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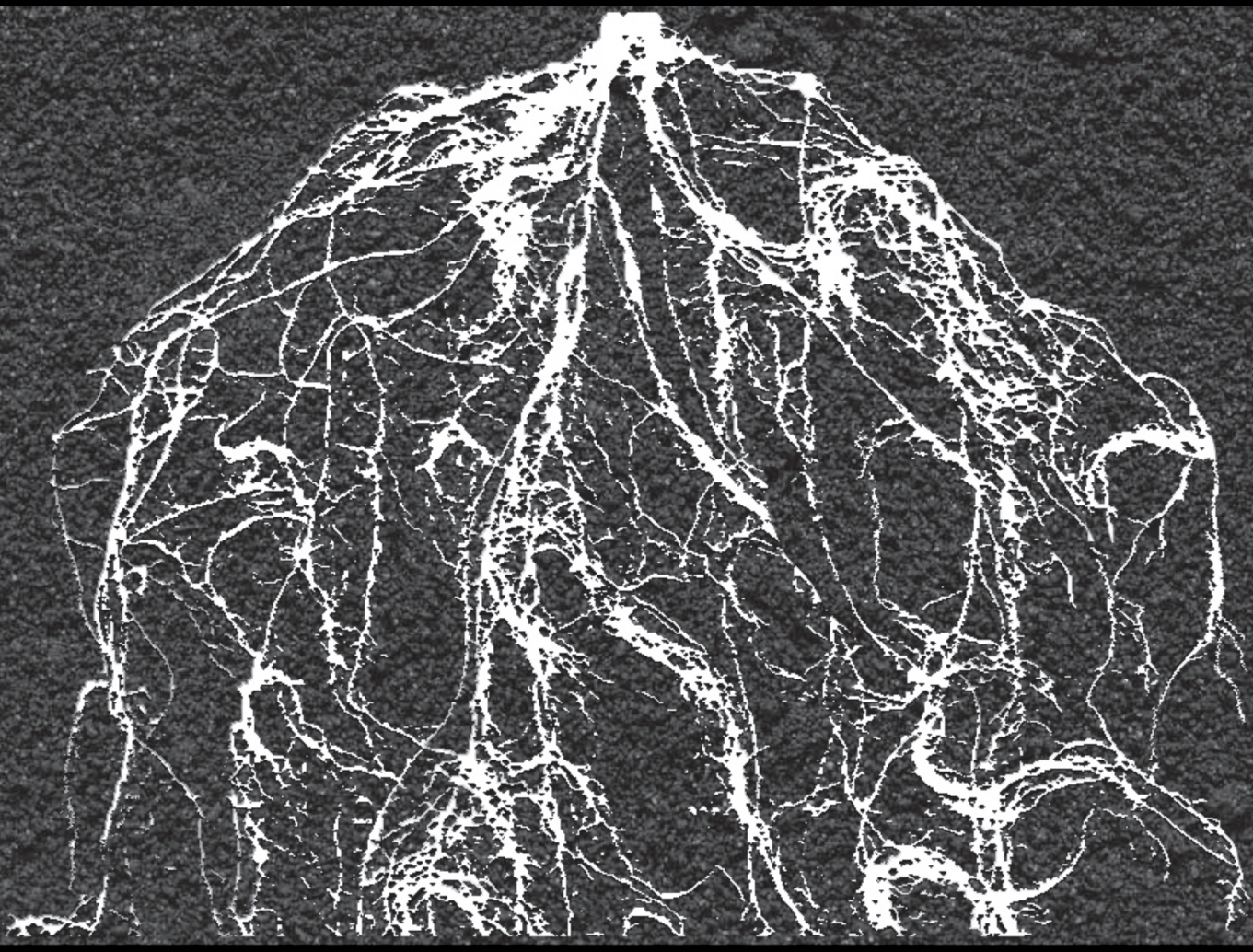
Biomass, Composition and Carbon Mineralization



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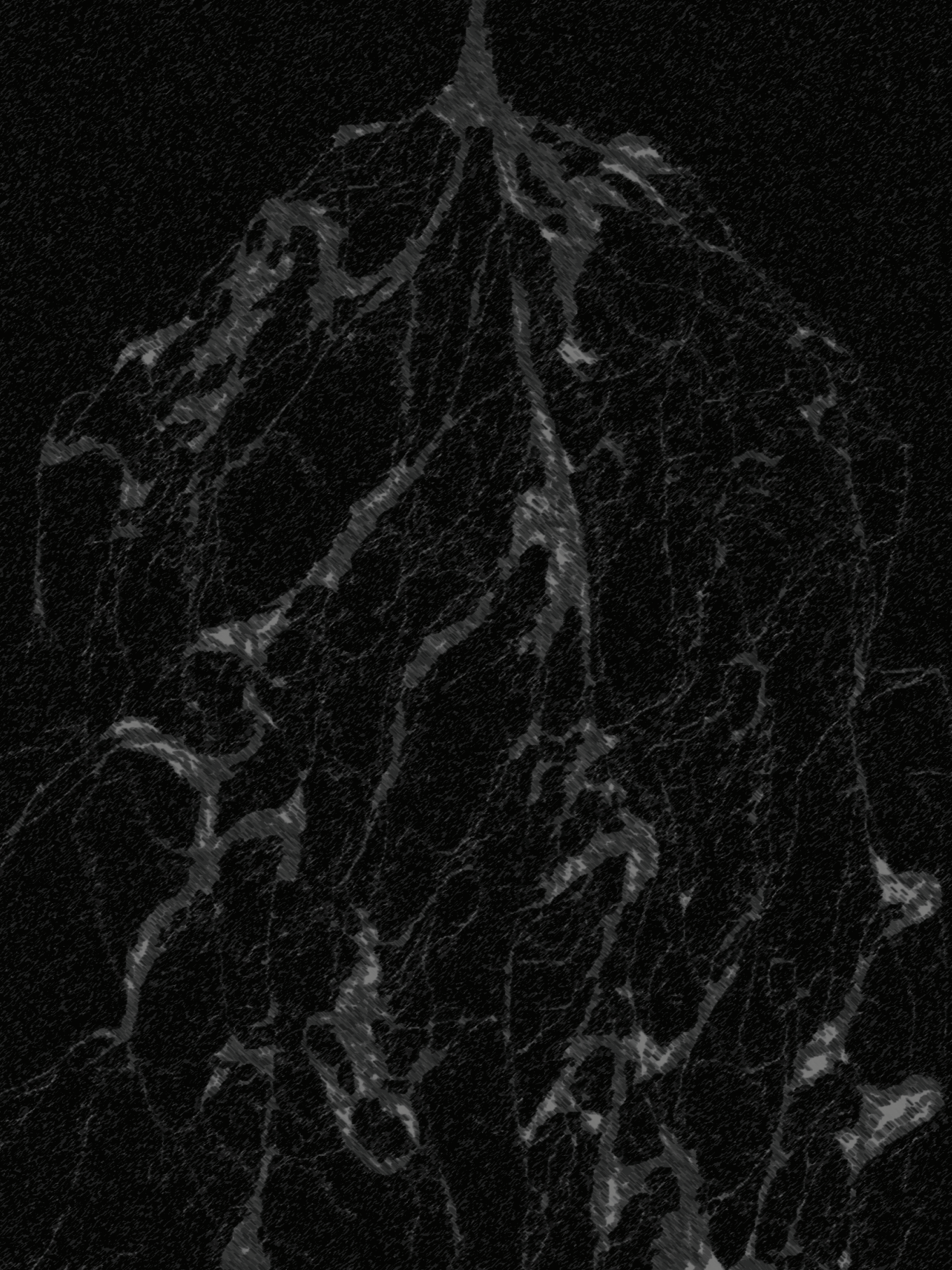

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CONTENTS

1. Introduction

The root system constitutes a major part of the plant body in terms of both function and bulk. Plant roots have received much less attention than above ground plant parts because they are hidden from view belowground and are intricately interspersed throughout the heterogeneous soil mass, which makes them extremely difficult to extract or to study *in situ*. Root systems perform several vital functions that are essential to growth and development of plants, the most important of which are:

1. Anchorage and support: The plant root system anchors the plant body to the soil and provides physical support against abiotic (wind, water) and biotic (animals and other plants) forces.

2. Absorption and conduction: The plant root system absorbs water, oxygen and nutrients from the soil in mineral solution, mainly through the root hairs. Roots are capable of absorbing inorganic nutrients in solution even against concentration gradient. After entry into the root, resources are conducted by radial transport to the central stele where they are released into xylem vessels and made available for long-distance (axial) transport.

3. Storage: Roots serve as storage organs for water and carbohydrates as in the modified, swollen roots of carrot, sweet potato, etc. Fibrous roots generally store less starch than taproots. Some roots are capable of storing large amounts of water.

4. Synthesis: Roots synthesize growth hormones such as cytokinins, gibberellins and abscicic acid (ABA) that regulate plant growth and development.

5. Sensing and signaling: Roots function as primary sensors of water stress. As the soil dries, changes in root metabolism such as a decrease in cytokinin production, increase in ABA production, and disturbance of nitrogen metabolism send biochemical signals to the shoots that induce physiological changes such as decrease in growth, stomatal conductance and rate of photosynthesis, regardless of the water status of the leaves.

In addition to the functions listed above, roots play a crucial role in the storage and turnover of carbon in the terrestrial ecosystem. About three quarters of terrestrial carbon is stored in the soil as soil organic matter. Roots are the primary vector for most carbon entering the soil carbon pool. It is very likely that most of the organic carbon in soil is derived from roots (Rasse *et al*., 2005).

In many arable systems, especially those in subtropical and tropical regions, since aboveground plant residues are grazed or removed, root-derived C is the primary C input to soil and contributor to soil organic carbon (SOC) (Heal *et al*., 1997). In agroecosystems where no aboveground crop residues or external sources of organic matter are added, roots are the only source of organic carbon in soil.

Since roots play such a significant role in soil organic matter formation and storage, strategies for removing carbon from the atmosphere and sequestering it in soil must essentially consider, or even centre around roots.

1.1 Carbon allocation belowground

Carbon taken up by the plant through photosynthesis is termed gross primary production (GPP). CO_2 uptake during photosynthesis is only temporary – respiration returns about half of the captured carbon to the atmosphere almost immediately. The remaining C, termed net primary production (NPP) is incorporated as structural material in shoots aboveground or allocated belowground. The fraction of C allocated belowground is significant. On a global scale, terrestrial plants allocate belowground some 60 Pg C out of the 120 Pg C fixed annually by terrestrial vegetation through photosynthesis, i.e., GPP (Schimel, 1995; Grace and Rayment, 2000). Studies indicate that roughly 40% of net fixed C (NPP) is allocated belowground (Jones *et al*., 2009). Net carbon allocated belowground is rhizodeposited or incorporated in structural material as root biomass.

1.1.1 Rhizodeposited C

Rhizodeposition consists of all material lost from plant roots, including water-soluble exudates, secretions of insoluble materials, lysates, dead fine roots, and gases, such as CO_2 and ethylene (Whipps and Lynch, 1985). The term rhizodeposition includes a wide range of processes by which C enters the soil including: (1) root cap and border cell loss, (2) death and lysis of root cells (cortex, root hairs etc), (3) flow of C to root-associated symbionts living in the soil (e.g. mycorrhizas), (4) gaseous losses, (5) leakage of solutes from living cells (root exudates), and (6) insoluble polymer secretion from living cells (mucilage) (Jones *et al*., 2009).

Rhizodeposited C may range between 30-90% of the carbon transferred belowground (Whipps, 1990). For cereal crops, rhizodeposited C can represent 50% or more of the total amount of C allocated below-ground (Keith *et al.*, 1986; Johansson, 1992; Swinnen *et al*., 1995). Buyanovsky and Wagner (1986) estimated that rhizodeposited C constitutes 40% of the total root-derived C (root biomass + rhizodeposits). Amos and Walters (2006) calculated that in field grown maize plants, net rhizodeposited C as a percentage of total net belowground root-derived C ranged from 37.2 to 48.0% with an average of 43.6%. Jones *et al.* (2009) presented an estimate of rhizodeposition at 11% of the net fixed C or 27% of C allocated to roots, corresponding to 400–600 kg C ha^{-1} for the vegetation period of grasses and cereals. Common assumptions relating to rhizodeposited C are that it is equivalent to 65 to 100% of the measurable root biomass (Bolinder *et al.*, 1999; Bolinder *et al*., 2007; Rasse *et al.*, 2005; Plénet *et al*., 1993). Some estimates suggest that rhizodeposition may be

as much as 2.5 to 6 times the amount of C incorporated into root biomass (Johnen and Sauerbeck, 1977; Molina *et al.*, 2001).

Rhizodeposited C may not contribute significantly to soil C stocks, as much of it is highly labile and therefore cycled through the soil food web during the growing season, with the respired portion of the C returned to the atmosphere as CO_2. Root exudates have especially low residence times in soil. Typically, low molecular weight root exudates are believed to have a residence time of a few hours in soil solution as they are rapidly consumed by the rhizosphere microbial community (Nguyen and Guckert 2001; Van Hees *et al*. 2005). Although higher molecular weight rhizodeposits have a slightly longer persistence time in soil, they are still mineralized within a few days (Mary *et al.,* 1992, 1993; Nguyen *et al.*, 2008). While most of the exuded materials are rapidly metabolized and respired by microorganisms (Kuzyakov and Cheng, 2001), some C is incorporated into the microbial biomass which has a slower turnover time (typically 30–90 days). However, carbon transferred to mycorrhizae may persist in the soil longer both through the production of significant amounts of the iron-containing glycoprotein glomalin that has a fairly long half life in soil (Nichols, *et al*., 2009) and may therefore contribute significantly to the recalcitrant soil C fraction (Treseder and Allen, 2000; Rillig *et al*., 2003), and through the effect of mycorrhizal hyphae on formation of stable soil aggregates (Wright and Upadhyaya, 1998) and physical protection of C in soil aggregates (Rillig *et al*., 2001).

1.1.2 Root biomass C

Root biomass C refers to the carbon present in live and dead coarse roots. In annual plants, the allocation of dry matter to roots changes during their life cycle and with growing conditions. Typically, relatively more assimilates are channeled to roots during early growth, but as development proceeds, the growing reproductive structures come to dominate and the amount of assimilate translocated to roots decreases. This change in allocation is particularly pronounced in cereal crops as the stem elongates and the ear develops. Several studies have shown that the proportion of carbon translocated to roots decreases with time as the ear grows and this is reflected in reduced root mass (Gregory, 2006).

Since the physical quantification of root biomass is difficult, C inputs from the root biomass at harvest are usually calculated using estimates of shoot to root (S:R) ratios or root:shoot (R:S) ratios at peak standing crop ((Bolinder *et al.* 1999). Johnson *et al.* (2006) estimated that the values of R:S ratio for wheat, maize and soybean, respectively, were 0.50, 0.33 and 0.37. Based on published information on studies conducted in Canada, Bolinder *et al*. (2007) estimated the shoot:root ratios for several annual crops. The mean S:R ratios for annual crops were typically around 5, and for forages they were typically 1-2, much lower than for annual crops. The S:R ratios for legumes were nearly twice those of grasses.

Estimates from S:R ratios as well as physical measurements of root biomass at harvest indicate that considerable amounts of C remain in root biomass at harvest. From a review of 45 studies, Amos and Walters (2006) estimated that in a range of climates and soil types, corn roots could contribute between 1.5 and 4.4 Mg C ha^{-1} $year^{-1}$. Prince *et al.* (2001) estimated that root biomass C represented an average of 15% of the aboveground biomass in maize. Root biomass C at harvest was estimated to be 45, 57 and 96 g m^{-2} for winter wheat, oats and barley respectively (Bolinder *et al*., 1997). Root biomass varies not only among species, but also among cultivars within a species (Xu and Juma, 1992). Gan *et al.* (2009) quantified the carbon in different plant parts of wheat, oilseeds and pulses and found that while straw represented the largest stock of C, belowground C was considerable.

