

# Lysenko's error about crop growth and development

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## Abstract

More than 60 years ago, the Ukrainian agronomist Trofim Lysenko asserted that wheat growth was independent of development. Field experiments reported by FAJ Harris and others at this conference disproved this assertion by showing that the *VRN1* genes, which control the developmental response to vernalisation, also affect growth. They showed that vegetative growth of wheat genotypes that possess the spring *Vrn-B1a* allele is 19% faster than genotypes with the winter *Vrn-B1v* allele. There was no such effect of the *VRN1* genes carried on the A or D genomes, or the *PPD1* genes. Previous research had cast doubt on the independence of growth and development, but this is the first conclusive evidence from field experiments that refute the supposed independence. The physiological mechanism linking assimilation and development is not clear, but while it is being investigated there is scope for using the result to manipulate vegetative growth. Rapid vegetative growth may be a valuable trait for late-sown crops in dry environments, for dual-purpose cultivars and for suppressing weeds, but a disadvantage where there is a risk of haying off.

## Keywords

Phenology, shoot growth, root growth.

## Introduction

The life cycle of annual crop species consists of a series of phases, each one of which has a distinct start and finish. Examples are the phases of germination, vegetative, reproductive and seed-filling., and more detailed phases also can be described, such as the development of each leaf, parts of the floral primordia, or microspores.

Development during each phase is mostly controlled by the interaction of genotype with photoperiod and temperature. Long photoperiod hastens development of some phases of long-day plants and retards development of short-day plants. High temperature generally hastens development of all phases and there is an additional effect of vernalisation, by which development of some phases of some species is hastened by low temperature. Phasic development is readily modified by selection and breeding, which can lead to improved adaptation to an environment, for example by enabling a crop to maximise capture of the resources of radiation and water, and in timing sensitive stages to avoid extreme temperatures.

In a series of papers written during the 1920s and 30s, the Ukrainian agronomist Trofim Lysenko asserted that phasic development and growth of annual crop plants were independent. The assertion followed experiments when vernalisation resulted in a change in phasic development with no apparent change in growth. Other assertions by Lysenko had been debunked earlier. One was that environment and management, not genetics, determined crop development. To avoid punishment, Soviet wheat breeders were forced to ignore evidence that development was inherited, so retarding genetic improvement for decades. Another assertion was the inheritance of acquired characteristics, the process now recognised as epigenetics. There is no evidence that epigenetics were involved in the crop development processes that Lysenko discussed, and geneticists rejected his assertions about inheritance of acquired characteristics (Graham 2016). The belief that growth and development were independent has persisted unchallenged for at least 60 years since Lysenko first asserted it.

Aitken (1974) reviewed phenological research in the two centuries before Lysenko's work, but did not report studies linking phasic development and growth, so Lysenko's assertion appears to be original. The most accessible review of Lysenko's work on this topic is by Whyte (1939) who suggested that development and growth were not totally independent, in that development was maintained only with a certain minimum of

growth. Even with this caveat the distinction between development and growth was a useful insight that has been picked up in textbooks on crop physiology (Hay and Porter 2006) and crop modelling (Thornley and France 2007).

The independence of phasic development and growth is coded in many, if not all, crop simulation models. For example DSSAT (Jones et al. 2003) and WOFOST (Diepen et al. 1989) simulate development during each phase, based on genotype-specific parameters combined with daily values of temperature and, when appropriate, photoperiod. Models simulate growth based on intercepted radiation, temperature, transpiration and nutrient status, but there is no explicit link between growth and development encoded in these models. The effect of development on yield is simulated in models through the duration of assimilation and allocation of assimilates to different organs, but not directly through assimilation.

