion of small pods or failure of one or more seeds to develop within the pods.

Figure 4–9. Frosted pods. Photo: Kathi Hertel

The actively growing tissues in developing seeds (and growing pollen tubes) are more sensitive than vegetative tissues to low temperatures. Because it is indeterminate and the flowers (and therefore the pods) do not all develop at the same time, lupin can compensate for cold damage by developing more flowers and pods on later-order laterals.

Well-developed pods will produce good-quality seed, provided that mild, moist conditions follow the frost. Seed in less-developed pods will shrivel and become brown in frosts.

Lupin plants can compensate for frost damage by increasing the number of pods on the later-order laterals. In one study, although pod numbers were reduced by 40% on the main shoot and first-order laterals in a section of a crop affected by frost, there was a 100% increase in the numbers of pods on the basal, second- and third-order laterals.

In addition, even though there can be up to 25% fewer seeds on the frosted plants, the seeds are heavier.

Heat stress

Both the canopy and the pods can experience temperatures higher than the surrounding air temperature (Figure 4–10). The pods, particularly those at the top of the canopy, can be between 3°C and 5°C hotter.

Heat stress, in the form of short bursts of high temperatures (>30°C) can reduce the size of individual seeds and therefore final yield (Table 4–3). Bursts of high temperature early in seed filling can cause seed abortion. During the later stages of seed fill, high temperatures can reduce the weight per seed in lupin. If moisture stress occurs at the same time, the impact is greater (Table 4–4). This may explain some of the season-to-season variability in lupin yields.

The reason for the decrease in seed weight in heat-stressed lupin is not known. In cereals, similar heat stress reduces starch synthesis and therefore grain weight. However, starch is a very small component (6%) of a lupin seed.

There is some evidence that seeds maturing at high temperatures (>28°C) establish more slowly when sown the next year. It is not known why, but temperatures during seed development may induce a temporary dormancy.

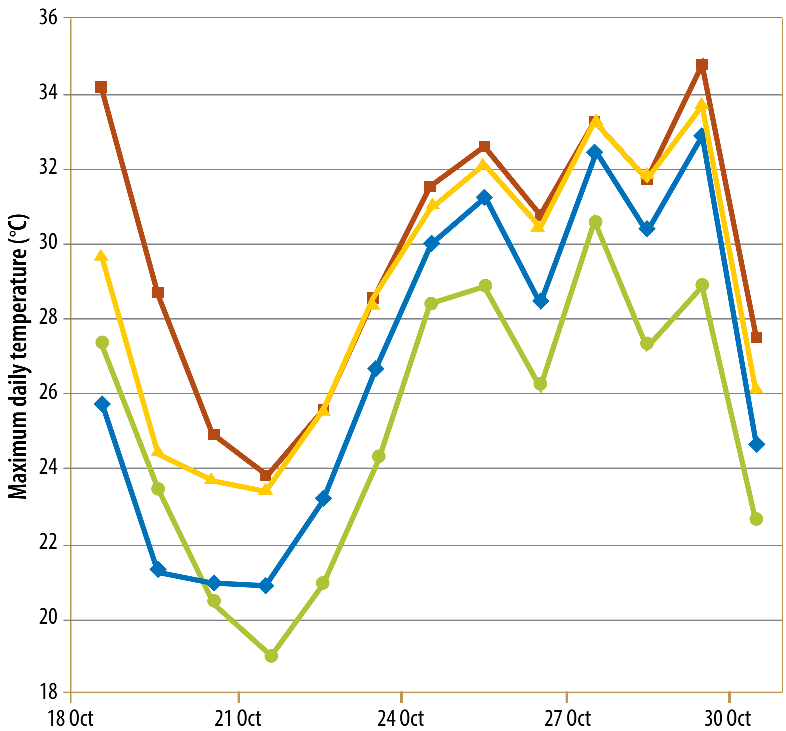


Figure 4–10. Maximum daily temperatures of the first-order pods (■), main stem pods (▲) and canopy (◆) of narrow-leafed lupin and in an adjacent meteorological screen (●) at East Beverly, WA in 2005. Source: Reader et al. (1997b)

Nutrition

Phosphorus

High phosphorus increases the number of pods set and the yield on lateral branches, but it has no effect on the number of seeds per pod or on pod size.

