

# THE GROWTH AND YIELD OF NARROW LEAFED LUPIN: MYTHS AND REALITIES

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## ABSTRACT

Narrow-leafed lupin (*Lupinus angustifolius* L.) is an important component of the sustainable farming system of the Mediterranean climatic region of southern Australia. Anecdotes on the growth and yield of the crop have discouraged its adoption among researchers, consultants and growers. An example of this is the idea that under well-watered and nutrient-rich conditions plants grow and accumulate biomass endlessly without converting this into seed yield. Another popular myth is that restricting growth and biomass accumulation in the apical branches lead to higher seed yields. In point of fact, neither of these suppositions is supported by hard data. Evaluation of the breeder's core collection under well-watered and nutrient-rich conditions in Western Australia showed that the indeterminate growth habit of narrow-leafed lupin ceased regardless of water and nutrient availability. Analysis of the growth and yield on mainstem and across all branches orders showed total seed yield is positive and strongly correlated ( $r^2=0.74$ ) with apical branch biomass rather than with mainstem biomass ( $r^2=0.011$ ). A strong and positive correlation ( $r^2=0.70$ ) between total seed yield and apical branch yield index was also found.

This paper reviews research data that demonstrates the untruth of these popular beliefs, and focuses on the facts that *do* determine productivity in narrow-leafed lupin, namely that seed yield is source- rather than sink-limited, and that the crop has little capacity to store and remobilise reserves to the seed during grain filling. Consequently a reduction in biomass and metabolic activity during seed filling leads to a marked reduction in yield.

## KEYWORDS

*L. angustifolius*, Source-sink ratio, core collection, growth and yield, myths and realities

## INTRODUCTION

Narrow-leafed lupin (*Lupinus angustifolius* L.) is the most important grain legume crop in Australia and a vital component of the sustainable farming system of

the Mediterranean climatic region. Australia is the only significant exporter of lupin and 85% is produced in Western Australia. Over the past decade, yields have been stagnant at 1.1 t/ha and the sown area has declined from a maximum of 1.3 million ha to 0.5 million ha in 2007. This is mainly because grower confidence in lupins has decreased due to low profitability as a consequence of low and variable yields, and low value of the grain on international markets. Crop adoption to new areas in Western Australia, particularly high rainfall southern areas, has been limited by prevailing myths on the growth and yield of narrow-leafed lupin. Despite this lupin remains in the farming system because of its value as a rotation crop for cereals, particularly wheat, on the coarse textured soils. It makes an important contribution to the nitrogen economy of the farming system as well as providing an important weed and disease break. With the increasing cost of energy, and therefore fertiliser nitrogen, lupin is expected to have an increasing value in the farming system. There is a critical need to address the profitability and long-term viability of narrow-leafed lupin in the cropping system, and to address its adoption to new areas, such as the high rainfall southern areas of Western Australia. An initial step in addressing its adoption to new areas is to scatter the myths and focus on the realities that the indeterminate growth and yield of narrow-leafed lupin has.

## THE INDETERMINATE GROWTH HABIT MYTH

The narrow-leafed lupin plant has an indeterminate growth habit composed of determinate structures with terminal inflorescences, such as the mainstem and lateral branches. During the vegetative stage the growth of the mainstem is slow, and determined by the elongation of the internodes. At flowering the mainstem accounts for only 10-15% of total biomass at physiological maturity, because of the determinate growth habit imposed by the terminal inflorescence. While mainstem growth therefore necessarily limited, the plant invests in rapid production and growth of apical branches after mainstem flowering. In the low and medium rainfall zones of Western Australia production and growth of apical branches after flowering is often limited by terminal drought. In the