The significant contribution of roots to stable soil organic carbon is not based on just the quantity of C input to soil, but also on the manner in which of root C resists decomposition. Biochemical recalcitrance of root material (biochemical quality), physico-chemical protection through interaction with minerals, physical protection from microbial decomposers through aggregation, and reduced decomposition due to location in lower soil depths are some possible mechanisms that explain the preferential preservation of root C in soil (Rasse *et al*., 2005).

Roots and aboveground plant parts (residues) recycled into the soil being the primary sources of organic carbon in soil, a comparison of their relative contribution to soil organic matter is inevitable. Several studies suggest that the relative contribution of plant roots to soil organic C stocks is larger than that of plant shoots. Long-term residue management studies suggest that above ground material has a limited impact on soil organic matter (SOM) levels as compared to root systems. Campbell *et al*. (1991) reported that 30 years of returning wheat straw to soils did not modify the carbon content of the soils. They suggested that root inputs may be more important in maintaining soil organic matter. Results from a 30-year maize experiment indicated that restitution of maize stalks vs. removal for silage had no impact on SOC contents (Reicosky *et al*., 2002). Although some studies indicated a significant contribution of crop shoot residues to SOC content (Barber, 1979; Hooker *et al*., 1982), this contribution was comparatively smaller than that of roots (Barber, 1979). A simulation study by Molina *et al*. (2001) suggested that maize root systems contributed 1.8 times more C to soils than the corresponding aboveground biomass. Johnson *et al*. (2006) proposed that 1.5–3 times more root C than shoot C is stabilized in the SOC pool, which suggests that root biomass makes a greater contribution to soil C sequestration than aboveground residues. Root biomass has considerable value for SOC storage because of the amount of C contained in these residues and the fact that they are less easily mineralized, thus more likely to become chemically or physically stabilized in deeper soil layers (Bolinder *et al*. 1999). In the corn–soybean agroecosystem of the Midwestern United States, Russell *et al*., (2009) found that although belowground net primary productivity (NPP)

comprised only 6–22% of total corn NPP, the quantity of belowground OC inputs was the best predictor of long-term soil C storage, leading them to conclude that selection of crops with high belowground NPP is a an effective management practice for increasing soil C sequestration. For roots to be the preponderant contributors to the soil organic carbon pool, the belowground C additions have to be large, and belowground C has to persist longer than aboveground C.

1.2 Factors contributing to the persistence of root derived C in soil

1.2.1 Biochemical recalcitrance (biochemical quality)

The importance of biochemical composition or 'quality' in determining the rate of decomposition and mineralization of nutrients from plant materials has long been recognized (Swift *et al.*, 1979). The chemical composition or quality of residues exerts a significant control over their decomposition (Vityakon and Dangthaisong, 2005). Plants generally contain the same classes of compounds, but the proportions of each, which depend upon the species and maturity, influence the degree and rate of decomposition (Kononova, 1966). Residues typically consist of three fractions which differ in decomposition rate; 1. easily decomposable sugars and amino acids, 2. slowly decomposable compounds comprising cellulose and hemicellulose, and 3. recalcitrant materials such as lignin (Van Veen *et al*., 1984). When plant residues enter soil, some components decay quickly, while others decay slowly. Simple compounds such as sugars, amino acids and low molecular weight phenolics are quickly decomposed, while polymeric molecules such as celluloses, hemicelluloses and lignin decompose slowly (Berg and McClaugherty, 2003).

The N concentration (and consequently C/N ratio) of residues is an important parameter determining their decomposability due to the influence of N availability on microbial metabolism (Parton *et al.*, 2007). Plant residues with a high C/N ratio are mineralized far more slowly than residues with low C/N ratio. However, over a wide range of plant materials, C/N ratio was found to be poorly correlated with litter decomposition (Wang *et al.*, 2004; Jalota *et al*., 2006).

The chemical recalcitrance of plant litter material is largely ascribed to lignin (Tegelaar *et al.*, 1989). Of all naturally produced organic chemicals, lignin is probably the most recalcitrant (Hammel, 1997). This is consistent with its biological functions, which are to give vascular plants the rigidity they need to stand upright, and to protect their structural polysaccharides (cellulose and hemicelluloses) from attack by other organisms. Lignin is known to inhibit microbial attack on holocellulose fraction physically, or by compounding the recalcitrant matrix by encrustation of cellulose (Adair *et al.*, 2008; Berg and McClaugherty, 2003; Sinsabaugh and Linkins, 1989). Lignin is a polyphenolic molecule that has stable ether and C-C bonds. Microbial decomposition of this structure requires strong oxidation agents and only a few soil microorganisms are able to completely mineralize lignin (Hammel, 1997).

Biodegradability of plant litter material is often characterized through biochemical fractionation, such as the method of Goering and Van Soest (1970). This method leads to the quantification of a series of organic molecule fractions displaying decreasing biodegradability. Within a given species, the lignin content of roots obtained by the method of Goering and Van Soest (1970) was reported to be more than double that of shoots (Rasse *et al*., 2005). Fernandez *et al.* (2003) investigated the chemical composition of roots and aboveground plant parts of ryegrass (*Lolium perenne*), *Pinus pinaster* and *Cocos nucifera* and observed that roots were more lignified than the aerial parts of the same species. Puget and Drinkwater (2001) found that root residues of hairy vetch had higher C/N and greater hemicellulose, lignin and cell wall contents while shoots had higher content of non-structural carbohydrates. From an analysis of root, stem and leaf samples of five plant species, Abiven *et al.* (2005) found that root residues were characterized by high values (>15%) of the lignin-like fractions and by low water soluble C and N content. Several other studies which compared initial root and leaf substrate quality reported higher lignin concentration in root litter compared to leaf litter (Bloomfield *et al*., 1993; Ostertag and Hobbie, 1999).

Due to the higher content of lignin in roots, root residues decompose more slowly than aboveground biomass and therefore have greater influence on long term soil organic matter dynamics. Silver and Miya (2001), using a global data set, reported that root chemistry appeared to be the primary controller of root decomposition while climate and environmental factors played secondary roles, unlike leaf litter, where climate and environment were the primary regulators. In a study of decomposition of above ground and below ground biomass of several plants, Jalota *et al.* (2006) found that as the lignin concentration increased, the proportion of plant materials decomposed decreased. For each 10% increase in lignin concentration, the proportion of the plant materials decomposed decreased by 25%. Also, for each 10% increase in plant lignin concentration, the litter and fine root turnover time in soil increased by 1.7 times. Abiven *et al.*, (2005) observed slower decomposition of roots, which had higher lignin content, compared to leaves. Fujii and Takeda (2010) analyzed the C fractions in leaves and roots of Japanese cypress (*Chamaecyparis obtuse*) and found that roots contained higher concentrations of the less decomposable fraction containing lignin, cutin, and suberin and polyphenols, while leaves contained higher concentrations of soluble carbohydrates. Litterbag studies using these residues revealed that mass loss of roots was considerably slower than that of leaves. Cusack *et al*. (2009) reported that roots of plant species with the slowest decomposition rate had the highest lignin concentration. Since root and shoot lignins possess similar molecular structure (Weichelt, 1981), it follows that the quantity of lignin itself (not the quality) is the main potential driver of differential degradation between roots and shoots.

The lignin to N ratio, which integrates the effects of the two most important characteristics governing plant residue decomposition, has been proposed as a better indicator of chemical recalcitrance than lignin content alone and has been used extensively to distinguish plant residues that are difficult to degrade, i.e. high lignin/N ratio, from those that are more easily biodegraded, i.e. low lignin/N ratio (Moore *et al.*, 1999; Parton *et al.*, 1987; Paustian *et al.*, 1992; Tietema and Wessel, 1992). In an evaluation of the decay rates of fine roots of four plantation tree species, Raich *et al.*, (2009) found a highly significant negative correlation between fine root decay and fine root lignin/N, which supports the use of lignin:N as a decay-controlling factor within terrestrial ecosystem models. Lignin/N ratio is currently used to modify detritus decay rates within soil organic matter models such as Century (Metherell *et al.*, 1993) and EPIC (Izaurralde *et al.*, 2006). Rasse *et al*. (2005) reported that across several plant species, the lignin/N ratio of root tissues was on average three times that of shoot tissues.

Numerous studies conducted under different conditions confirm the slower mineralization of root C. For instance, Lu *et al.* (2003) reported that the decomposition of intact root systems was extremely slow. This finding is supported by other field results obtained for root residue C (Balesdent and Balabane 1996; Bolinder *et al.*, 1999; Puget and Drinkwater 2001). These findings clearly indicate that the proportional contribution of root C to the sequestration of C in soil, through long-term buildup of soil organic matter, is greater than that of other plant parts.

1.2.2 Physico-chemical protection through interaction with minerals

Although close interaction of root tissues with the soil minerals has been suggested to be the main soil-specific protection pathway for root C (Balesdent and Balabane, 1996; Oades, 1995), Farrar *et al.* (2003) showed that roots interact with mineral soil in a manifold manner. Plant roots produce many organic acids; lactate, acetate, oxalate, malate and citrate being the primary anion components. These molecules are generally considered as labile compounds that are mineralized within a few hours following release by roots (Chabbi *et al.*, 2001; Grayston *et al.*, 1996). It is often ignored that due to their negative charge, these substances may become rapidly and readily sorbed to the mineral phase through cation bonding (Jones, 1998). For citrate, it was demonstrated that interaction with clay minerals and Fe oxides inhibits degradation (Jones and Edwards, 1998). Di- and tri-carboxylic acids were found to be readily adsorbed to the solid phase, particularly in subsoil horizons containing abundant Fe and Al oxyhydroxides (Van Hees *et al.*, 2003). Fe oxides are effective sorbents of soluble organic matter (Kaiser and Zech, 1998). These soil minerals possess most of the available surface area in mineral soils (Kaiser and Guggenberger, 2000). Available surface area seems to govern the stabilization of organic compounds (Saggar *et al.*, 1996; Torn *et al.*, 1997). In forest

podzols of coastal British Columbia, Canada, Stephanie and Lavkulich (2011) found that although clay content was low (<5%), the clay fraction accounted for one third of the SOC, suggesting that organo-mineral interactions, especially Al and Fe complexes, were an important factor for SOC storage. Sorption of root-derived organic acids to the mineral phase may be more effective in subsoils with low contents of organic matter because mineral surfaces are not yet saturated with organic matter. Thus, root-released compounds appear to have a selective advantage for stabilization through binding to the mineral phase, more so in deeper soil horizons.

1.2.3 Physical protection from decomposition through aggregation

The organic material released by roots plays a major role in the interaction between root, microorganisms and the mineral soil. Roots improve aggregation directly by enmeshing soil particles and indirectly by stimulating microbial biomass which in turn synthesizes polymers that act as binding agents (Jastrow *et al.*, 1998; Tisdall and Oades, 1979). The existence of stable macroaggregates in soil is very important for the stabilization of SOM, because the formation of stable microaggregates is fostered within macroaggregates. Formation of stable aggregates may be attributed to rhizosphere polysaccharides and the network of root associated fungal hyphae. Stable aggregates protect SOC from biodegradation by reducing the access of decomposers to these encapsulated substrates (Elliott, 1986; Oades, 1988). As microbes break down the organic materials in the soil, they form polysaccharide gels and exopolymers that help glue and stabilize soil aggregates. Stable aggregates are more likely to protect and store carbon for longer periods than fragile aggregates. Root tip mucilage influences soil physical characteristics such as aggregation, and creates a continuous sphere of contact between the root and soil. This mucilage is high molecular weight polysaccharide and has been shown to increase stable aggregates in soil up to 40% by acting as a glue to hold aggregates together (Aiken and Smucker, 1996; Young, 1998).

Watteau *et al.* (2006) observed that silt and clay-sized aggregates were drawn, along with water, towards the central cylinders of decomposing coarse roots for distances of up to 15 µm, a process they postulated, could initiate the formation of soil aggregates. They observed that many fine roots were colonized by bacteria, whose decomposition upon death resulted in granulofibrillar residues which formed associations with silt and clay minerals. They inferred that roots are not just simple structures holding preformed aggregates together but roots act as centres for the formation of aggregates and nucleation of SOC in such aggregates. The inclusion of organic matter within aggregates reduces its decomposition rate (Krull *et al.*, 2003; Oades, 1984; Six *et al.*, 2002a). In a $^{13}CO_2$ labeling study of root and shoot decomposition of hairy vetch, Puget and Drinkwater (2001) found a greater proportion of root-derived C as occluded POM and associated with the clay and silt fraction. The

persistence of this C was attributed to the nature of root material and the root-soil association. Roots have an intimate association with the soil and are more likely to become coated by clay films, which help protect root derived POM from further decomposition (Puget and Drinkwater, 2001). Six *et al.* (2002b) found that the absolute contribution of roots to the total particulate organic matter occluded within soil aggregates ranged between 1.2 and 6.1 times that of shoots.

1.2.4 Reduced decomposition in deeper soil layers

The recognition that substantial (possibly 10 or even 20 fold) decreases in atmospheric CO_2 over geological time, especially during the Devonian (416.0–359.2 million years ago) may have largely been effected via the production of deep-rooted trees (Kell, 2011) can be taken as proof of the strong effect that deep roots can have on the terrestrial carbon cycle. Similarities in the depth distribution of roots and SOC (Olupot *et al*., 2010), further confirm this. Vegetation types differ in their vertical root distribution leaving distinct imprints on the depth distribution of SOC (Lorenz and Lal, 2005).

Depending on the plant species, roots can transfer C to considerable depth in the soil profile. Organic carbon input into subsoil horizons occurs as root litter and root exudates, dissolved organic carbon (DOC) and/or bioturbation. In addition, there may be translocation of particulate organic matter and transport of clay-bound organic matter in certain soil types (Rumpel and Kogel-Knabner, 2011). There is considerable variation between both plant types and individual plant strains (cultivars) as to the maximum depth to which they produce roots, but 2 m for angiosperms (and much deeper for trees) is not at all uncommon (Kell, 2011). Most presently cultivated agricultural crops have root depths that do not extend much beyond 1 m, but a few crop plants can produce roots exceeding 2 m (Kutschera *et al.*, 2009). Rooting depths of annual crops range from 0.5 to 3.0 m (Borg and Grimes, 1986; Dardanelli *et al.*, 1997; Merrill *et al.*, 2002; Stone *et al.*, 2002). Roots of pigeonpea are deep and wide spreading in the soil, with well-developed lateral roots and may extend down to more than 2 m (Singh and Oswalt, 1992). Using data from experimental root measurements and modeling, Metselaar *et al.* (2009) estimated the rooting depths of globally important agricultural crops and found that averaged across all crops, the depth within which 95% of roots were present (D95) was 90 cm, while depth within which 50% of roots were present (D50) was 19 cm. There was considerable variation in rooting depth of different crops, and D95 ranged from 32 cm for sunflower to 162 cm in cotton. Deeper root systems have the potential to sequester SOC deeper in the soil profile, where the time of SOC turnover to atmospheric CO_2 can be slower.

Environmental conditions prevailing in the deep soil profile are detrimental to the decomposition of plant tissues. While there is no clear evidence in literature for oxygen limitations for SOM decay in subsoils, it was postulated that unfavourable conditions with regards to temperature, nutrients and

energy could limit the degradation of OM stored in subsoil horizons (Rumpel and Kogel-Knabner, 2011). Gill and Burke (2002) observed that the decomposition rate of *Bouteloua gracilis* roots at 1 m depth was slower than at 0.1 m depth, with estimated residence times of 36 and 19 years, respectively. In subsoil horizons, the amount and activity of soil microorganisms was found to be minimal, with fungi being absent from the deep soil (Taylor *et al.*, 2002, Fang and Moncrieff, 2005). Soil organic carbon stored deeper than 2 m can have very long residence times (Follet *et al.*, 2003).