Nitrogen

Nitrogen fixation stops with the onset of pod filling. Nitrogen is translocated from the stems, leaves and pods to the growing seed. Nitrogen deficiency early in pod filling reduces seed protein levels.

Lupin yield is generally more sensitive to early nitrogen deficiency than deficiency during flowering or seed-filling.

Manganese

Seed yields of lupin can be substantially reduced by manganese deficiency. Narrow-leafed lupin has a poor ability to accumulate manganese in its seed. The resulting deficiency can cause the seed to split.

Table 4–5 shows the amount of nutrients removed in each tonne of lupin seed.

Table 4–3. Effect of 6 hours of heat treatment on yield components of narrow-leafed lupin.

	TEMPERATURE NIGHT/ MAXIMUM DAY	YIELD COMPONENT WEIGHT PER SEED (MG)	SEEDS PER POD	SEEDS PER PLANT	SEED YIELD (G DRY SEED PER PLANT)
Experiment 1	15°C/20°C	180	3.94	7.14	5.1
	15°C/38°C	159	2.47	7	2.7
	l.s.d. ($P = 0.01$)	*14*	*0.4*	*2*	*1.2*
Experiment 2	15°C/20°C	190	4.07	9.13	7.1
	15°C/34°C	182	4.07	9.65	7.1
	15°C/36°C	174	4.08	9.78	6.9
	l.s.d. ($P = 0.01$)	*5.9*	*0.1*	*1*	*0.6*

Source: modified from Reader et al. (1997a)

- Plants were exposed to higher temperatures for 3 hours each day for 2 days.
- Heat treatment occurred when seeds were 4.3% of their final weight.
- Increasing temperature to 34 to 38°C caused a seed weight reduction of between 4% and 12%.

Table 4–4. Effect of temperature on seed yield of the main stem and branches of narrow-leafed lupin.

	SEED YIELD (G PER PLANT)	
	MAIN STEM	BRANCHES
Well watered at 20°C	1.50	1.70
Well watered at 25°C	1.75	0.60
Water stress at 20°C for 5 days at early pod filling	1.65	0.50
Water stress at 25°C for 5 days at early pod filling	1.00	0.15

Source: Modified from Gladstones et al. (1998)

Table 4–5. Nutrient removal (kg) for each tonne of lupin seed

	NITROGEN	PHOSPHORUS	POTASSIUM	SULFUR	CALCIUM	MAGNESIUM
Narrow-leafed lupin	51.2	3.0	8.0	2.3	2.2	1.6
Albus lupin	57.3	3.6	8.8	2.5	2.0	1.3

Source: Price (2006)

Disease

There are several diseases that can infect lupin during the reproductive stages and cause yield losses.

Phomopsis infection of the stems and pods (Figures 4–11 to 4–15) can cause stem collapse and reduce yield if there is a water deficit at the end of the season. Current breeding is directed towards producing resistant types.

Until recently, this disease was known to occur only in narrow-leafed lupin. Symptoms usually become obvious only at maturity or after harvest. Infected seed is discoloured and may have mould growth. The fungus has a major impact on germination percentage (Figure 4–16). Sowing of seed free of this disease is currently the only method available to growers to minimise potential yield losses.

Infected stubble can be highly toxic to livestock, causing lupinosis, particularly if it is grazed under very humid or wet conditions following rain. Phomopsis levels can increase in stubble of all lupin varieties – whether resistant or susceptible – following rain after harvest.

In 2004, an isolate of the fungus capable of infecting albus lupin was detected. Luxor and Rosetta have good resistance. Kiev Mutant is moderately resistant to susceptible. At the time of publishing, the strain of Phomopsis that can infect albus lupin represents a minor risk.