high rainfall zones the growth restriction by terminal drought is considerably reduced, but adoption of the crop to these zones has been restricted by the belief that under an abundance of soil water and nutrients, narrow-leaved lupin will grow continuous vegetative matter like trees and yield less than in the northern zones. In fact, there is good evidence that there is a limit to the number of branch order produced even when lupin is grown under well watered, high fertility conditions. Glasshouse experiments (Palta and Ludwig, 1996; Palta and Plaut, 1999) and field trials (Dracup *et al.* 1998; J. Palta and C. Ludwig, 2000, unpublished) in which narrow-leaved lupin was grown free of water shortage and nutrient deficiency showed that production and growth of apical branches ceased after the emergence of the fifth order apical branches. Similar results were found when narrow-leaved lupin was exposed to elevated CO<sub>2</sub> after flowering and under adequate watering and nutrient conditions (Palta and Ludwig, 2000). The signal for ending the indeterminate growth habit in lupin is not known. In pot-grown plants it is possible that the signal comes from the roots after extensive root growth occupies the limited soil volume (Ternes *et al.* 1994). However, this is not the case under field conditions. Narrow-leaved lupin has the reputation for exploring the soil thoroughly with roots been found at depth of 2 m during podding (Lefroy *et al.* 2001). It is possible then that the signal comes from changes in ambient temperature (Reader *et al.* 1997) or perhaps triggered during flowering (J. Berger, pers. comm.). This is an issue that requires research.

#### THE RESTRICTING BRANCHING MYTH

The average yield of narrow-leaved lupin in Western Australia is 1.1 t/ha and it is often measured against the average yield of wheat of 2.0 t/ha. This ongoing comparison has given rise to another myth relating to the growth and yield of lupin. Narrow-leaved lupin has the reputation of producing large biomass on the branches and it has been suggested that this reduces total yield by reducing the productivity of the mainstems. The underlying misconception here is that mainstem yield is the principal source of plant productivity, and that branches compete with the mainstem for resources. Research programs aimed to improve narrow-leaved lupin yields by restricting branching have not been successful. For instance, the yield of Tallerack, a restricted branching cultivar released in 1997, is not higher than the yield of Belara, a non-restricted branching cultivar also released in 1997 (Berger *et al.* 2008). Further, Tallerack yield is lower than that of Mandelup, a high yielding, non-restricted branching cultivar released in 2000. Several reasons may be responsible for the lack of impact of restricted branching lupins. Firstly, the importance of mainstem yield in determining the crop yield was over emphasised and the competition between developing branches and mainstem yield for resources not determined. As a result, the mainstem yield advantage of restricting lateral branch growth remained an unknown quantity. In any case, water shortage after podding, which often

occurs in many environments where lupin is grown in Western Australia, reduces branch development *per se* (French and Turner, 1991; Palta and Plaut, 1999). Therefore, the need for genetic options to restrict branch growth as a means to improving yield in narrow-leaved lupin is questionable.

Competition for resources between the developing branches and mainstem yield in lupin has been suggested from several studies (Pate and Herridge, 1978; Pate *et al.* 1980; French and Turner, 1991; Palta and Ludwig, 1996). However, this competition is not strong and continuous through the development and growth of apical branches to have a substantial effect on mainstem yield (Palta *et al.* 2000). The use of the stable isotopes of <sup>13</sup>C and <sup>15</sup>N has made it possible to measure the carbon and nitrogen contribution from the mainstem to the branches (Palta *et al.* 2000; Palta, 2001). The numbers are very small. The mainstem only contributes 6% of its assimilated carbon and 4% of its stored nitrogen to the vegetative development of the first order apical branches, and then only during the first two weeks of branch development (Palta *et al.* 2000). Essentially the lateral branches become autonomous in their carbon economy early on in development. Thus, there is *no* carbon and nitrogen contribution from mainstem to seed production in any of the lateral branch orders, including the first order apical branches (Palta *et al.* 2000). The inability of lupin to export resources outside branch orders appears to be a fixed trait that does not respond to manipulation of source-sink relationships. Labelling studies indicate that branches from which flowers were removed to avoid pod set and hence reduce sink size were unable to remobilise the available carbon to either higher or lower branch orders, including the mainstem (J. Palta and C Ludwig, 2002, unpublished).