Soil deposition of C through allocation to deep roots and their slow turnover constitutes a means for substantial long-term C sequestration. Subsoil horizons with low C concentrations may not yet be saturated in organic C. The possibility of root derived anions being sorbed on unsaturated mineral surfaces, which are more abundant at greater soil depths has already been discussed. It has been suggested that subsoil horizons may have the potential to sequester organic carbon for centuries through higher C input into subsoil by roots and DOC (Lorenz and Lal, 2005). Introducing relatively deep rooted vegetation into shallow rooted systems may result in carbon storage deep in the soil, acting as a potential C sink for centuries. Potential examples include shrub encroachment of grasslands or afforestation of areas dedicated to annual crops or pasture.

1.3 Root derived C vs shoot derived C in SOM

The preferential preservation of root C compared with shoot C has been emphasized by several researchers (Wilhelm *et al.*, 2004; Rasse *et al.*, 2005; Johnson *et al.*, 2006). Johnson *et al.* (2006) proposed that 1.5–3 times more root C than shoot C is stabilized in the SOC pool. Balesdent and Balabane (1996) reported that although the estimated aboveground corn residue (345 g C m^{-2} yr^{-1}) was higher than the belowground (152 g C m^{-2} yr^{-1}), the latter contributed more to the SOM pool (57 g C m^{-2} yr^{-1}) than the aboveground (36 g C m^{-2} yr^{-1}) corn residue. From an analysis of long term experiments on maize, Bolinder *et al.* (1999) estimated that 17% of root derived C was retained as SOM as against 12.2% for shoot derived C. Puget and Drinkwater (2001) labeled hairy vetch (*Vicia villosa* Roth subsp. *villosa*) *in situ* with $^{13}CO_2$ and followed both root and shoot derived C in total soil organic C (SOC) and labile C pools for the first growing season following hairy vetch incorporation and found that at the end of the growing season, nearly one-half of the root derived C was still present in the soil, whereas only 13% of shoot derived C remained.

From an analysis of soils under long term experimentation, Katterer *et al.* (2011) found that the humification coefficient, the fraction of plant material converted into more stabilized soil organic material, was 2.3 times higher for root derived C (including rhizodeposits, estimated at 35%) than that for aboveground plant residues, indicating that that roots contribute relatively more to refractory

soil organic matter than aboveground residues. Based on the analysis of several *in situ* root growth experiments, Rasse *et al.* (2005) reported that the relative root contribution to SOC was, on an average, 2.4 times that of shoot, with a minimum of 1.5 and a maximum of 3.7, confirming the dominant role of root C in soils.

Since root contribution to stable SOC is significant, strategies for increasing soil organic matter and transferring atmospheric C to soil must essentially consider the crucial role roots play. In agroecosystems, some idea of how much carbon can be sequestered in soil under different cropping systems can be obtained by quantifying root biomass of crops, determining the biochemical composition of the roots and studying their decomposition patterns. A research project entitled 'Understanding the role of plant roots in soil C sequestration' was undertaken at CRIDA, Hyderabad under the National Initiative on Climate Resilient Agriculture (NICRA) during the period January 2012 to May 2015 with the following objectives

1. Quantification of plant root biomass in important crops and crop varieties
2. Biochemical characterization of roots and shoots of major crops
3. Studies on carbon mineralization behavior of roots and shoots

2. Methodology

2.1 Determination of shoot and root biomass

Two varieties each of eight rainfed crops were grown at Hayathnagar Research Farm of the Central Research Institute for Dryland Agriculture (CRIDA) over a 3 year period (*kharif* seasons of 2012, 2013 and 2014) in plastic containers under open field conditions. The details of the crops and varieties are given in Table 1.

In sorghum, sunflower, maize, castor and pigeonpea crops in which hybrids were available, the selected varieties consisted of one hybrid and one non-hybrid variety. In greengram, cowpea and horsegram which have no hybrids, a new variety and an old variety were selected in greengram and cowpea, while the two varieties of horsegram were mutant selections released by CRIDA.

Plants were grown in 64 cm tall 100 L plastic containers filled up to 55-60 cm depth depending on the crop (~100-120 kg soil). To allow free drainage, 7 holes were drilled in the bottom of the container. A single plant was grown in each container. Plants were grown in conditions identical to rainfed and were irrigated only when they exhibited symptoms of water stress.

Table 1. Details of crops and varieties

Year	Crop	Variety	Description
2012	Sorghum *Sorghum bicolor* (L.) Moench	**V1** SPV 462	Variety
		V2 CSH 16	Hybrid
	Greengram *Vigna radiata* (L.) R. Wilczek	**V1** ML 267	Old variety
		V2 LGG 460	New variety
	Sunflower *Helianthus annuus* L.	**V1** Morden	Variety
		V2 KBSH 44	Hybrid
2013	Maize *Zea mays* subsp. *mays* L.	**V1** Varun	Variety
		V2 DHM 117	Hybrid
	Pigeonpea *Cajanus cajan* (L.) Millsp.	**V1** PRG 158	Variety
		V2 ICPH 2740	Hybrid
	Castor *Ricinus communis* L.	**V1** Kranthi	Variety
		V2 PCH 111	Hybrid
2014	Cowpea *Vigna unguiculata* (L.) Walp.	**V1** C 152	Old variety
		V2 APFC 10-1	New variety
	Horsegram *Macrotyloma uniflorum* (Lam.) Verdc.	**V1** CRHG 4	Mutant derivative of Hyderabad local
		V2 CRIDA 18R	Mutant derivative of K 42

The biomass of plants grown in large containers is not representative of field grown plants, but this approach was chosen based on experience with field grown plants. Sorghum and greengram were grown in the field in *kharif*, 2011 and roots were extracted by washing exposed monoliths.

The procedure of exposing large monoliths by excavation and extraction of roots by washing was not only laborious and time consuming, but also prone to error of serious underestimation of root biomass. For deep rooted crops like castor and pigeonpea, it is extremely difficult to extract the roots. Hence the procedure of growing the plants in large containers was adopted for two major reasons, 1. It allows a more complete recovery of roots and thus, a more realistic estimation of shoot:root ratio, and 2. It allows better recovery roots of all sizes - coarse, fine, etc, which is generally not possible in field grown plants where most of the fine roots are lost during extraction. Using the shoot:root ratios obtained from container grown plants, the root biomass of plants under field condition can be estimated. Further, the biochemical composition of container grown plants is likely to be more

Overview of experiments conducted over the three years – 2012, 2013 and 2014

realistic since most of the roots are recovered, unlike field grown plants where the sample is likely to contain proportionately more coarse root material. To test the hypothesis that shoot:root ratios will be identical for container and field grown plants, cowpea and horsegram were grown in the field in 2014, concurrently with container grown plants, and the roots were extracted by washing exposed monoliths.

Root systems of the plants were extracted at two stages, maximum biomass stage (late flowering) and crop maturity, by washing away the soil in the containers with a jet of water on a wire mesh with 2 mm openings). Fragments of roots separated from the root system during washing and collected on the wire mesh were recovered and added to the root portion. Root and shoot system at late flowering stage, and roots, stems+leaves and reproductive parts at maturity were separated, dried and weights were recorded, and shoot:root ratios were determined.

For comparing plants grown in the containers and plants grown in the field, cowpea and horsegram were also grown in the open field in 2014. At late flowering stage, roots of the field grown plants were extracted by washing exposed monoliths.

The photographs of the whole plants of the 8 crop species included in this study are shown in the following pages. It is to be noted that the length of the root systems as evident from the photographs is not necessarily an indication of the rooting depth. The photos are intended to give a general picture of the root systems. The red markings on the scale are feet.

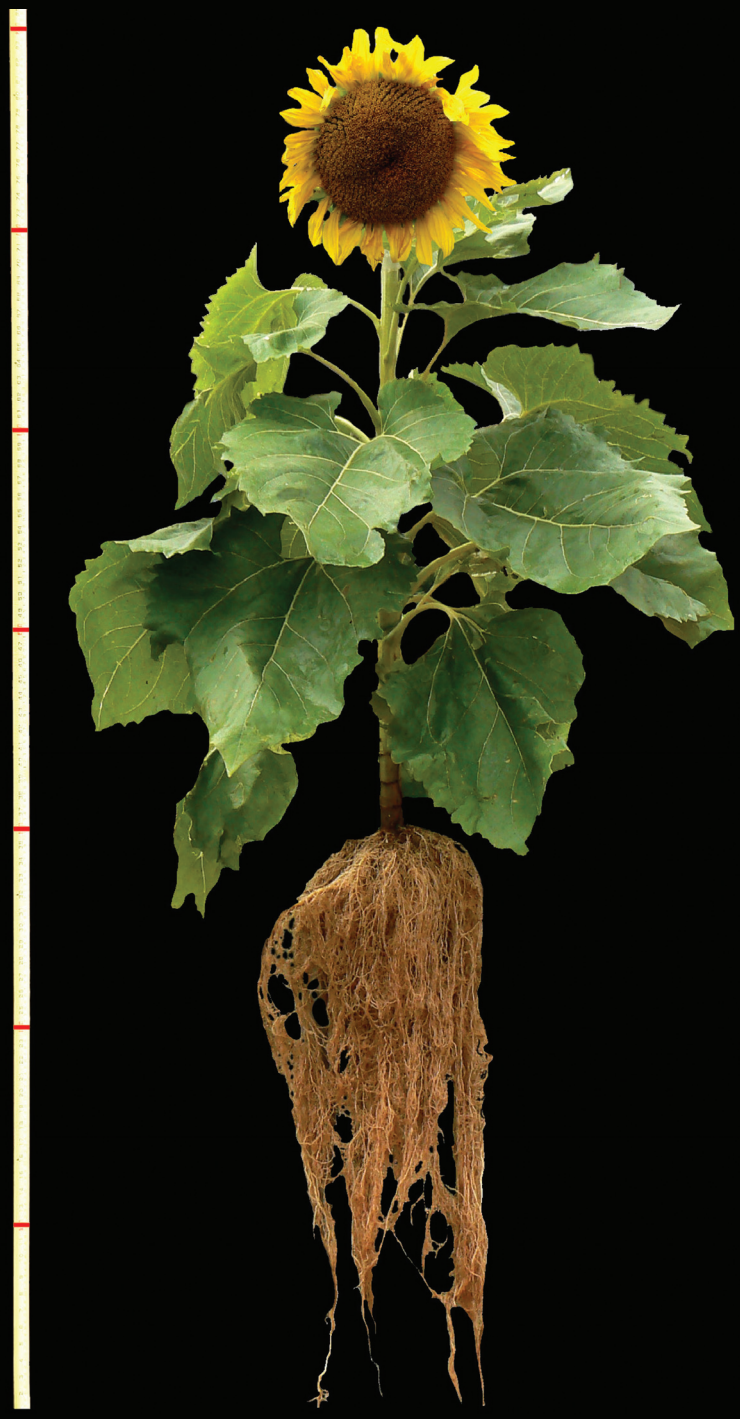
Extraction of sunflower roots at late flowering stage

Exposed soil monolith with cowpea plants at late flowering stage

Extraction of roots of field grown cowpea by washing the exposed monolith

Sorghum, SPV 462

Greengram, ML 267



Sunflower, KBSH 44

Maize, DHM 117

Pigeonpea, ICPH 2740

Castor, PCH 111

Container-grown Cowpea, APFC 10-1

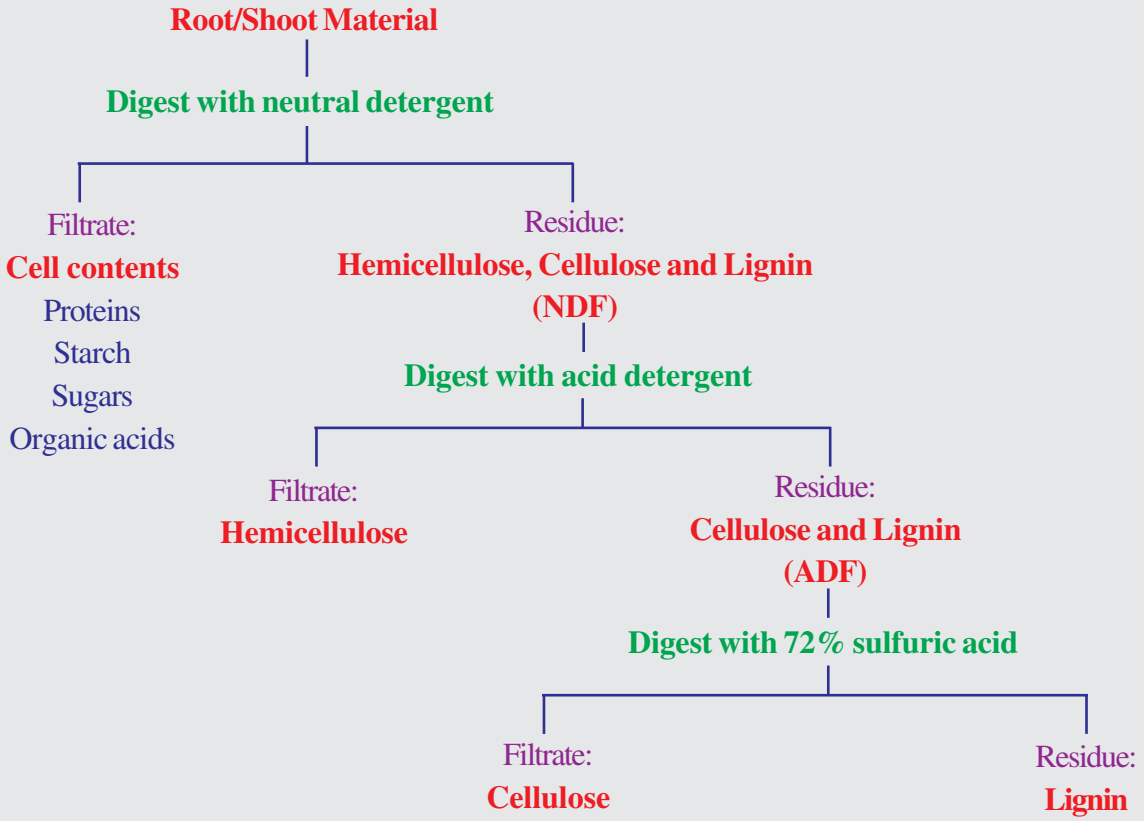
Field-grown Cowpea, APFC 10-1

Container-grown Horsegram, CRIDA 18R

Field-grown Horsegram, CRIDA 18R

2.2 Determination of biochemical composition

For determining biochemical composition, plant parts were ground to pass 1 mm sieve and tissue fractions were determined using the detergent fibre fractionation procedure (Goering and Van Soest, 1970) as described by Dutta (1999). The concept behind detergent fibre analysis is that plant cells can be divided into cell walls (comprising hemicellulose, cellulose and lignin) and cell contents (comprising starch and sugars). The components can be separated by using two detergents: a neutral detergent and an acid detergent. A schematic representation of the residue fractionation procedure is given below.



Plant tissue fractionation scheme

Carbon and nitrogen in the samples were determined by solid sample dry combustion – gas chromatography method. C/N ratio and Lignin/N ratio as indicators of decomposability were calculated.

2.3 Carbon mineralization study

For studying decomposition behavior, ground 1 mm sieved root and shoot material (late flowering stage) were mixed into soil @ 5 g/500 g and incubated at water content equivalent to field capacity in sealed plastic jars along with alkali solution for trapping CO_2 released upon decomposition. Jars were opened at 4, 10, 18, 28, 38, 48, 58, 68, 78, 88, 98, 108 and 120 days after start of incubation and trapped CO_2 was determined by precipitating carbonate with barium and titrating the remaining alkali with acid (Singh *et al*., 1999). Per cent of added C mineralized at the end of 120 days of incubation was calculated as

$$\frac{\text{cumulative C mineralized in treated} - \text{cumulative C mineralized in control}}{\text{C added}} \times 100$$

Simple correlations were worked out between %C mineralized and relevant residue quality parameters.