Figure 4–11. Albus lupin pods infected with Phomopsis (top) and brown leaf spot (bottom; see Chapter 2). Photo: Raymond Cowley I&I NSW

Figure 4–14. Pods and seeds heavily infected with Phomopsis. Within an infected pod there can be differences in the level of disease on each seed. Photo: Raymond Cowley I&I NSW

Figure 4–12. Comparison of albus lupin variety resistant to Phomopsis (right) and the susceptible breeding line WK264 (left). Note the darkened and shrivelled pods. Photo: Raymond Cowley I&I NSW

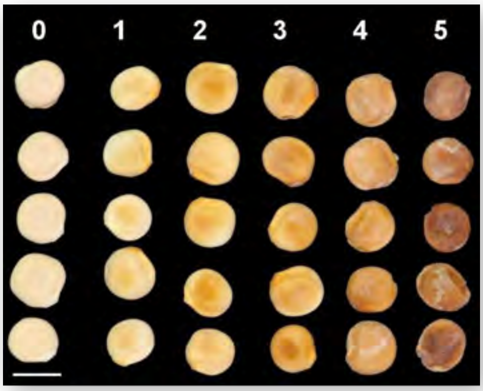


Figure 4–15. A 0 to 5 seed infection (discolouration) scale used to determine the severity of Phomopsis infection of a seed lot. Photo: Raymond Cowley I&I NSW

Figure 4–13. Characteristic pycnidia ('leopard spotting') of Phomopsis on albus stubble. Stems such as these contain the toxins responsible for lupinosis. Photo: Raymond Cowley I&I NSW

- As seed infection percentages rise, the ability of the seeds to germinate falls.
- Seed at discoloration category 1 (a 65% infection level) has an unacceptably low germination %.
- Moderately infected and heavily infected seeds (categories 2 to 5) do not germinate.

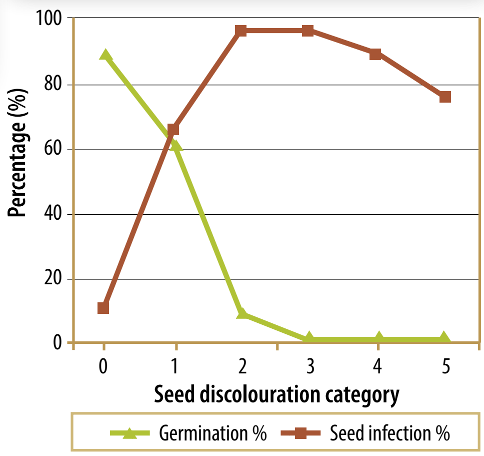


Figure 4–16. Effect of Phomopsis seed infection on germination, and levels of seed-borne Phomopsis in a heavily infected sample of Kiev Mutant. The seed was sorted into the seed discolouration categories shown in Figure 4–15. Source: Cowley et al. (2010)

Insects

Insects can cause serious damage during pod and seed development. Caterpillars (in particular those of *Heliothis* and lucerne seed web moth) can cause significant yield losses (See Figure 4–17). They eat their way through the walls of the young pods and feed on the developing seeds. Very young pods may abort. Seeds suffer physical seed damage that affects the quality of the harvested seed. It also affects the germination percentage of the sowing seed for the following year.

Feeding of large populations of thrips on the developing pods can have a detrimental impact on yield through increased pod abortion. See Chapter 3.

The native budworm (*Helicoverpa punctigera*) is a major pest of lupin crops. Narrow-leafed lupin crops will not be damaged until they are close to maturity and the pods are losing their green colouration. Pod walls are not penetrated until the caterpillars are over 15 mm long. Large caterpillars (25 mm) eat holes in the pods and seeds (Figures 4–18 and 4–19). The decision to spray a lupin crop should not be made until the caterpillars are greater than 15 mm long. At this size they are capable of penetrating the walls of the pods.

Figure 4–17. Lucerne seed-web moth damage. Photo: I&I NSW

Figure 4–18. Caterpillar damage to lupin pods. Photo: Ray Cowley, I&I NSW

Figure 4–19. Damage to albus lupin seeds caused by heliothis. Source: Lowan Turton, I&I NSW

Measuring crop performance

Yield

Seed yield from a lupin crop is determined by the amount of seed produced per unit area. The three components influencing this are:

- number of pods per square metre (pod density)
- number of seeds per pod
- seed weight.

The yield components develop in sequence, although there is some overlap.

Pod density

Pod density is a function of the number of plants and the number of lateral branches, which sets the number of flowering spikes.

Growth before pod initiation influences the potential number of pods through its effect on the number of leaves, which influences the number of potential sites for flowering branches in the leaf axils.

Final pod density is controlled by water availability (and therefore assimilate supply) before and during flowering. Although pod number is usually set by the end of flowering, pods can be aborted up to maturity.