Another argument that counteracts the belief that yield of narrow-leaved lupin may be improved by restricting branching growth arises from the evaluation of a breeders core collection for competition between mainstem and branch yield (J. Palta, J. Berger and C. Ludwig, 2005, unpublished). The evaluation included 27 commercial cultivars released from 1967 to 2004 in Western Australia and 67 wild genotypes collected from Greece, Spain, Morocco, Italy, Portugal, Syria, Turkey, France, Cyprus, Israel and Germany. Across all genotypes total grain yield decreased with increasing mainstem yield (Fig. 1a). Modern high yielding cultivars released from 1995-2004 had lower mainstem yield than older cultivars. In contrast total grain yield increase with increasing the yield on the branches, particularly on the second order apical branches (Fig. 1b). Modern high yielding cultivars released from 1995-2004 had higher yields on the branches than older cultivars. Reducing biomass, particularly branch biomass will reduce grain yield in narrow-leaved lupin. This is because grain yield was correlated to biomass production, particularly branch biomass rather than to mainstem biomass (Fig. 2a, b and c). Modern breeding

in narrow-leaved lupin has improved biomass and grain yield on the apical branches as a result of decreasing the time to flowering and podding (Fig. 2a, 1b and 3). Since flowering coincides with branching, early flowering allows more time for branches to develop, increasing yield potential (J. Palta, J. Berger and C. Ludwig, 2005, unpublished). This is particularly important for lupin grown in dry areas and dry seasons because it allows the branches to grow and set seed before terminal drought develops (Palta *et al.* 2004).

The importance of branch growth in grain yield of narrow-leaved lupin is also apparent in seasons in which every single young pod on the mainstem is aborted. Under these circumstances grain yield depends entirely on the plasticity of the crop to produce branches and spread the yield risk over time.

### THE REALITIES

Pre-anthesis growth of narrow-leaved lupin is slow, accounting for almost half the pre-anthesis growth of wheat when both crops are grown free of water shortage and at the same location (Eastham *et al.* 1999). Drought spells, low temperature and solar radiation early in the cropping season often reduces the growth of lupin (French and Turner, 1991; Palta *et al.* 2004), and this is likely to be exacerbated by the high proportion of assimilated carbon allocated below ground. Studies in which canopies of narrow-leaved lupin were fed with <sup>13</sup>CO<sub>2</sub> showed that roots were receiving 62% of the daily assimilated carbon at the 5 leaf stage, reducing to 51% at floral initiation, 72-80% of which was used in root respiration (J. Palta and C. Ludwig, 1997, unpublished). Compared to wheat, which has a more abundant root system than lupin (Dracup *et al.* 1992), the allocation and use of assimilated carbon by roots of lupin is much higher. Wheat receives 42% of its assimilated carbon before tillering and 20% at floral initiation (Gregory and Atwell, 1991; Palta and Gregory, 1996). Allocation and use of assimilated carbon in respiration of nodulated roots of narrow-leaved lupin is likely to be due to nitrogen fixation. Nitrogen fixation is expensive. Nodulated roots of white lupin utilised 5.0–6.5 g C to fix 1 g of nitrogen (Pate and Herridge, 1978).

Measures are being sought to improve the pre-anthesis growth of narrow-leaved lupin. Selecting lupin cultivars with vigorous seedling growth is probably one option since this has been shown to increase biomass accumulation and yield in wheat, particularly in drier environments and seasons (Rebetzke and Richards, 1999; Richards and Lukacs, 2002). A possible advantage of improving early growth in narrow-leaved lupin may be the provision of a carbon store for subsequent pod development and grain filling during periods of water shortage after flowering. However, consideration should be taken to prevent a reduction in the fixing nitrogen capacity of narrow-leaved lupin while improving early growth.