3. Results and Discussion

3.1 Biomass

Root and shoot biomass at were determined by destructive sampling at late flowering and maturity stages. The late flowering stage was selected for sampling because annual crops generally attain maximum root biomass at this stage (Gregory, 2006). However, the stage when plants attain maximum biomass, or for that matter, late flowering stage, are not clearly evident in indeterminate plants that accumulate vegetative as well as reproductive biomass simultaneously and extend the production of vegetative biomass and reproductive structures when resources (water, nutrients, etc) are abundant. The determination of biomass of shoots as well as roots at maturity presents a different set of problems. With regard to shoots, dicots, especially plants like pigeonpea, shed their leaves as they age or when they experience abiotic stresses, mainly water deficit stress. So the standing biomass does not truly represent the maximum biomass attained by the plants (unless leaves and other parts separated from the plant are systematically collected). In case of roots, as the plants approach maturity, roots begin to lose their integrity and root losses during extraction are considerable. Further, as roots lose their vitality towards maturity, they are attacked by soil microflora and micro and macro fauna to varying degrees. Such problems are minimal at late flowering stage. Accordingly, more focus is placed on measurements made at late flowering stage in this publication.

The biomass of roots for all the crops and varieties was much lower than the respective shoot biomass (Table 2, Figure 1) at both the stages of sampling. Roots accounted for 12.07% (Horsegram, CRHG 4) to 35.26% (Maize, DHM 117) of total biomass at late flowering stage. In reality, root

biomass and root contribution to total plant biomass are likely to be higher for two reasons, 1. The roots of most of the plants grew out of the drainage holes at the bottom of the containers and extended into the soil below. While these are mostly fine roots that do not contribute greatly to root biomass, in plants like pigeonpea, which are inherently deep rooted, they may account for a significant fraction of the total root biomass. 2. The measurement of root biomass based on root extraction from soil by washing leads to underestimation of the root biomass as considerable root material is lost during washing and subsequent handling. While the extent of loss depends on several factors such as the nature of the roots themselves, the properties of the soil and the washing process, the losses can be as high as 20% and in some cases as high as 40% (Judd *et al*., 2015). Van Noordwijk and Floris (1979) indicated that measured root weights are one third lower than actual weights. The extent of loss can be minimized by washing the soil gently without using excessive force, and employing sieves or mesh screens to retain and recover root fragments separated from the root system. The process of extracting roots by washing is a painstaking and laborious task, and patience and time determine how much of the root biomass is captured. Other methods of estimation of root biomass, especially root biomass of fully grown plants, have their own limitations, and currently there is no method that can give a 100% quantitative measurement of root biomass in contrast to shoot biomass, whose quantitative measurement presents no difficulty whatsoever.

While the loss of root material leads to underestimation of root biomass, the adherence of mineral soil particles to the roots leads to an overestimation of the root biomass. Vanguelova (2002) indicated that mineral soil adherent to the roots can overestimate root biomass by up to 19%. Jackson and Chittenden (1981) reported that even for visually clean fine roots of *Pinus radiata* obtained after repeated washing, the mineral component (after ashing in a furnace) was as high as 30%. Soil particles, especially finer particles adhere to the roots as a coating on the root surface and also by becoming lodged in the enmeshed root mass. This tendency is pronouncedly greater in case of the fibrous root systems of monocots. It may be possible to remove most of the soil particles by washing more vigourously, but that would lead to loss of root material. Therefore the researcher has to strike a balance and optimize the washing intensity in such a way that root loss and at the same time soil adhering to roots, are minimized.

At maturity stage, root biomass as percentage of total plant biomass, including reproductive parts, was less than at late flowering stage in all the crops and varieties (Table 2) and ranged from 6.87% (Horsegram, CRIDA 18 R) to 23.23% (Sorghum, CSH 16). Averaged across crops and varieties, roots accounted for 18.31% of the total plant biomass at late flowering, and only 12.36% at maturity. The change in biomass from late flowering to maturity differed with crops and even varieties, increasing in some and decreasing in others (Figure 2). The most conspicuous changes were a steep decline in

Table 2. Root and shoot biomass (g/plant) of crops and varieties at late flowering and maturity

Crop	Variety	Late flowering				Maturity					% change in root biomass @#
		Root	Shoot	Total	Root (% of total)	Root	Shoot	*Rep. part	Total	Root (% of total)	
A	B	C	D	E	F	G	H	I	J	K	L
Sorghum	SPV 462	152.75	488.49	641.24	23.82	153.76	598.25	96.37	848.38	18.12	-0.66
	CSH 16	105.86	311.96	417.82	25.34	161.32	382.55	150.63	694.50	23.23	-52.39
Greengram	ML 267	13.47	81.63	95.10	14.16	6.52	62.63	9.69	78.84	8.27	51.60
	LGG460	10.85	69.22	80.07	13.55	8.01	73.85	20.11	101.97	7.86	26.18
Sunflower	Morden	32.45	157.27	189.72	17.10	27.45	121.93	136.70	286.08	9.60	15.41
	KBSH 44	45.99	259.26	305.25	15.07	46.63	189.42	230.25	466.30	10.00	-1.39
Maize	Varun	41.33	102.96	144.29	28.64	48.36	130.34	168.77	347.47	13.92	-17.01
	DHM 117	100.66	184.84	285.50	35.26	106.70	187.30	262.40	556.40	19.18	-6.00
Castor	Kranthi	35.48	206.27	241.75	14.68	88.63	266.43	377.07	732.13	12.11	-149.80
	PCH 111	49.10	256.55	305.65	16.06	110.47	295.03	429.10	834.60	13.24	-124.99
Pigeonpea	PRG 158	160.83	819.87	980.70	16.40	184.50	723.27	535.83	1443.60	12.78	-14.72
	ICPH 2740	155.63	724.96	880.59	17.67	163.67	681.97	520.20	1365.84	11.98	-5.17
Cowpea	C 152	16.52	95.39	111.91	14.76	16.24	68.15	54.50	138.89	11.69	1.69
	APFC 10-1	18.96	99.62	118.58	15.99	17.51	77.97	58.53	154.01	11.37	7.65
Horsegram	CRHG4	4.85	35.34	40.19	12.07	5.81	32.78	38.27	76.86	7.56	-19.79
	CRIDA 18R	5.63	39.85	45.48	12.38	6.54	41.90	46.77	95.21	6.87	-16.16
Mean					**18.31**					**12.36**	

* Reproductive part - Earhead in sorghum; pods in greengram; capitulum in sunflower; cob in maize; capsules in castor; pods in pigeonpea, cowpea and horsegram

@ % change in root biomass from flowering to maturity, calculated as L = ((C-G)/C)*100)

Negative values indicate increase in biomass from late flowering to maturity, positive values indicate decrease

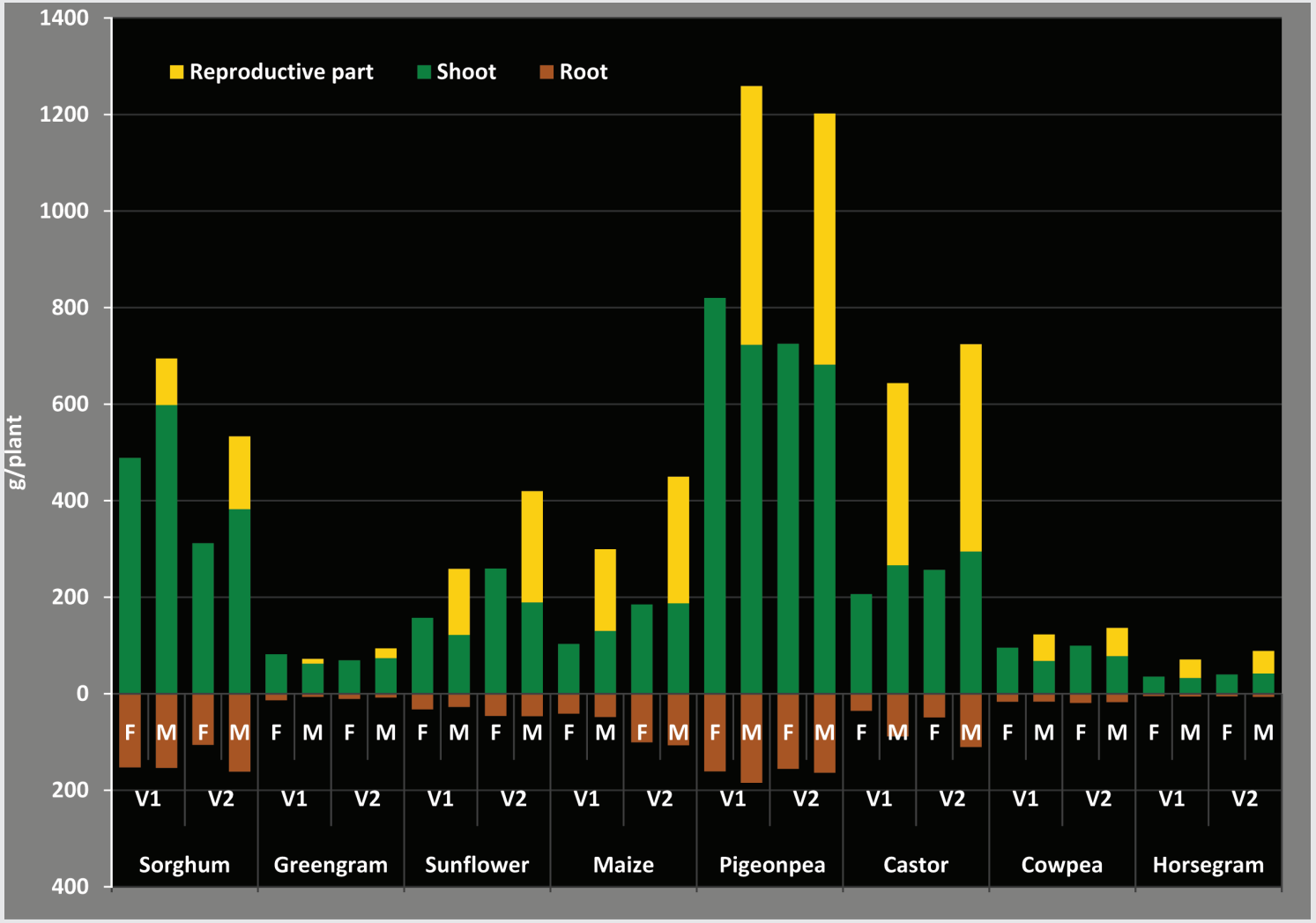


Figure 1. Root and shoot biomass at late flowering (F) and root, shoot and reproductive parts biomass at maturity (M) of crops and varieties (V1, V2)

root biomass of greengram from late flowering to maturity (51.60% decrease in ML 267), and a substantial increase in root biomass of castor (149.80% increase in Kranthi). In crops/varieties whose root biomass increased from late flowering to maturity, evidently the stage chosen as late flowering stage was not the peak root biomass stage. This was especially so in castor which produces flowers on branches of different order, i.e., primary, secondary and tertiary, over a long span of time, making it difficult to identify the maximum root biomass stage. Varieties within crops also differed in the nature and extent of change in biomass from late flowering to maturity. While the root biomass of sorghum SPV 462 increased by only 0.66%, that of CSH 16 increased by 52.39%. In case of sunflower, while the root biomass of KBSH 44 increased by 1.39%, that of Morden decreased by 15.41%.

Root biomass varied widely with crops (Figure 3), ranging from as low as 5.24 g/plant (Horsegram) to as high as 158.23 g/plant (Pigeonpea). The root biomass of the 8 crops (mean of two varieties) at late flowering stage was in the order pigeonpea > sorghum > maize > castor > sunflower > cowpea > greengram > horsegram (Figure 3). Crops are known to vary widely in root biomass (Welbank *et al.*, 1974; Biscoe *et al.*, 1975; Gregory *et al.*, 1978; Buyanovsky and Wagner, 1986, 1987; Paustian *et al*., 1990; Xu and Juma, 1992; Amato and Pardo, 1994). Buyanovsky and Wagner (1986) reported that the post harvest C input to the soil from maize roots was more than twice that of wheat or soybean roots. Iwama and Yamaguchi (1996) also reported large differences in root biomass of different crop species.

Shoot:root ratios (Table 3, Figure 4) at late flowering ranged from 1.84 (Maize, DHM 117) to 7.29 (Horsegram, CRHG 4) and at maturity, from 1.76 (Maize, DHM 117) to 9.61 (Greengram, LGG 460). Shoot:root ratios, averaged across crops and varieties, were 4.98 at late flowering and 4.53 at maturity. Changes in shoot:root ratios from late flowering to maturity differed with crops and even varieties within crops. The shoot:root ratio of greengram increased markedly from late flowering to maturity, while that of castor decreased noticeably. The shoot:root ratio of sorghum SPV 462 increased, while that of CSH 16 decreased. There were significant differences in shoot:root ratios among crops and even varieties within crops. Shoot:root ratios of crops, averaged over varieties, were in the order horsegram > greengram > castor > cowpea > sunflower > pigeonpea > sorghum > maize (Figure 5). The monocots - sorghum and maize, with fibrous root systems, had lower shoot:root ratios than the dicots with tap root systems, indicating a higher percentage allocation of photosynthetically fixed carbon to roots in the monocots. Shoot:root ratios in this study are in general agreement with values in published literature for different crops (Welbank *et al.*, 1974; Gregory *et al.*, 1978; Buyanovsky and Wagner, 1986; Paustian *et al.*,1990; Johnson *et al.,* 2006; Bolinder *et al*., 2007).

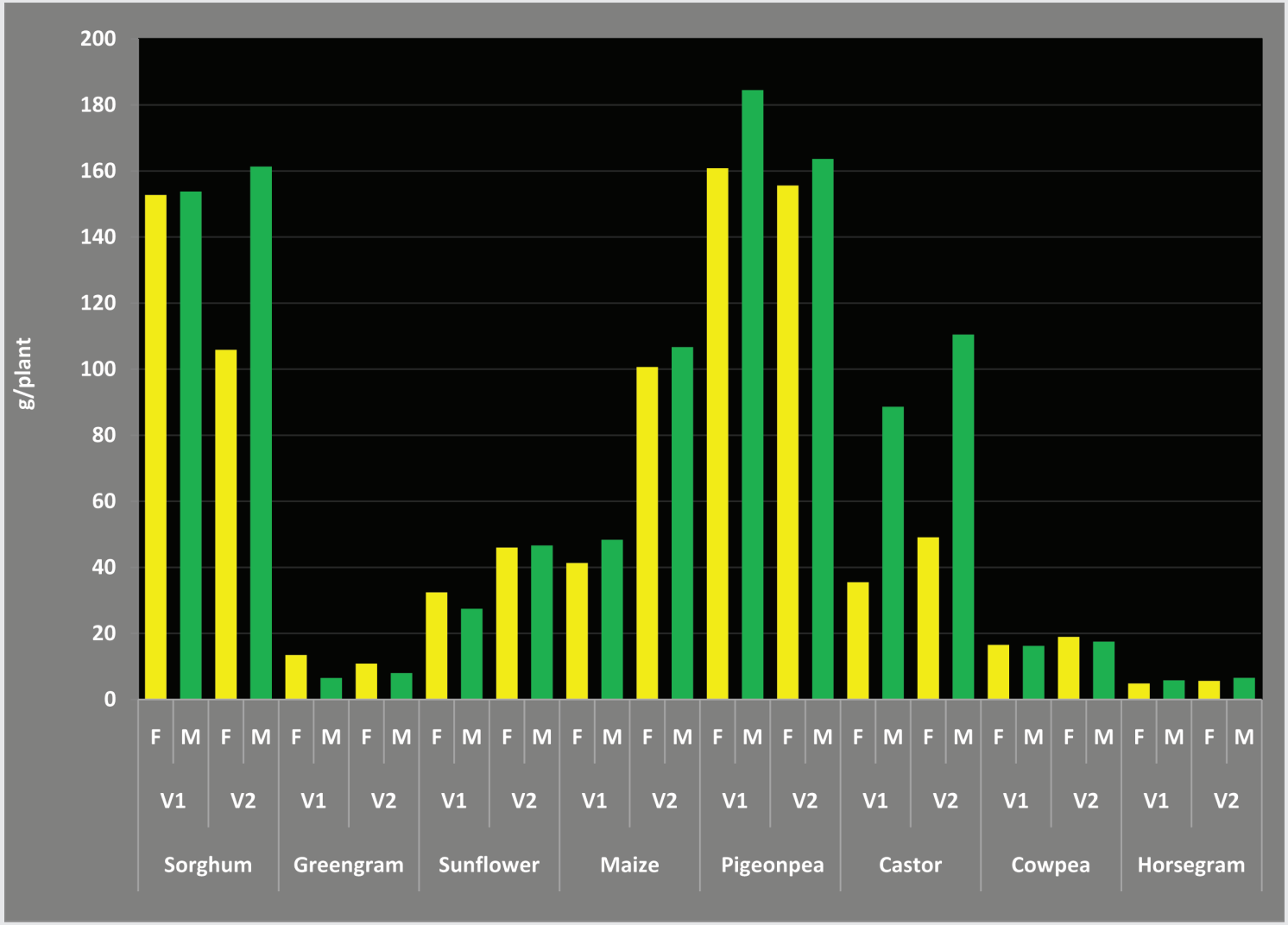


Figure 2. Root biomass of crops and varieties (V1, V2) at late flowering (F) and maturity (M)