The first suggestion that phasic development and growth may not be independent came from an experiment where an early-maturing wheat cultivar grew faster than a winter cultivar when both were growing in plots during autumn in south-eastern Australia (Davidson et al. 1990). A similar experiment with more cultivars showed similar results (Karimi and Siddique 1991) but since the later-maturing cultivars had generally been released before the earlier maturing cultivars it was not clear whether faster growth was due to earliness or unrelated genetic changes. Experiments under controlled conditions with wheat (Gómez-Macpherson et al. 1998) and barley (Soltész et al. 2013) showed that early maturing cultivars grew shoots faster than later maturing cultivars and Gómez-Macpherson et al. (1998) also showed that their roots grew more slowly. Plants in this experiment were grown in pots so it was possible that root growth was limited in the confined space and Gómez-Macpherson et al. (1998) suggested that experiments be conducted in the field to test these results. Such experiments were reported for field experiments with flooded rice, which has shallow roots that can be collected relatively easily (Angus et al. 2002). In this experiment shoot growth was similar for six cultivars of differing maturity, but root growth of early cultivars was less than half that of late cultivars. Collectively these studies raise a question about the independence of phasic development and growth but the diversity of the results suggests that the topic needs to be clarified. The objective of this research was to confirm and quantify the effect of development and growth and explain the mechanism.

## Methods

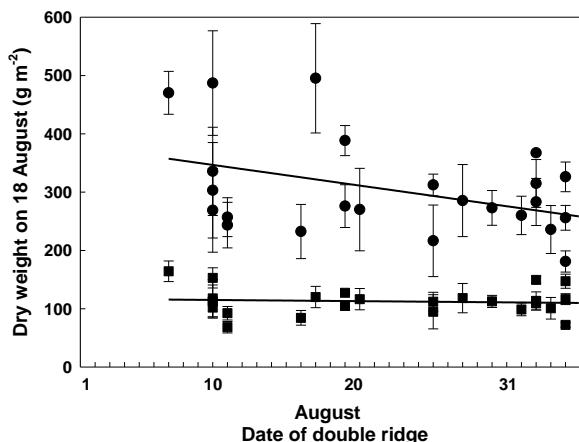
The experimental site was on a dryland farm at Marrar in southern NSW ( $34^{\circ} 45' 23''S$ ;  $147^{\circ} 20' 52''E$ ). The experiment compared 25 bread wheat (*Triticum aestivum* L.) cultivars that had been released in the previous five years and current breeders' lines; all are described here as cultivars. Seeding was on 1 June 2005 in plots with dimensions 20 m x 1.8 m and a row width of 0.18 m. There were four replications. Applications of fertiliser and agrochemicals followed local recommendations. The mean plant density was  $158 \text{ m}^{-2}$ . Observations of phasic development were microscopic identification of the double ridge stage on the main stem from samples collected every two or three days (Moncur 1981). The date of anthesis was when half the spikes in a  $1 \text{ m}^2$  quadrat extruded anthers. Growth was measured 79 days after sowing in quadrats 0.40 m long in the central six rows in each plot. Roots in the top 0.10 m of soil were collected from these plants using a trowel. Soil was washed off and the roots separated from the tops before drying and weighing.

## Results

The 25 cultivars included 12 with spring habit and 13 with winter habit. The spring types were generally earlier than the winter types but there was considerable variation in development within each group. The duration of the vegetative phase, from sowing to the double ridge stage, varied between 58 and 85 days and duration of the reproductive phase, from double ridge until anthesis, varied from 54 to 69 days. Cultivars with slow vegetative development tended to develop more rapidly in the reproductive phase and the correlation coefficient between the durations of the two phases was -0.57. The probable reason was that cultivars with a longer vegetative phase experienced higher temperatures and longer photoperiod than those with a shorter vegetative phase, and so developed more rapidly during the reproductive phase.

Growth was measured on all cultivars on the same day (18 August) when about half had reached the double ridge stage. Shoot growth decreased significantly for later developing cultivars (Figure 1). A linear equation fitted to the data indicates a decrease in shoot dry matter of about 1% for each day's delay in forming double ridges. There appeared to be more variation in growth among the earlier, faster growing and spring cultivars than among the later, slower growing and mostly winter types. There were three early spring cultivars (Ventura, Diamondbird and Sunzell) that produced more biomass than other cultivars. Ventura and

Diamondbird have the *a* allele of *VRN1* on the B genome but the allele for this gene on Sunzell is unknown (see below). If these outliers are removed from the data, biomass still decreased with later development, although the decrease is not statistically significant. Root growth was unrelated to maturity.