Sensitivity to terminal drought is another reality of the growth and yield of narrow-leaved lupin. Terminal drought or 'end-of-season drought' is a common feature of the lupin cropping regions of Australia and occurs when rainfall decreases and evaporation increases in the spring, when lupin enters its reproductive stage (Fitzpatrick, 1970; Reader *et al.* 1995). Current assimilation in narrow-leaved lupin is very sensitive to water deficit (Turner and Henson, 1989) and that sensitivity causes the end of vegetative growth of the apical branches and the end of reproductive growth (French and Turner, 1991; Palta and Plaut, 1999). This ending of both vegetative and reproductive growth causes most of the yield reduction and variability (Palta and Dracup, 1994; Dracup *et al.* 1998; Palta and Plaut, 1999). Yield under terminal drought is often reduced through pod and seed abortion due to a shortage of carbon assimilates (Palta and Ludwig, 1996, 2000). Varietal selection has ensured early flowering in narrow-leaved lupin (Gladstones, 1994), providing more time for pod filling before the severe effects of drought occurs on carbon assimilation (Palta *et al.* 2004). Terminal drought escape is characteristic of modern narrow-leaved lupin cultivars such as Belara, Quinilock and Mandelup, with early flowering and podding and higher rates of seed filling than other cultivars. However, terminal drought escape may limit yield improvement because grain yield in narrow-leaf lupin is carbon limited and there is little capacity to store and remobilise carbon to the grain (Palta and Ludwig 2000). Finishing the growing season early limits the time available for biomass accumulation, generating a tension between drought escape and maximising source potential.

The yield of narrow-leaved lupin is source rather than sink-limited (Palta and Ludwig, 2000). Increasing the number of pods (sink size) by application of cytokinin (Atkins and Pigeaire, 1993; Palta and Ludwig, 1996) does not necessarily increase the grain yield because many pods failed to fill their seeds (Palta and Ludwig, 1996). The failure to fill extra pods arises from a limited capacity to accumulate carbon in vegetative parts for remobilisation to the developing grain (Palta *et al.* 2000). Increasing the availability of carbon assimilates (source) by exposing plants with an increase number of pods (large sink) to elevated CO<sub>2</sub> during pod filling increased grain yield by 42% (Palta and Ludwig, 2000). Pod filling is almost entirely dependent on current assimilation (Pate *et al.* 1980) rather than on pre-anthesis stored carbon (Palta and Ludwig, 2000). Therefore, grain yield is often reduced through a reduction in the availability of carbon assimilates (Palta and Ludwig, 1996, 2000). A reduction in the availability of carbon after pod set causes pod and seed abortion mainly because narrow-leaved lupin does not store or uses enough reserves to support reproductive growth under shortages of carbon assimilates (J. Palta and C. Ludwig, 1997, unpublished; Berger *et al.* 2008). This is apparent in some environments and some seasons where lupin crops abort young pods ( $\leq 20$  mm) after 2-3

successive overcast days ( $\leq 430 \mu\text{m m}^{-2} \text{s}^{-1}$ ; PAR) (Berger *et al.* 2008). The limited use of reserves may be due to an anatomical constriction between stems and pods (C. Atkins, per. comm.).

### CONCLUSIONS

There is good evidence from glasshouse experiments (Palta and Ludwig, 1996; Palta and Plaut, 1999) and field trials (Dracup *et al.* 1998; J. Palta and C. Ludwig, 2000, unpublished) that there is a limit to the number of branch order produced even when lupin is grown under well watered and high fertility conditions. Several reasons may be responsible for the lack of impact of restricted branching on improving seed yield in lupins. Whilst the mainstem yield advantage of restricting branching growth remained unquantifiable, the need for genetic options to restrict branch growth as a means to improving yield in narrow-leaved lupin is questionable. Competition for resources between the developing branches and mainstem yield in lupin is not strong and continuous through the development of apical branches to have a substantial effect on mainstem yield. The inability of lupin to export resources outside branch orders appears to be a fixed trait that does not respond to manipulation of source-sink relationships. A possible advantage of improving early growth in narrow-leaved lupin may be the provision of a carbon store for subsequent pod development and grain filling during periods of water shortage after flowering. However, consideration should be taken to prevent a reduction in the fixing nitrogen capacity of narrow-leaved lupin while improving early growth.