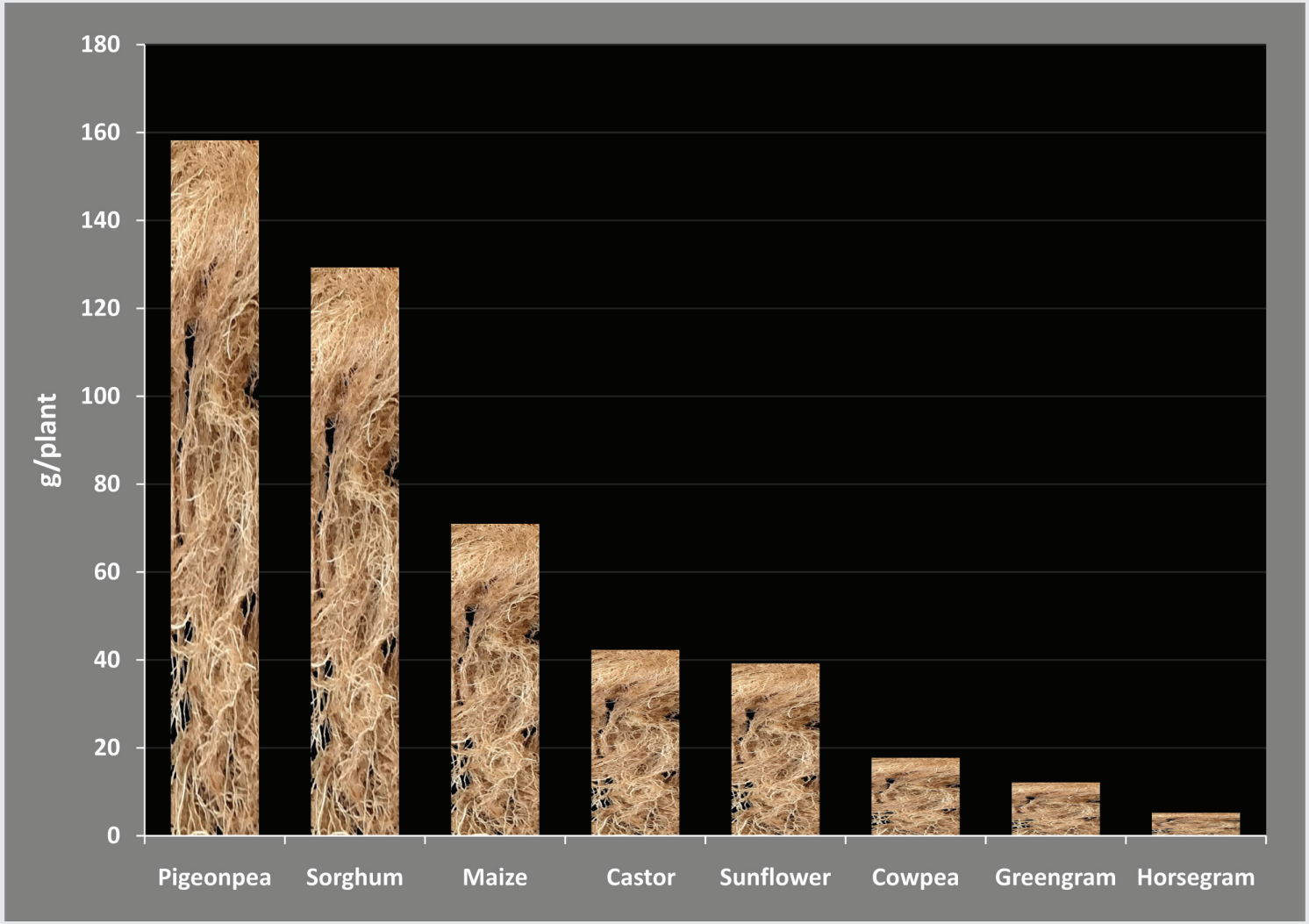


Figure 3. Cropwise (mean of 2 varieties) root biomass at late flowering stage

Table 3. Shoot:root ratios at late flowering and maturity

Crop	Variety	Late flowering	Maturity*
Sorghum	SPV 462	3.20	3.89
	CSH 16	2.95	2.37
Greengram	ML 267	6.06	9.61
	LGG 460	6.38	9.22
Sunflower	Morden	4.85	4.44
	KBSH 44	5.64	4.06
Maize	Varun	2.49	2.70
	DHM 117	1.84	1.76
Castor	Kranthi	5.81	3.01
	PCH 111	5.23	2.68
Pigeonpea	PRG 158	5.09	3.92
	ICPH 2740	4.68	4.18
Cowpea	C 152	5.77	4.20
	APFC 10-1	5.25	4.45
Horsegram	CRHG 4	7.29	5.64
	CRIDA 18R	7.08	6.41
Mean		**4.98**	**4.53**

* Shoot at maturity does not include reproductive parts

Field grown cowpea and horsegram plants were considerably smaller than container grown plants and their root and shoot biomass were 1/3rd to 1/4th of container grown plants (Table 4). This is attributable to the fact that field grown plants experienced stiff competition for resources – light, water and nutrients, whereas container grown plants had no such constraints. However, shoot:root ratios were not so much different, although the ratios were larger for field grown plants, most probably due to underestimation of root biomass under field condition explained earlier. These findings suggest that shoot:root ratios of container grown plants may be used to get a reasonable estimate of root biomass under field conditions (by measuring shoot biomass), especially when other means of root biomass estimation are not available.

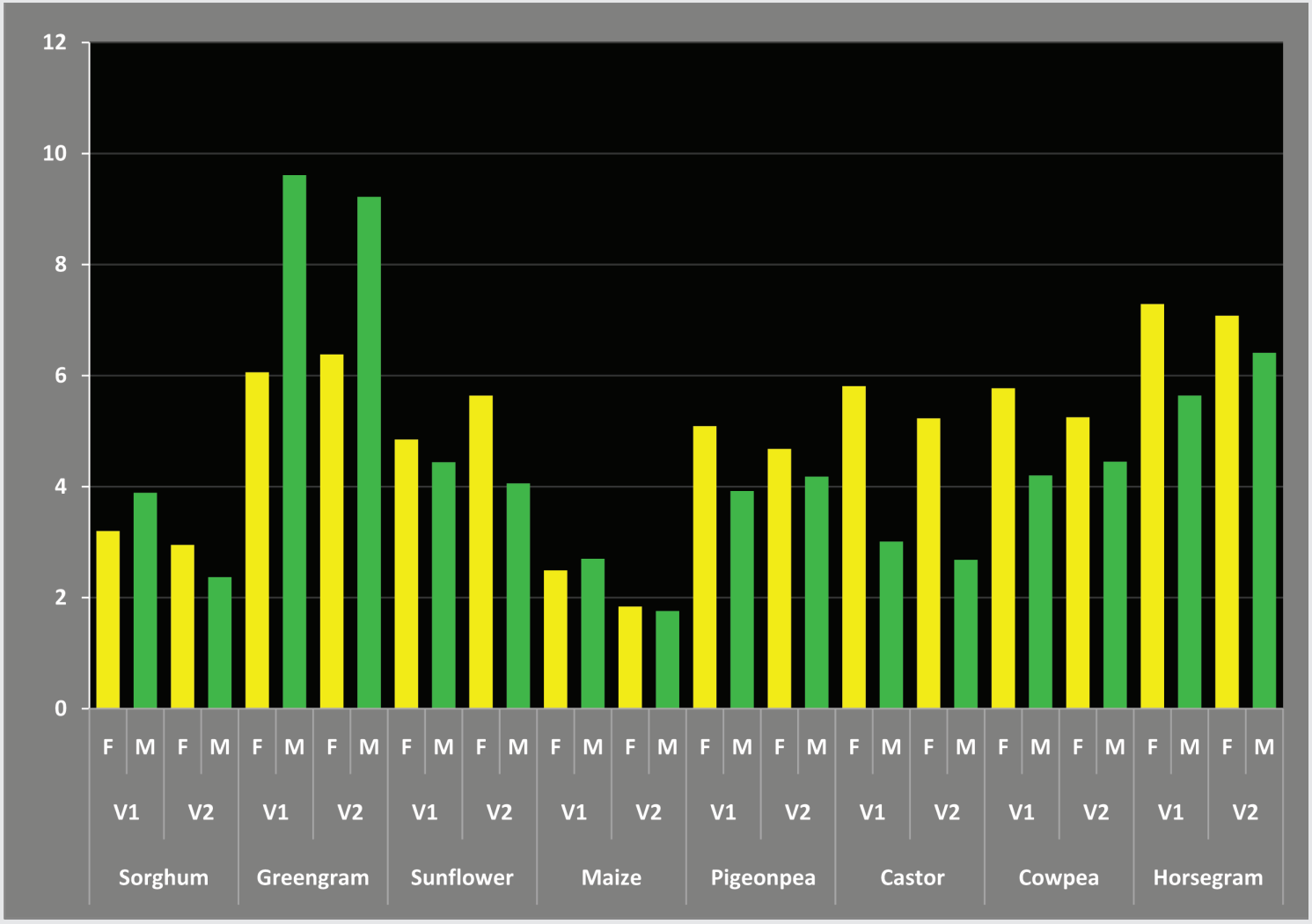


Figure 4. Shoot:Root ratios of crops and varieties (V1, V2) at late flowering (F) and maturity (M)

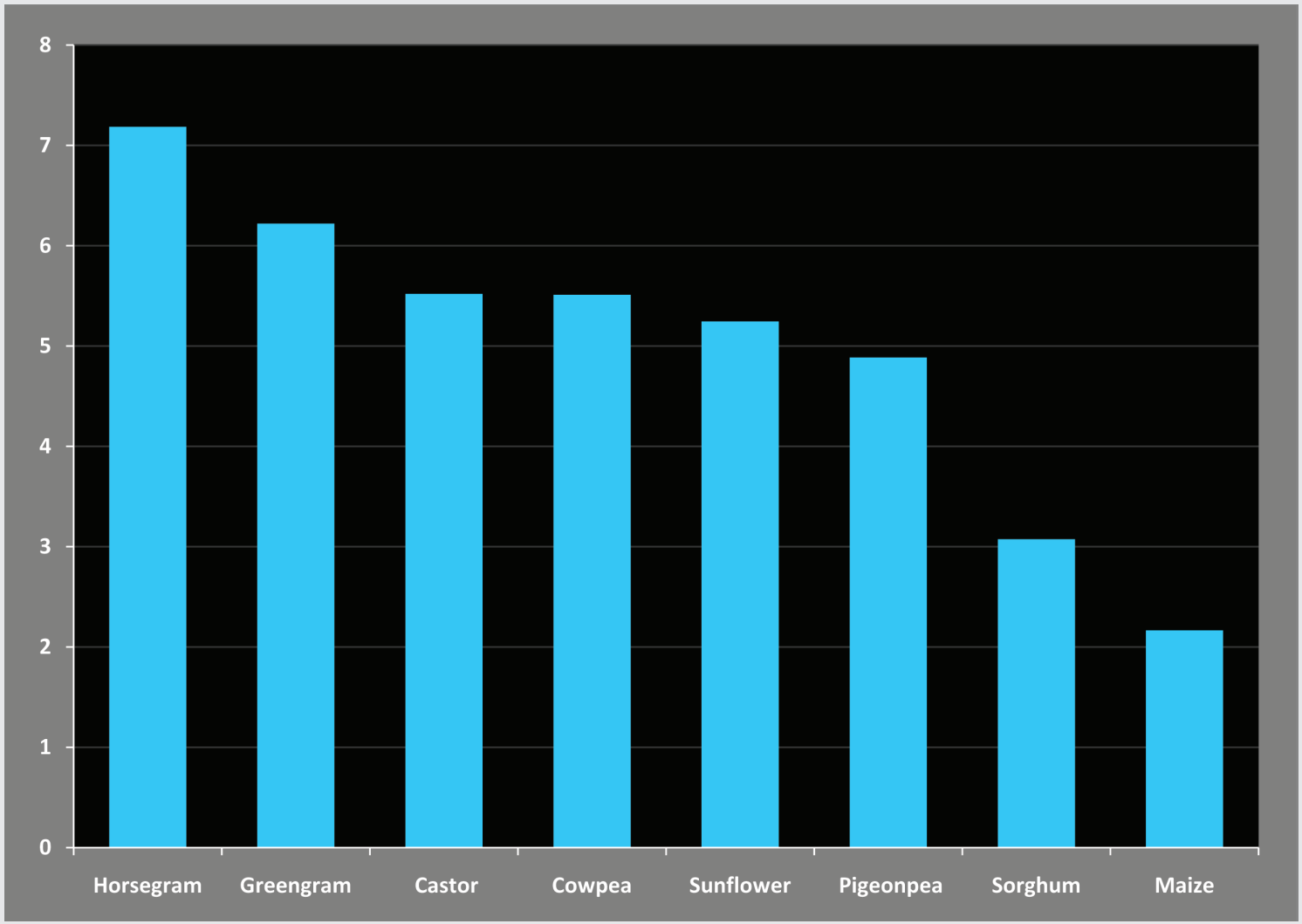


Figure 5. Cropwise shoot:root ratios (mean of 2 varieties) at late flowering stage

Table 4. Root and shoot biomass (g/plant) and shoot:root ratios of container and field grown cowpea and horsegram at late flowering stage

Crop	Variety	Root biomass		Shoot biomass		Shoot:root ratio	
		Container grown plant	Field grown plant	Container grown plant	Field grown plant	Container grown plant	Field grown plant
Cowpea	C 152	16.52	4.37	95.39	27.28	5.77	6.24
	APFC 10-1	18.96	5.06	99.62	31.32	5.25	6.19
Horsegram	CRHG 4	4.85	1.65	35.34	13.10	7.29	7.93
	CRIDA 18R	5.63	1.84	39.85	14.22	7.08	7.72

3.2 Biochemical composition

Plant cells have two major components: cell contents and cell walls. The cell content fraction contains most of the organic acids, soluble carbohydrates, proteins, fats and soluble ash. The cell wall fraction includes hemicellulose, cellulose, lignin and insoluble ash. In most crop residues, the cell wall fraction accounts for 60-80 percent of dry matter (Xiong, 1986). Cell walls of crop residues consist mainly of hemicellulose, cellulose and lignin. These substances, with small amounts of other components, like acetyl groups and phenols, are organized in a complex three-dimensional structure. Other wall components include suberin, cutin, tannins, waxes and minerals.

Hemicellulose is constituted by sugars (xylans) and comprises 20-25 per cent plant biomass on dry weight basis (Meng, 2002). In addition, it also contains glucose and several other hexoses (galactose and mannose) and pentoses (xylose and arabinose). The proportion of these constituents varies plant to plant. Degree of polymerization in hemicellulose does not exceed 50 units and the polymers have branched chains. It occurs as amorphous mass around the cellulose strands. Hemicellulose is insoluble in water but easily soluble in alkali.