**Figure 1. Dry weight of above-ground (●) and below-ground (■) tissue of 25 wheat cultivars growing in the field, measured on 18 August when about half the cultivars had reached the double-ridge stage.**

## Discussion

The result of the experiment confirms previous observations that early cultivars grow more rapidly than late cultivars. The experiment is more conclusive than previous studies for several reasons. The difference between the growth habits of cultivars were less than the extreme differences between the early spring wheat and the obligate winter wheat compared by Davidson et al. (1990), so the differences in growth they found may have been related to radiation interception. All cultivars in our experiment were bred over a short period, so growth differences are not due to genetic improvements in growth, a possible explanation of the results of Karimi and Siddique (1991). There was no effect of development on below-ground growth as was shown by Gómez-Macpherson et al. (1998) in a controlled environment, possibly indicating more allocation of assimilates to shoots than roots in early maturing cultivars. The result suggests that, under field conditions, the effect of earliness on above-ground growth is not due to preferential allocation of assimilates to shoots following stem elongation. By rejecting hypotheses about radiation interception, breeding for rapid growth and allocation of assimilation between shoots and roots, we are left with the possibility that genetic control of development directly affects vegetative growth of wheat.

Field experiments at two locations, described by Harris et al. (2017), showed that rapid vegetative growth in a doubled haploid series of wheat lines was due to the presence of the *a* allele on *Vrn-B1*. There were no effects on growth-of *Vrn-A1* or *Vrn-D1*, nor effects of *Ppd-B1* or *Ppd-D1*. They concluded that a pleiotropic effect of *Vrn-B1a* was responsible for rapid growth.

The developmental effects of the three *VRN1* genes provide flexible sowing windows from late summer until mid-winter for cultivars that still flower close to the optimum time. Late maturity generally provides a yield advantage in long growing seasons and early maturity in short growing seasons, but until recently there had been no evidence of a direct association between a maturity gene and yield. Eagles et al. (2014) showed that *Vrn-B1a* conferred a yield advantage for a large number of cultivar comparisons in low-rainfall environments. None of their experiments were sown before 1 May, with the mean a relatively late 4 June. Harris et al. (2017) suggested that this yield advantage may be related to faster vegetative growth in low-rainfall environments.

Rapid seedling growth of wheat is likely to be valuable for late-sown crops in dry environments, in dual-purpose crops and for suppressing weeds, but may reduce yields when the water used to produce additional vegetative dry matter leads to water deficit during grain filling. This is similar to the process of haying-off when additional N leads to reduced yield (van Herwaarden et al. 1998) and when cultivation leads to faster seedling growth than direct drilling, but lower yields (Mason and Fischer 1986).

The results of these studies lead to questions. The physiological mechanism by which the *Vrn-B1a* stimulates wheat growth is not known. It is not clear why the *VRN1* gene on the B genome, but not on the A or D genomes, affects growth. It would be interesting to see the effect of homologous genes in barley or other winter crops with a single genome. We still lack an explanation of how early maturity reduces the vegetative root biomass of rice but not the above-ground vegetative biomass (Angus et al. 2002). Rice is known to carry the *VRN1* gene but vernalisation, as found in wheat, is unknown in rice.

## Conclusion

The finding by Harris et al. (2017), that the *a* allele on *Vrn-B1* stimulates vegetative growth of wheat helps to explain previous observations that early maturing cultivars grow faster than late cultivars. Knowledge of this effect will enable wheat breeders to produce cultivars with the vegetative growth appropriate for the environment in which they are grown. The result is also the first example that we know of where growth rate is related to a developmental process and disproves the long-held belief, originating from Lysenko, that growth and development are independent.

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