Terminal drought escape is characteristic of modern narrow-leaved lupin cultivars, but this trait may limit yield improvement because grain yield is carbon limited and there is little capacity to store and remobilise carbon to the grain. Finishing the growing season early limits the time available for biomass accumulation, generating a tension between drought escape and maximising source potential.

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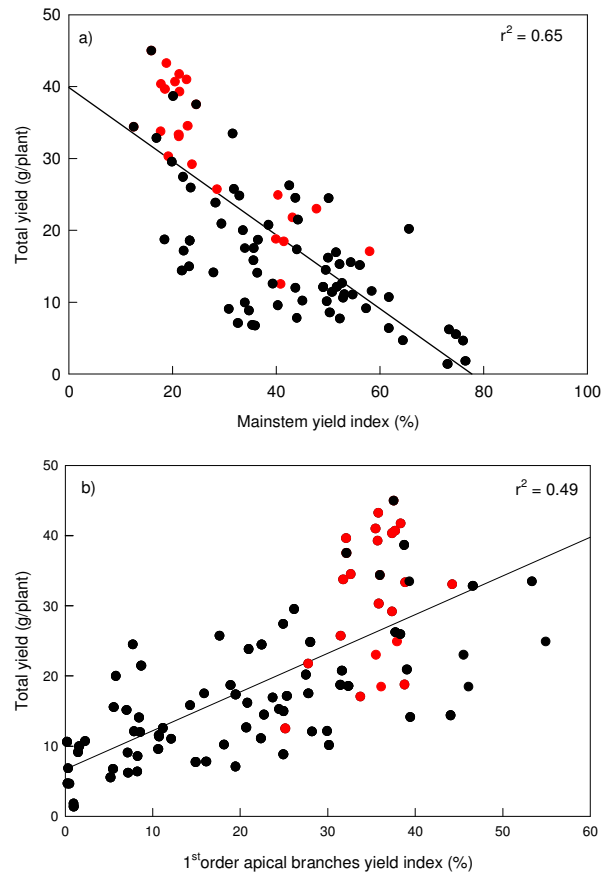
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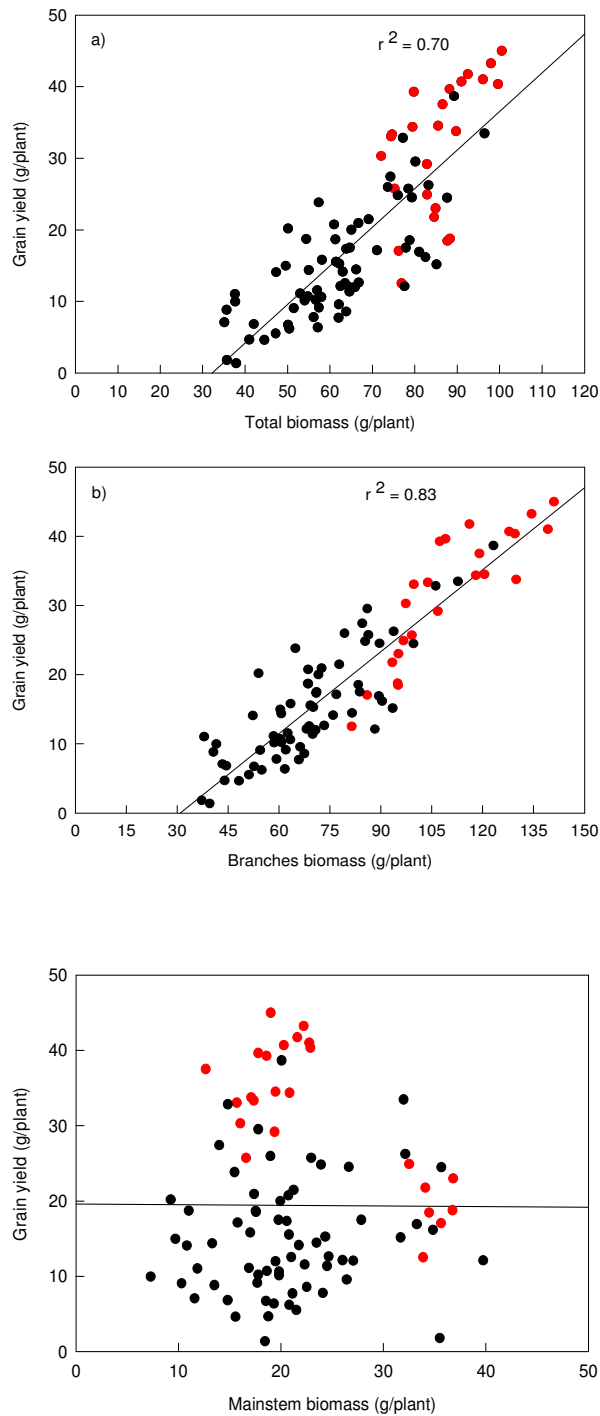
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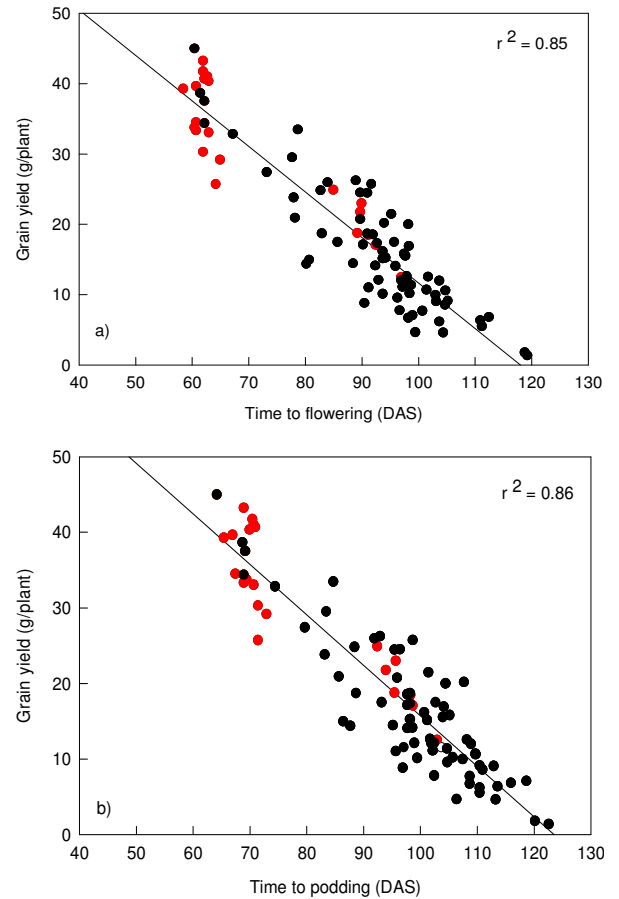
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**Fig. 1.** Relationship between total grain yield and a) grain yield on the mainstem and b) grain yield on the apical branches of the 'old breeders' core collection of narrow-leafed lupin'. Data in red represent commercial cultivars released from 1967-2004 and data in black represent wild genotypes.



**Fig. 2.** Relationship between grain yield and a) total biomass b) biomass on the branches and c) biomass on the mainstem for the ‘old breeders’ core collection of narrow-leaved lupin’. Data in red represent commercial cultivars of narrow-leaved lupin released from 1967-2004. Data in black represent wild genotypes.



**Fig. 3.** Relationship between grain yield and a) time to flowering and b) time to podding for the ‘old breeders’ core collection of narrow-leaved lupin’. Data in red represent commercial cultivars of narrow-leaved lupin released from 1967-2004. Data in black represent wild genotypes.