Cellulose constitutes the major portion of plant cell wall, the fundamental unit of which is glucose (Meng, 2002). Cellulose is a highly ordered linear homopolymer of glucose linked by β $(1\rightarrow4)$ bonds. In all higher plants, cellulose in primary and secondary walls exists in the form of microfibrils. Cellulose molecules in primary cell walls are heterogeneous in their degree of polymerization, between 2-6000, but in secondary walls they are longer and more homogeneous (up to 14000).

Lignin represents between 5-20 percent of crop residue dry matter (Meng, 2002). Lignin is a complex and high molecular weight polymer with three-dimensional networks of phenylpropane units. It is

generally recognized that the precursors of lignin are coniferyl, sinapyl, and *p*-coumaryl alcohols, which are transformed into lignin by a complex dehydrogenative polymerization process. These three aromatic monomers in lignin are referred to as *p*-hydroxyphenyl, guaiacyl and syringyl residues, respectively. Depending upon the number and type of functional groups on the aromatic rings and propane side chains, lignin has variable solubility. Lignin is phenolic in nature; it is very stable and difficult to isolate.

Lignin occurs between the cells and cell walls and is physically and chemically associated with cell wall polysaccharides. It is deposited during lignification of the plant tissue and gets intimately associated with the cell wall cellulose and hemicellulose and imparts strength and rigidity to the plant. The association between lignin and polysaccharides includes glycosidic linkages, ether cross-linkages, ester cross-linkages and cinnamic acid bridges. The strong linkage between lignin and polysaccharides prevents cell wall components from enzymatic hydrolysis by micro-organisms and thus limits the decomposition of cell walls.

The process of microbial breakdown of plant residues in soil is identical to the degradation of plant material in the rumen of livestock. Most of the methods for fractionation of residues have in fact been developed for animal feeds and fibres. Biodegradability of plant litter material is often characterized through biochemical fractionation, such as the method of Goering and Van Soest (1970). This method leads to the quantification of a series of organic molecule fractions displaying decreasing biodegradability, lignin being the most resistant fraction.

Biochemical analysis of root and shoot samples in the present study revealed that cell wall was the dominant fraction of the plant tissue, except in a few cases of shoot material at late flowering stage, where the soluble cell contents slightly exceeded the cell wall contents (Table 5). In majority of the cases, especially in roots, cell wall contents accounted for 2/3rd to 3/4th of the tissue (Table 5, Figures 6 and 7). The proportion of cell wall increased from late flowering to maturity across all plants and varieties. Cellulose was the dominant cell wall constituent accounting for up to 40% of the plant material. Root samples had high ash content, as high as 19.36% in maize, DHM 117. Much of this ash is due to mineral soil adhering to roots as discussed earlier. Ash contents were higher in roots of maize and sorghum – monocots with fibrous root systems. Correction for ash content due to mineral soil would result in higher values of all the other fractions, including lignin, in root samples.

Regardless of crops, varieties and stage of sampling, roots had lower soluble cell contents and higher cell wall contents than shoots. Lignin, the constituent most important in terms of decomposition, soil organic matter formation and long-term C sequestration, was considerably higher in roots than in

shoots irrespective of crop, variety and stage (Figures 8 & 9). Averaged across crops and varieties, lignin content of roots at late flowering stage was 13.76% as against 8.38% for shoots (Figure 10). The lignin content of both roots and shoots increased from late flowering to maturity to 16.55% in roots and 10.60% in shoots.

Higher lignin content of roots over shoots has been reported earlier by several researchers. Rasse *et al*. (2005) indicated that within a given species, the lignin content of roots obtained by the method of Goering and Van Soest (1970) was on average more than double that of shoots. Fernandez *et al.* (2003) investigated the chemical composition of roots and aboveground plant parts of ryegrass (*Lolium perenne*), *Pinus pinaster* and *Cocos nucifera* and observed that roots were more lignified than the aerial parts of the same species. Puget and Drinkwater (2001) found that root residues of hairy vetch had higher C/N and greater hemicellulose, lignin and cell wall contents while shoots had higher content of non-structural carbohydrates. From an analysis of root, stem and leaf samples of five plant species, Abiven *et al.* (2005) found that root residues were characterized by high values (>15%) of the lignin-like fractions. Several other studies which compared initial root and leaf substrate quality reported higher lignin concentration in roots compared to leaves (Bloomfield *et al*., 1993; Ostertag and Hobbie, 1999).

Crops differed significantly in the lignin content of their roots, which ranged from 8.25% in maize to 19.15% in pigeonpea at late flowering stage (Figure 11). The dicots with taproot systems (castor, sunflower, greengram, cowpea, horsegram, pigeonpea) had higher lignin content than the monocots with fibrous root systems (maize, sorghum). Root lignin content of crops at late flowering stage was in the order pigeonpea > horsegram > cowpea > greengram > sunflower > castor > sorghum > maize. Differences in lignin content among crops have important implications for carbon sequestration. Choice of crops like pigeonpea, which have deep root systems, large root biomass and high lignin content, or their inclusion in cropping systems, can lead to greater sequestration of carbon in soil.

While all of the constituents influence decomposition, residue N content and lignin content exert the greatest control over the decomposition process. Residue N concentration (and consequently C/N ratio) is an important parameter determining decomposability due to the influence of N availability on microbial metabolism (Parton *et al.*, 2007). Plant residues with a high C/N ratio are mineralized far more slowly than residues with low C/N ratio. However, over a wide range of plant materials, C/N ratio was found to be poorly correlated with litter decomposition (Wang *et al.*, 2004; Jalota *et al*., 2006). The lignin to N ratio, which integrates the effects of the two most important characteristics governing plant residue decomposition, has been proposed as a better indicator of chemical recalcitrance than lignin content alone and has been used extensively to distinguish plant residues that

are difficult to degrade, *i.e.* high lignin/N ratio, from those that are more easily biodegraded, *i.e.* low lignin/N ratio (Moore *et al.*, 1999; Parton *et al.*, 1987; Paustian *et al.*, 1992; Tietema and Wessel, 1992). In an evaluation of the decay rates of fine roots of four plantation tree species, Raich *et al.* (2009) found a highly significant negative correlation between fine root decay and fine root lignin:N, which supports the use of lignin:N as a decay-controlling factor within terrestrial ecosystem models. Lignin:N currently is used to modify detritus decay rates within soil organic matter models such as Century (Metherell *et al.*, 1993) and EPIC (Izaurralde *et al.*, 2006).

In the present study, the concentration of C in plant material ranged from 32.15% to 37.66% in roots and 37.97% to 48.2% in shoots across crops, varieties and sampling stages (Table 5). The lower C content of roots is likely to be due to root contamination with mineral soil particles discussed earlier. Nitrogen content was distinctly lower in roots of all the crops and varieties across stages, excepting sorghum CSH 6, whose root N content was slightly higher than shoots (Table 5, Figure 12). Averaged across crops, varieties and stages, N content was 1.65% in roots and 2.30% in shoots. N content of roots as well as shoots decreased from late flowering to maturity. Variations in N content among crops were consistent with crop type, being higher in leguminous crops, and lower in the others. C/N ratios (Table 5, Figure 13) followed a pattern inverse to N%, because C% is relatively constant at around 40%.

Lignin/N ratios of roots were 2-3 times higher than those of shoots (Table 5, Figure 14). Averaged across crops, varieties and stages, lignin/N ratio was 10.02 in roots and 4.59 in shoots. Values of lignin/N ratio increased from late flowering to maturity. Rasse *et al*. (2005) reported that across several plant species, the lignin/N ratio of root tissues was, on an average, three times that of shoot tissues. The high lignin/N ratios of roots make them more difficult to decompose because not only is the carbon of lower quality (recalcitrant) due to higher lignin content, but also nitrogen that soil microorganisms require is in short supply.

3.3 Carbon mineralization behaviour

Due to the higher content of lignin in roots, root residues decompose more slowly than aboveground biomass and therefore have greater influence on long term soil organic matter buildup. In a study of decomposition of above ground and below ground biomass of several plants, Jalota *et al.* (2006) found that as the lignin concentration increased, the proportion of plant materials decomposed decreased. For each 10% increase in lignin concentration, the proportion of the plant materials decomposed decreased by 25%. Also, for each 10% increase in plant lignin concentration, the litter and fine root turnover time in soil increased by 1.7 times. Abiven *et al.*, (2005) observed slower decomposition of roots, which had higher lignin content, compared to leaves. They suggested that roots decompose less easily because of the presence of the suberin–lignin complex. Slower

Table 5. Biochemical composition of roots and shoots of crops and varieties at late flowering and maturity

Crop	Stage	Variety	Plant part	NDF %	Solubles %	Hemi-cellulose %	Cellulose %	Lignin %	Ash %	C %	N %	C/N	Lignin/ N
Sorghum	Late Flowering	SPV 462	Root	71.61	28.39	15.06	33.19	8.54	14.82	32.28	0.90	35.87	9.49
			Shoot	63.96	36.04	21.03	37.27	4.91	0.76	41.29	1.32	31.28	3.72
		CSH 16	Root	69.89	30.12	13.67	31.09	9.16	15.96	32.51	1.02	32.03	9.02
			Shoot	66.53	33.47	20.80	39.10	5.76	0.88	41.23	1.37	30.20	4.22
	Maturity	SPV 462	Root	77.68	22.32	15.83	35.38	10.49	15.98	34.23	0.74	46.56	14.27
			Shoot	70.06	29.94	24.40	38.90	5.91	0.84	43.31	0.77	56.24	7.68
		CSH 16	Root	76.57	23.43	16.19	33.70	10.91	15.78	33.83	0.79	43.10	13.90
			Shoot	72.76	27.24	23.39	41.45	6.99	0.92	42.86	0.74	58.31	9.51
Greengram	Late Flowering	ML 267	Root	64.89	35.11	17.40	25.43	15.16	6.90	35.37	2.92	12.13	5.20
			Shoot	48.78	51.22	15.53	24.15	8.38	0.72	39.99	3.50	11.44	2.40
		LGG 460	Root	62.12	37.88	15.21	26.30	13.82	6.79	35.92	2.85	12.62	4.86
			Shoot	45.96	54.04	13.15	22.40	9.40	1.01	40.49	3.60	11.26	2.61
	Maturity	ML 267	Root	70.81	29.19	18.33	26.56	17.64	8.27	35.33	2.20	16.06	8.02
			Shoot	54.04	45.96	17.45	25.93	9.81	0.85	42.08	2.58	16.34	3.81
		LGG 460	Root	67.38	32.62	15.79	27.73	16.17	7.68	34.77	2.18	15.95	7.42
			Shoot	50.40	49.60	13.26	24.60	11.58	0.95	42.96	2.68	16.03	4.32
Sunflower	Late Flowering	Morden	Root	60.86	39.14	11.87	27.35	13.28	8.37	32.15	1.32	24.45	10.10
			Shoot	49.53	50.47	14.25	24.53	9.90	0.85	38.11	2.24	17.05	4.43
		KBSH 44	Root	57.90	42.10	11.24	27.37	12.47	6.82	33.20	1.19	28.01	10.52
			Shoot	50.02	49.98	16.13	23.59	9.57	0.73	37.97	2.21	17.22	4.34
	Maturity	Morden	Root	65.79	34.21	12.53	29.04	16.26	7.96	33.75	1.01	33.41	16.10
			Shoot	54.55	45.45	15.09	25.85	12.67	0.94	40.97	1.57	26.18	8.10
		KBSH 44	Root	64.16	35.84	10.99	29.67	14.93	8.57	34.19	1.05	32.72	14.29
			Shoot	55.71	44.29	18.63	24.90	11.30	0.87	40.86	1.62	25.22	6.98
Maize	Late Flowering	Varun	Root	77.02	22.98	19.73	32.27	7.79	17.23	33.59	1.01	33.42	7.75
			Shoot	72.79	27.21	30.84	36.41	4.62	0.92	42.22	1.45	29.22	3.20
		DHM 117	Root	77.11	22.89	16.59	32.46	8.70	19.36	34.09	1.06	32.16	8.21
			Shoot	71.66	28.34	29.47	36.88	4.26	1.06	42.16	1.55	27.28	2.75
	Maturity	Varun	Root	78.18	21.32	18.31	32.08	9.54	18.74	36.72	0.80	45.89	11.93
			Shoot	76.67	23.33	29.98	39.59	6.21	0.89	41.34	0.83	50.10	7.52
		DHM 117	Root	78.26	21.74	18.48	30.68	10.17	18.93	36.64	0.75	48.85	13.55
			Shoot	74.52	25.48	29.43	38.00	6.15	0.93	42.89	0.88	48.73	6.99

Castor	Late Flowering	Kranthi	Root	69.19	30.82	16.17	31.85	12.41	8.76	36.87	1.540	23.94	8.06
			Shoot	55.48	44.52	17.29	31.04	6.30	0.84	42.24	2.54	16.63	2.48
		PCH 111	Root	67.80	32.20	14.35	35.54	10.83	7.08	37.51	1.65	22.73	6.56
			Shoot	53.94	46.06	17.41	30.73	5.23	0.58	43.88	2.68	16.40	1.96
	Maturity	Kranthi	Root	72.39	27.61	18.10	29.89	14.06	10.33	36.99	1.11	33.47	12.72
			Shoot	63.89	36.11	19.72	36.28	7.25	0.63	41.19	1.90	21.74	3.83
		PCH 111	Root	69.53	30.47	16.84	30.69	13.91	8.09	37.42	1.19	31.45	11.69
			Shoot	62.33	37.68	19.09	36.26	6.40	0.57	42.61	1.98	21.52	3.23
Pigeonpea	Late Flowering	PRG 158	Root	73.23	26.77	16.64	27.66	19.44	9.50	36.98	2.40	15.44	8.12
			Shoot	65.53	34.47	18.76	30.44	15.97	0.37	48.04	3.54	13.57	4.51
		ICPH 2740	Root	72.23	27.77	13.26	32.00	18.86	8.10	35.81	2.42	14.83	7.81
			Shoot	62.86	37.14	18.32	28.01	16.07	0.46	47.90	3.66	13.09	4.39
	Maturity	PRG 158	Root	76.14	23.86	15.38	28.92	20.97	10.87	36.38	1.84	19.82	11.43
			Shoot	69.99	30.01	21.14	33.69	14.60	0.56	47.58	2.67	17.82	5.47
		ICPH 2740	Root	74.51	25.49	12.77	32.45	19.90	9.39	35.39	1.77	20.05	11.27
			Shoot	67.30	32.70	18.14	33.61	15.31	0.25	48.20	2.59	18.65	5.92
Cowpea	Late Flowering	C 152	Root	68.08	31.92	16.64	28.35	15.79	7.30	35.14	2.60	13.52	6.07
			Shoot	51.42	48.58	13.37	28.69	8.79	0.58	38.95	3.60	10.82	2.44
		APFC 10-1	Root	73.89	26.11	16.74	31.68	17.11	8.36	35.23	2.51	14.04	6.82
			Shoot	46.86	53.14	15.43	22.82	7.91	0.70	38.19	3.34	11.43	2.37
	Maturity	C 152	Root	74.13	25.87	15.99	31.18	19.55	7.41	36.17	1.87	19.34	10.45
			Shoot	62.03	37.97	17.00	31.72	12.62	0.69	40.11	2.53	15.85	4.99
		APFC 10-1	Root	79.25	20.75	15.66	33.70	22.79	7.10	36.84	1.77	20.81	12.88
			Shoot	65.09	34.91	16.25	32.80	15.34	0.70	39.49	2.49	15.86	6.16
Horsegram	Late Flowering	CRHG 4	Root	76.90	23.10	18.53	31.49	17.99	8.90	36.30	2.40	15.13	7.50
			Shoot	49.59	50.41	15.01	25.84	7.94	0.80	39.82	3.23	12.33	2.46
		CRIDA 18R	Root	76.46	23.54	18.32	31.22	18.80	8.13	37.08	2.49	14.89	7.55
			Shoot	50.79	49.21	17.02	24.05	9.04	0.68	40.93	3.21	12.75	2.82
	Maturity	CRHG 4	Root	80.08	19.92	17.24	33.00	23.39	6.46	37.12	1.71	21.71	13.68
			Shoot	59.94	40.06	12.39	33.28	13.24	1.04	41.88	2.39	17.52	5.54
		CRIDA 18R	Root	82.72	17.28	18.32	32.64	24.04	7.72	37.66	1.80	20.92	13.36
			Shoot	61.17	38.83	16.99	29.15	14.20	0.82	40.78	2.42	16.85	5.87