High plant populations tend to produce plants with fewer branches and a greater number of pods on the main stems. As a result, a greater proportion of the yield is derived from the pods on the main stem.

Number of seeds per pod

The potential number of seeds per pod ranges from three to six, depending on the location on the plant. As branch order increases up the plant, the number of seeds per pod decreases. Seed set is determined mainly by temperature and moisture during flowering, both of which affect assimilate supply. Pollination and fertilisation generally do not limit the potential number of seeds per pod.

There is a correlation between total dry matter production at flowering and seed density.

Weight per seed

Seed weight is the last component to be set, and is the least variable. It is largely determined by the genetic potential of the variety. The two additional impacts on seed weight are the location of the pod on the plant and the timing and severity of environmental stress. Seeds are generally smaller on the later-order laterals.

Yield compensation

The lupin plant responds to improving or deteriorating conditions almost to maturity by increasing or decreasing its yield components.

This ability to compensate means that the plant produces yield even when one or more of the yield components is affected by environmental conditions.

For example, if a transient stress aborts some of the early-formed flowers and pods, the plant will put its existing resources into the remaining seeds, which will tend to be larger. If conditions are favourable, the flowering and seed-fill period can be extended. This will allow the later seeds to develop. How large they get depends on how long the conditions last.

Although the plant can adjust according to conditions, maximum yield is most likely when the plant has to do the least amount of compensation.

If the lower nodes on a flower spike fail to set pods because the flowers are destroyed, then an equivalent number of pods will form higher up the flower spike.

Reducing the supply of carbohydrates around the time of flowering reduces the number of pods that develop and also restricts the pods' capacity for compensatory growth when the supply returns to normal.

The supply of carbohydrates regulates the yield of seeds and pods. Prolonged stress results in smaller pods and fewer, lighter seeds.

Harvest index

Lupin has a lower harvest index than other pulse crops such as peas, chickpeas and lentils. This is because lupin has higher vegetative biomass.

In lupin, the weight of the pod wall itself makes up a much greater percentage of the total pod weight at maturity than in other pulses such as soybean. This also contributes to a low harvest index.

A low harvest index can also result from a low plant population. If the plant population is low, the lupin puts more resources into vegetative growth, resulting in a lower harvest index.

Water-use efficiency

Water-use efficiency in lupin crops is lower than in cereal crops. The process of fixing nitrogen requires more energy and therefore uses more water. Lupin also has a high protein content in its seed. Plants need more energy to produce 1 g of protein than to produce 1 g of carbohydrate. Protein production also requires more nutrients, and therefore water.

Lupin does have some adaptations to make it more water-use efficient. Lupin has been bred to flower early and set pods and seeds before the onset of moisture stress. Early flowering also leaves more time and moisture available for use after flowering. This results in larger seeds, and improved water-use efficiency and harvest index.

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IN THE PADDOCK

Pod mapping

Aim: To map pod location and number of pods on primary and lateral flower spikes.

1. Count the number of plants in 1 m of row in five locations in the paddock.
2. Collect 10 plants.
3. Including the primary flower spike, count the number of each branch order laterals on each plant.
4. Count the total number of pod-bearing flower spikes, including the primary flower spike, that have developed on each of the plants.
5. Count the total numbers of pods that have developed on each plant.
6. From the 10 plants collected, select one that is a representative, average plant.
7. From this plant, select three pods (one from the bottom, one from the centre and one from the top) from **each** order of flower spike (i.e. three pods from the primary flower spike and three pods from a flower spike from a first-order lateral, three pods from a flower spike from a second-order lateral, etc.), keeping the pods from each flower spike separate.
8. Compare the differences in size among the three pods from each flower spike and between the pods from each of the flower spikes from the different laterals.

LOCATION	NO. OF PLANTS/METRE
1	
2	
3	
4	
5	
Average	

PLANT	NO. OF DIFFERENT-ORDER LATERALS	TOTAL NO. OF POD-BEARING FLOWER SPIKES	TOTAL NO. OF PODS ON EACH PLANT
1			
2			
3			
4			
5			
6			
7			
8			
9			
10			
Average			

IN THE PADDOCK

Seed mapping

Aim: To identify the relationship between pod location on laterals and pod size and seeds per pod.