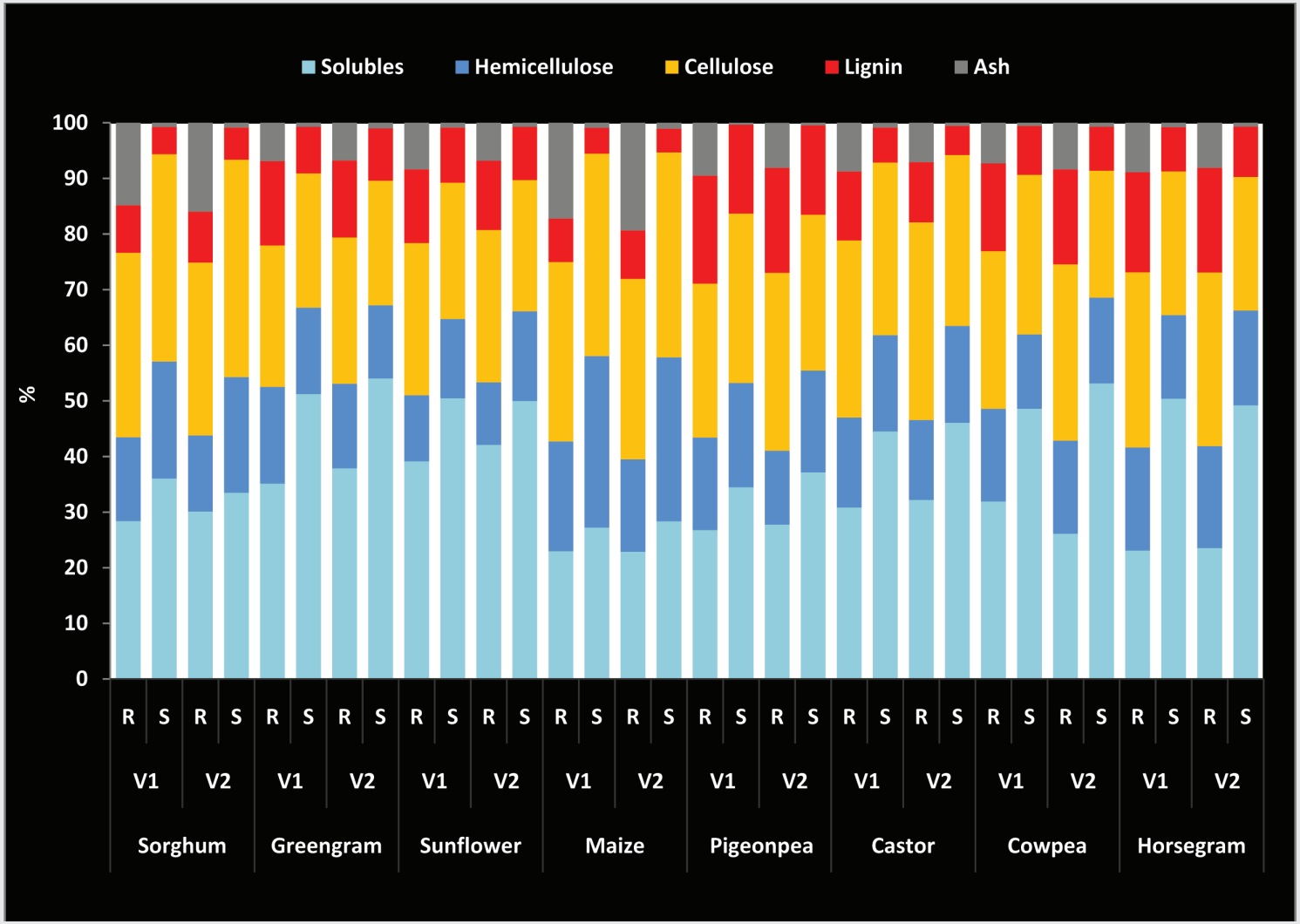


Figure 6. Biochemical composition of roots (R) and shoots (S) of crops and varieties (V1, V2) at late flowering stage

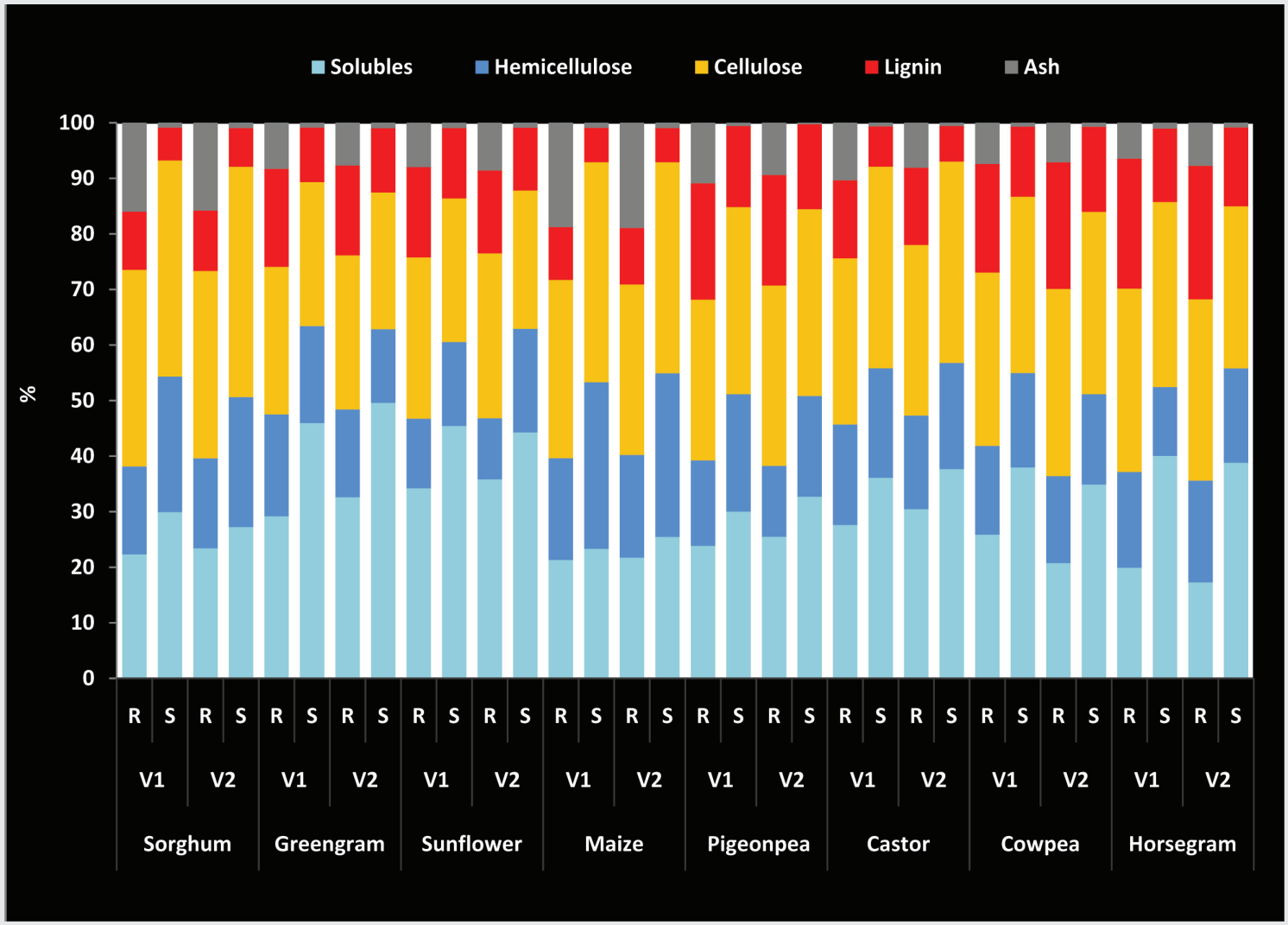


Figure 7. Biochemical composition of roots (R) and shoots (S) of crops and varieties (V1, V2) at maturity stage

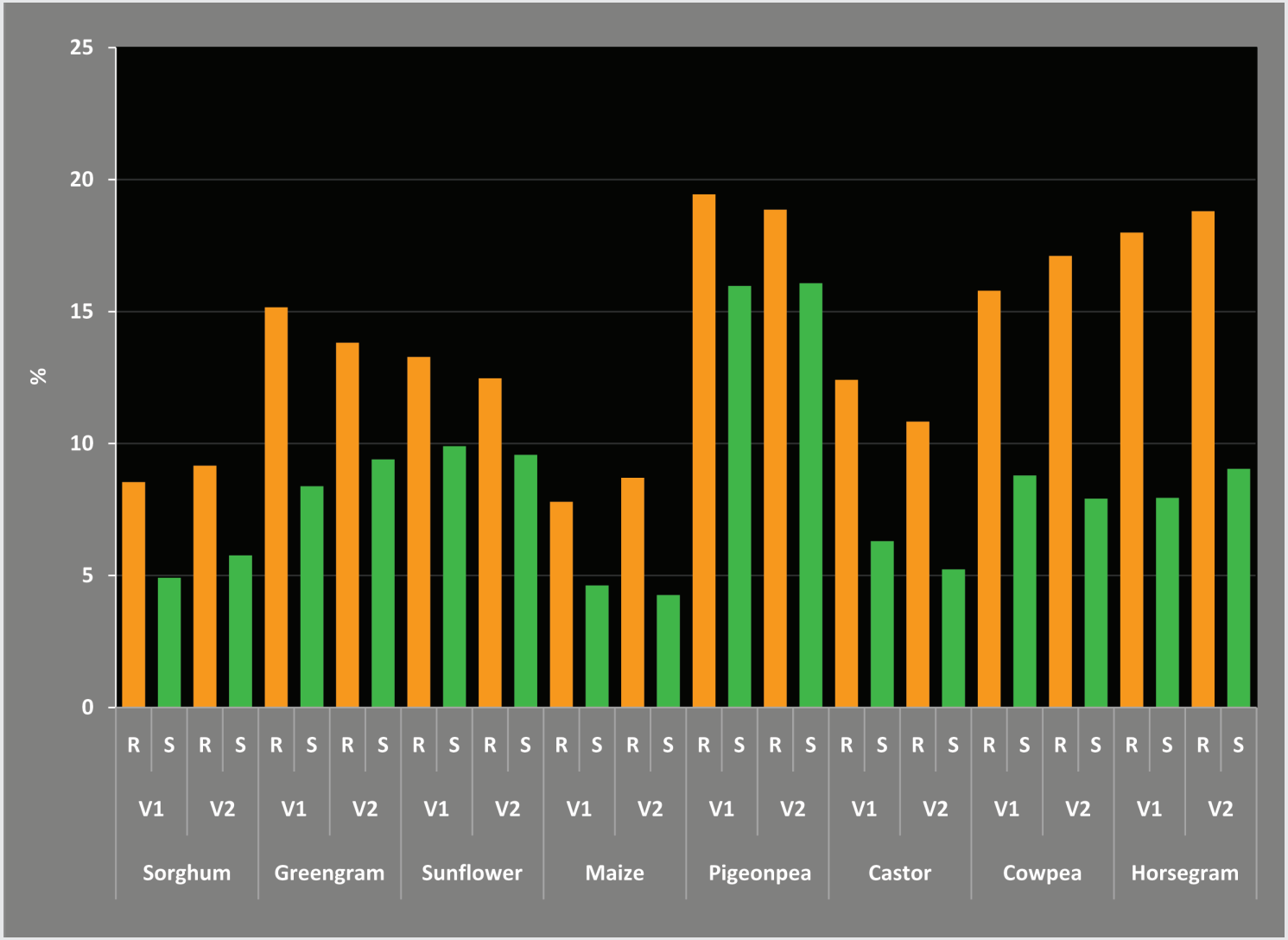


Figure 8. Lignin content of roots (R) and shoots (S) of crops and varieties (V1, V2) at late flowering stage

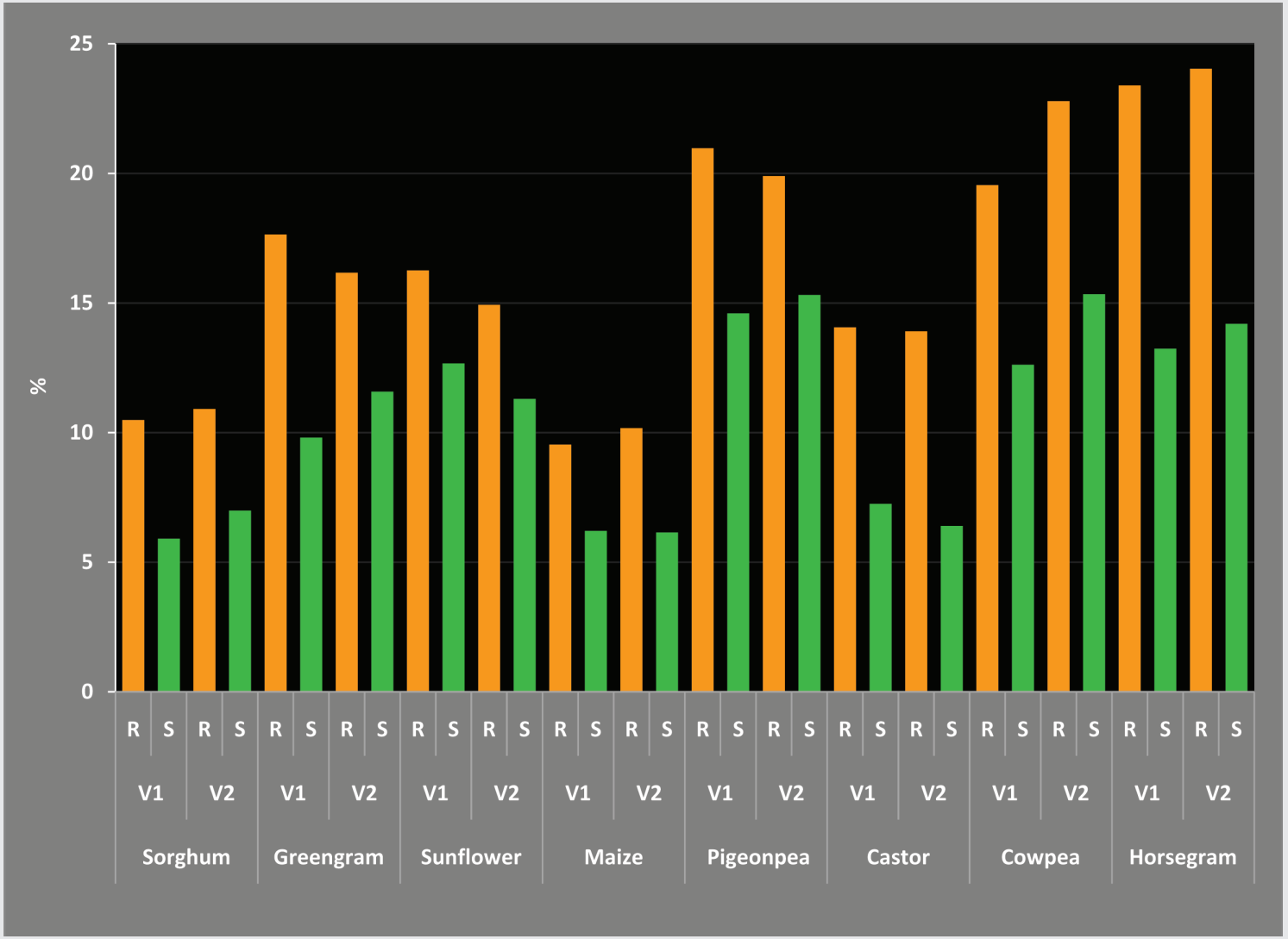


Figure 9. Lignin content of roots (R) and shoots (S) of crops and varieties (V1, V2) at maturity stage