1. Using the three pods selected from each of the different flower spikes in step 7 of the pod mapping section above, carefully open them and count the number of seeds in each pod. Determine the total number of seeds per pod number. Now determine the average number of seeds per pod by dividing the total number of seeds by the number of spikelets with seeds (i.e. primary + first-order lateral + second-order lateral + third order lateral etc.).
2. Check if there is any difference between the size of seed from the different pods, and note which pod, if any, has the largest seed and which has smallest seed. Note which lateral, and the location on the lateral, that these pods came from.

FLOWER SPIKE	NUMBER OF SEEDS			COMMENTS ON SEED SIZE COMPARISON AMONG PODS AND BETWEEN LATERALS
	POD 1	POD 2	POD 3	
Primary				
First-order lateral				
Second-order lateral				
Third-order lateral				
Fourth-order lateral				
Fifth-order lateral				
Total number of seeds				
Average number of seeds/pod				

Seed maturity

Aim: To identify the stages of maturity in developing lupin seeds. Determine which have reached physical maturity.

1. Taking one seed from each of the pods opened at step 1 in the exercise above, note the seed coat colour.
2. If possible, carefully cut open each seed and note the colour of the cotyledons. The seed moisture content will determine whether this can be done easily. If the seed is too hard to open, it can be assumed that the cotyledons will be yellow. Colours other than yellow may indicate development or disease issues.
3. Identify the different components of the seed, including the cotyledons, radicle, shoot apex and seed coat.

POD LOCATION	SEED COAT COLOUR			COTYLEDON COLOUR		
	SEED 1	SEED 2	SEED 3	SEED 1	SEED 2	SEED 3
Primary flower spike						
First-order lateral						
Second-order lateral						
Third-order lateral						
Fourth-order lateral						
Fifth-order lateral						

IN THE PADDOCK

Estimating yield

Aim: To estimate a lupin crop yield from the counts of pods and plants above.

1. Using the figures obtained in Step 1 of Pod mapping, calculate the number of plants per square metre by multiplying the number of plants per metre of row by the factor corresponding to the crop row spacing.

LOCATION	NUMBER OF PLANTS/M	NUMBER OF PLANTS/M^2
1		
2		
3		
4		
5		
Average		

Conversion factors for determining number of plants per square metre:

ROW SPACING	FACTOR	ROW SPACING	FACTOR
15 cm (6 in.)	6.7	25 cm (10 in.)	4
17.5 cm (7 in.)	5.7	30 cm (12 in.)	3.3
20 cm (8 in.)	5	40 cm (15.7 in.)	2.5
22.8 cm (9 in.)	4.4	50 cm (19.6 in.)	2

2. Determine the total number of seeds per square metre by using the numbers already determined above:

   Total seeds/m^2 = average no. pods per plant × average no. seeds per pod × no. plants per m^2

Average no. of pods/plant		From 'Pod mapping' step 5
Average no. of seeds/pod		From 'Seed mapping' step 1
Average no. plants/m^2		From 'Estimating yield' step 1
Total seeds/m^2		

3. Calculate estimated yield
   For narrow-leafed lupin: Yield (kg/ha) = total seeds/m^2 × 1.6
   (Calculation is based on an average of 6000 seeds/kg for narrow-leafed lupin.)

   For albus lupin: Yield kg/ha = total seeds/ m^2 × 3.3
   (Calculation is based on an average of 6000 seeds/kg for albus lupin.)

	NARROW-LEAFED LUPIN	ALBUS LUPIN
Total seeds/m^2		
x conversion factor	x 1.6	x 3.3
Yield (kg/ha)		

IN THE PADDOCK

Checking seed quality

Aim: To check the quality of harvested seed to determine whether there has been any damage from low moisture or incorrect harvester speed.

One way to test for cracked or damaged seed is to soak the seed in 1 part ink and 9 parts methylated spirits. After being washed in clean methylated spirits, cracked seeds retain the colour of the ink that has penetrated through the damaged seed coat.

Glossary

Aerenchyma

Air channels in the roots of lupin that enable the exchange of gases between the roots and the shoots.

Allelopathy

Allelopathy occurs through the release by one plant species of chemicals that affect other species in its vicinity. The effect is usually negative, such as reduced growth and development, reduced germination rates; reduced root and shoot extension.

Anther

The terminal part of a stamen, producing pollen, in pollen sacs.

Anthesis

The moment when pollen is released from the anthers. In lupin this occurs before flower opening. Pollination and fertilisation occur immediately after anthesis.

Apex

The tip of an organ.

Apical meristem / apical dome

Growing point; a zone of cell division at the tip of the stem or root.

Arbuscular mycorrhizae

Arbuscular mycorrhizae (AM) are fungi that occur naturally in soil and help make soil nutrients available to a plant by acting as an extension of the plant's root system. AM increase the volume of soil so that the roots can explore and improve the uptake of nutrients, particularly phosphorus and zinc. AM are particularly important in northern New South Wales.

Basal or lower branch

Branch arising in the axil of the cotyledons or lowest 4 to 6 leaves on the main shoot.

Base temperature

The temperature below which the plant will not perform some function, e.g. germinate, emerge or grow.

Bract

A modified leaf, or leaf-like structure, that covers the flower in the early stages of its development.

Carbohydrates

A group of compounds that include sugars, starches and celluloses and serve as major energy sources in plants.

Carpel

The female part of the flower. A carpel consists of three parts: the ovary, which becomes the seed after fertilisation; styles, which are extensions of the ovary; and stigmas, which are specialised filaments on which the pollen falls and germinates.

Corolla

Part of the flower between the calyx (sepals) and organs (i.e., the petals)

Cotyledon

The food store for the germinating plant, and the largest part of the seed. Cotyledons form the seed leaves directly from the embryo. Lupin and all broad-leafed plants are known as dicots, because they have two cotyledons.

Degree-days

The unit of thermal time (accumulated temperature). Degree-days (°Cd) are used to explain the relationship between plant development and temperature.

Determinate growth

Growth that stops (terminates) once a genetically predetermined structure (e.g. a flower) has been produced.

Dicotyledon

Plant with seeds that have two cotyledons (e.g. canola and pulses). Also known as 'dicots'.

Embryo

Part of the seed that contains the main plant structures. It is made up of the scutellum, plumule and radicle.

Embryo shoot

Shoot that will form the above-ground plant.

Endosperm

A nutritive tissue within the seed that surrounds the embryo and provides energy for germination.

Epigeal emergence

Seed germination and emergence where the cotyledons are pushed above the ground surface (e.g. in lupin and canola). The seedling develops with the cotyledons above the ground.

Fertilisation

The union of male and female reproductive cells during the process of sexual reproduction.

Field capacity

The capacity of soil to hold water at atmospheric pressure, i.e. the maximum volume of water a well-drained soil can hold. It is measured as the ratio of the weight of water retained by the soil (after saturated soil has been allowed to drain) to the weight of the dry soil.

Filament

The stalk of a stamen.

First-order branch

A branch originating in a leaf or cotyledon axil on the main shoot or stem.

Harvest index

The ratio of the seed weight to the total plant weight at harvest.

Harvest ripe

State in which the seed has dried off and is ready to be harvested.

Hilum

The scar on the seed left when the seed separates from the seed stalk in the pod.

Hypocotyl

The length of stem that links the cotyledons and the root system. It is long and white. The junction of the hypocotyl and the root can be indistinct, as the hypocotyl can have some root-like features such as root hairs.

Hypogeal emergence

Occurs when the hypocotyl grows away from the cotyledons and the cotyledons remain below ground level (e.g. in field peas and cereals).

Imbibe

Absorb water.

Indeterminate growth

Ability of a plant to produce more branches or flower spikes after the plant has reached the reproductive phase. If conditions (water, nutrients and sunlight) remain favourable, the plant will produce flowers over an extended period of time and multiple stages of reproductive development will occur on the plant at the same time, all competing for limited resources.

Flower spike

The flower cluster.

Internode

The part of a plant stem between two nodes.

Keel

A pair of united petals of legume flowers that is shaped like the keel of a boat. It is part of the trigger mechanism in insect-pollinated legume plants.

Leaf area index (LAI)

A measure of the upper surface area of leaves of a crop in comparison with the surface area of the ground the plant grows above.

Leaf axil

The point where the leaf joins the stem.

Leaflet

A section of leaf that is highly segmented.

Leghaemoglobin

An organic molecule that controls the supply of oxygen to the *Bradyrhizobium* bacteria.

Lupin

The name commonly used for all species of the genus *Lupinus*. 'Lupin' is derived from the Latin word lupus, meaning 'wolf'.

Meristem

Growing point where active cell division takes place and permanent tissue is formed.

Metaxylem

The outer part of the primary xylem, or woody tissue, of a plant consisting of thick-walled or pitted cells.

Monocotyledon

Plants with seeds that have only one cotyledon (e.g. cereal crops). Also known as 'monocots'.

Nitrogenase

An essential component of the process by which atmospheric nitrogen is converted to ammonium nitrogen. Nitrogenase requires a low-oxygen environment within the nodule to function.

Node

The part of a plant where one or more leaves grow. The nodes are separated on the stem by the internodes.

Order

Describes when and where branches develop on the plant. The branches that develop on the main stem are called first-order branches. The branches that develop on the first-order branches are called second-order branches, and so on, usually up to order number five.

Ovary

The part of the carpel that holds the ovule(s).

Ovule

The part of the plant that, after fertilisation, develops into the seed.

Pedicel

The stalk of an individual flower in the flower spike.

Peduncle

The final internode of the plant stem between the highest leaf and the lowest flower that bears the flower.

Petiole

The stalk attaching the leaf to the stem.

Photoperiod (Daylength)

The relationship between the length of light and dark in a 24-hour period. Photoperiod is expressed as the number of hours of daylight in a 24-hour period. For example, 'The plant was exposed to a 14 h photoperiod'.

Physiological maturity

The stage at which the seed-filling period has ended and the seed has reached its maximum dry weight.

Plumule

Growing point of the seed that develops into the shoot bearing the first true leaves.

Pollen

The male gametes, which are produced in the stamens.

Pollination

The transfer of pollen from an anther (the terminal part of a stamen, producing pollen in pollen sacs) to a stigma (the receptive part of the female reproductive organ).

Primordia

Organs or tissues in their earliest recognisable stage of development.

Proteoid (cluster) roots

Root clusters that develop along the primary lateral roots and increase phosphorus acquisition in low-phosphorus soils.

Raceme

A cluster of flowers, consisting of a single central stem (unbranched) along which individual flowers grow on small stalks called pedicels. The growing point continues to add to the flower spike, so that the youngest flowers are nearest the apex.

Radicle bump

Small bump below the hilum from which the radicle will emerge.

Radicle

Shoot that will form the root system.

Radicle

The part of a plant embryo that develops into the primary root.

Rhizosphere

The area of soil immediately around the plant roots.

Root exudates

Organic acid phosphatases, like citrate, malate, malonate, tartarate, succinate, fumarate, acetate and lactate, as well as protons (hydrogen ions) and phenolics, that are secreted from the roots.

Second-order branch

A branch originating in the axil of a leaf of a first-order branch.

Sepal

Part of the flower, usually green, that surrounds and protects the flower in the bud. The sepals together are called the calyx.

Shoot apex

See Apical meristem.

Stamen

The structure in a flower that produces pollen grains, consisting of a stalk (filament) and an anther.

Stigma

The glandular sticky surface at the tip of the carpel of a flower, which receives the pollen.

Staminate tube

Tube formed by the fusing of the filaments of the stamens.

Stipules

Outgrowths found on either side of the base of the leaf stalk (petiole).

Stomata

Pores found in the leaf and stem epidermis and used for gas exchange.

Style

The part of the carpel bearing the stigma at its tip.

Symbiosis

A close and often long-term interaction between different species, in this case between the lupin plant and *Rhizobium* soil bacteria that fix nitrogen.

Terminal flower spike

The last flower spike produced, marking the completion of the flower spike initiation phase. It is at right angles to the other flower spikes.

Testa

The seed coat.

Thermal time

A way of expressing accumulated temperature. It helps to explain the relationship between plant development and temperature. It is calculated as the mean daily temperature minus a base temperature and is given in degree-days (°Cd). The base temperature used to calculate thermal time is 3°C for albus lupin and 0°C for narrow-leafed lupin.

Vernalisation

A period of cold temperature that triggers the switch from vegetative growth to reproductive development, and therefore flowering.

Water potential

The potential of water molecules to move between regions of different concentrations across a semi-permeable membrane. In a plant cell the cell wall is a semi-permeable membrane.

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