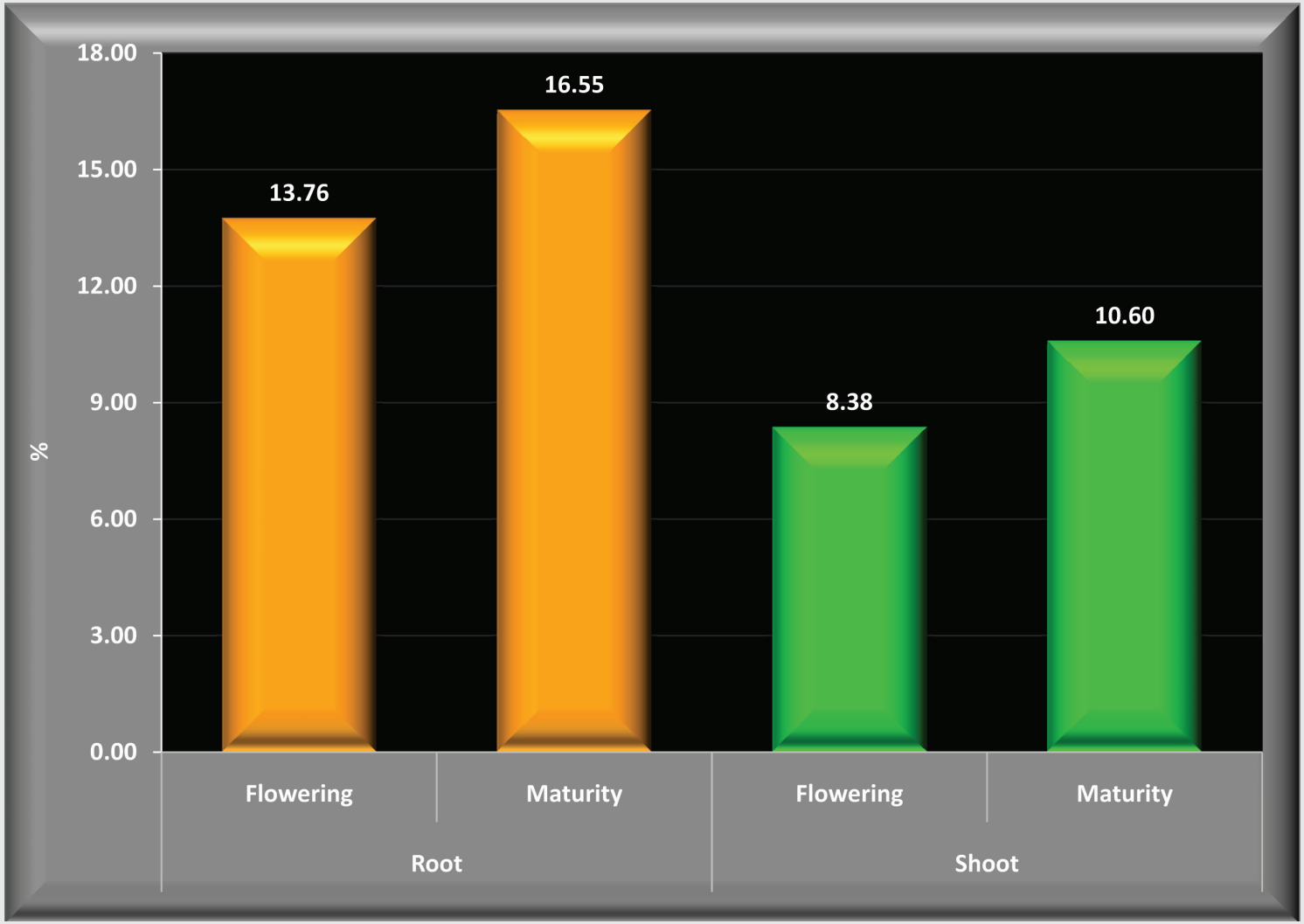


Figure 10. Stagewise lignin content of roots and shoots (averaged across plants and varieties)

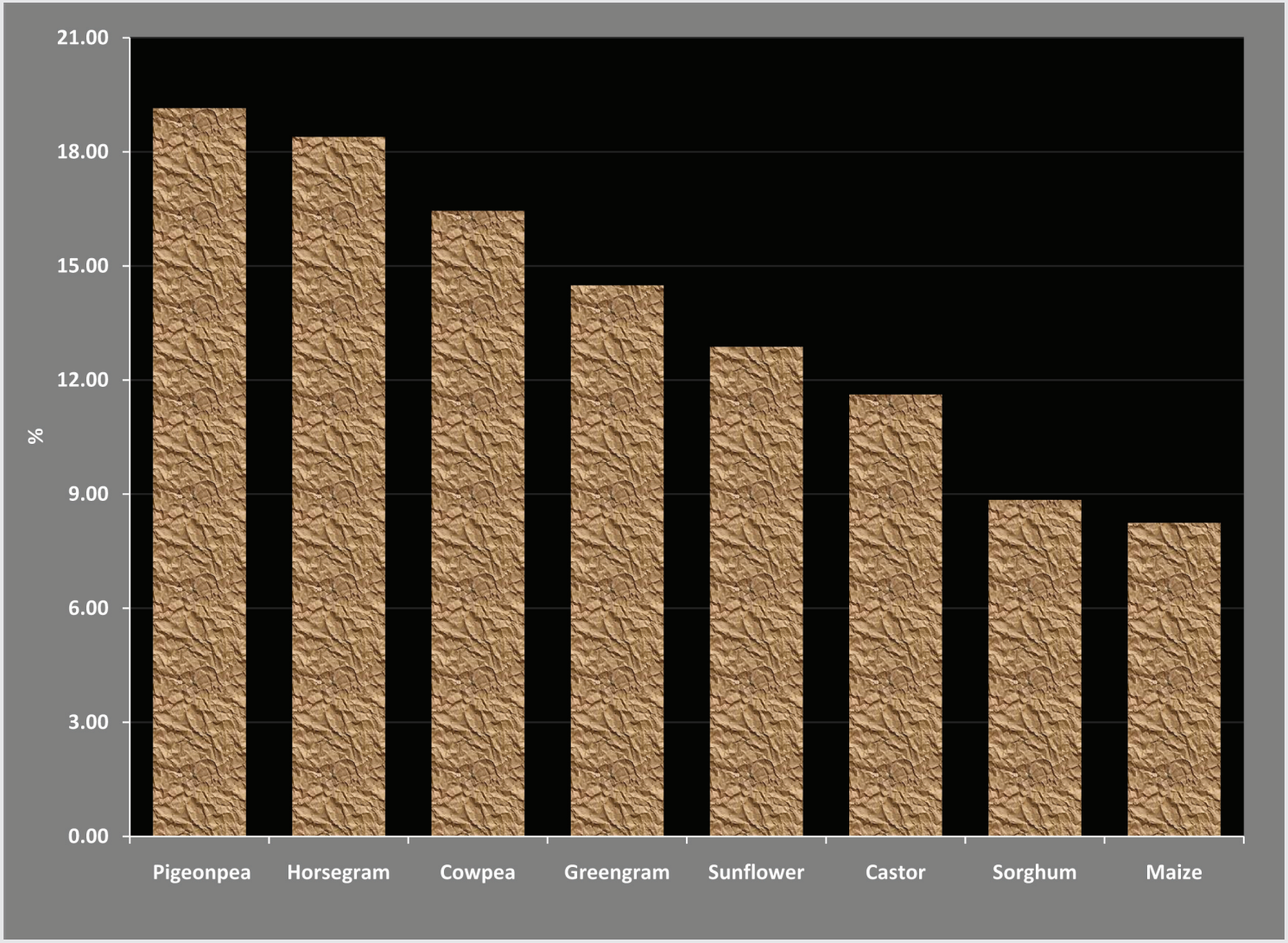


Figure 11. Cropwise lignin content of roots (mean of 2 varieties) at late flowering stage

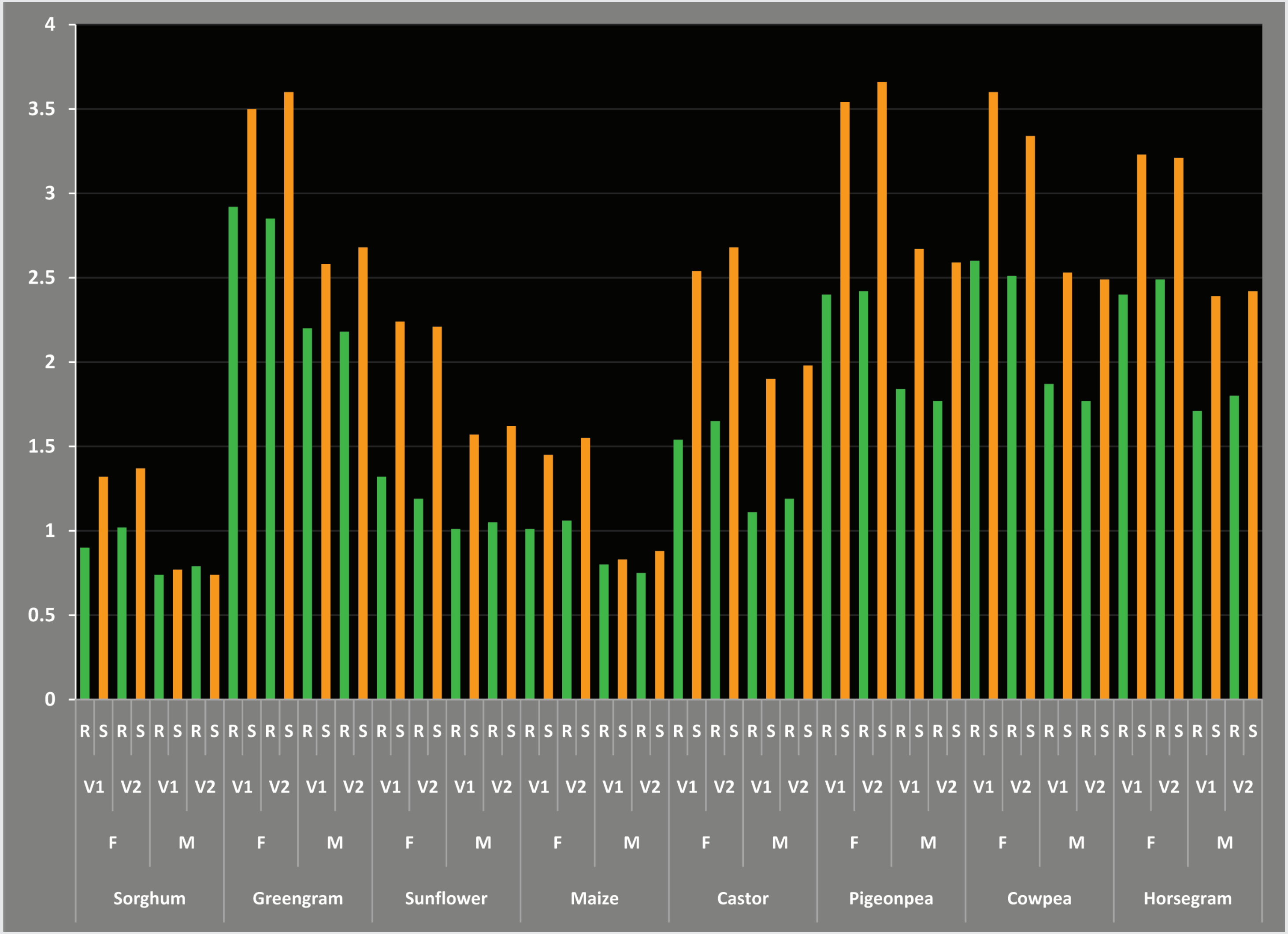


Figure 12. Nitrogen content (%) in roots (R) and shoots (S) of crops and varieties (V1, V2) at late flowering (F) and maturity (M) stages

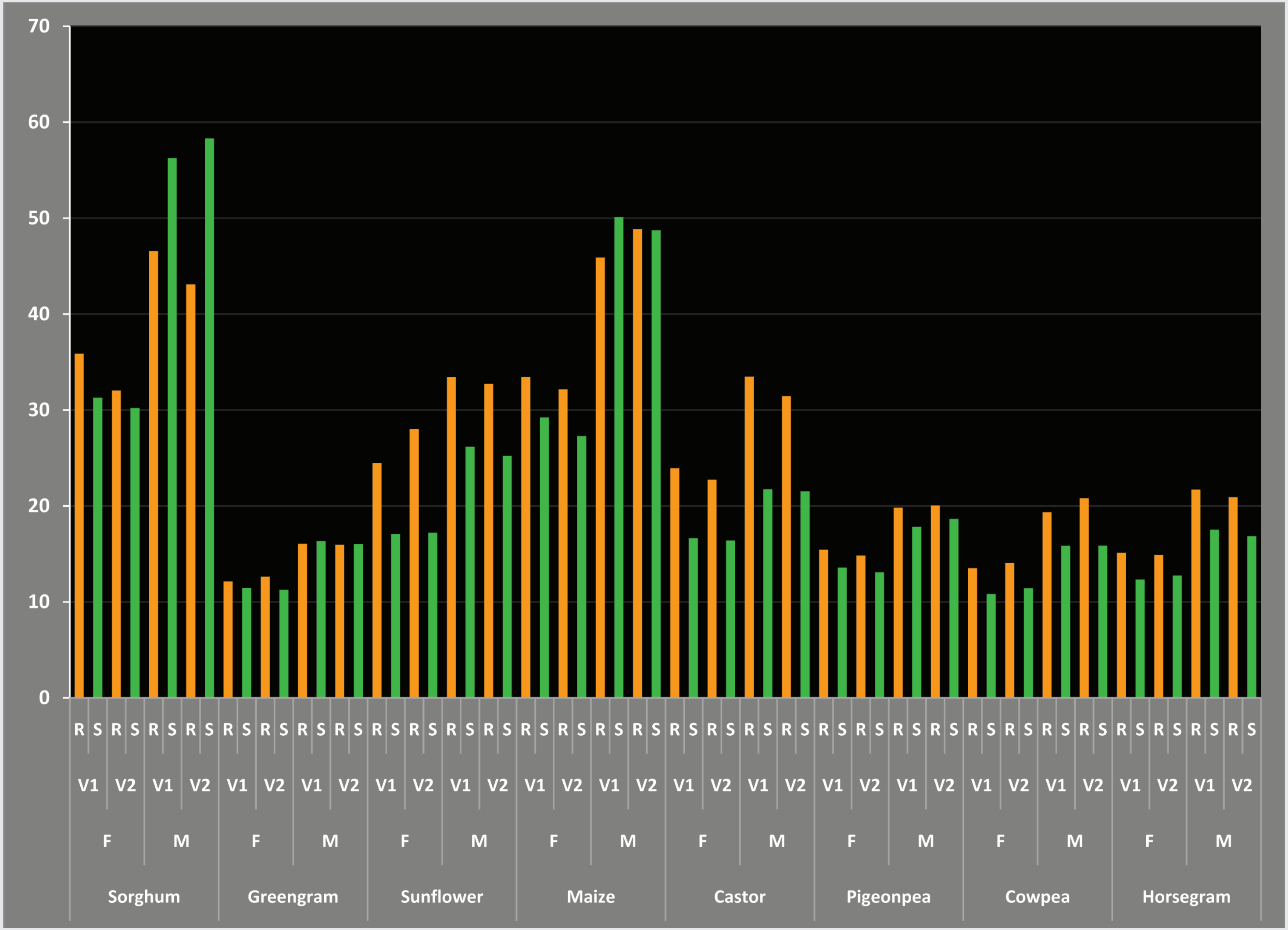


Figure 13. C/N ratio of roots (R) and shoots (S) of crops and varieties (V1, V2) at late flowering (F) and maturity (M) stages

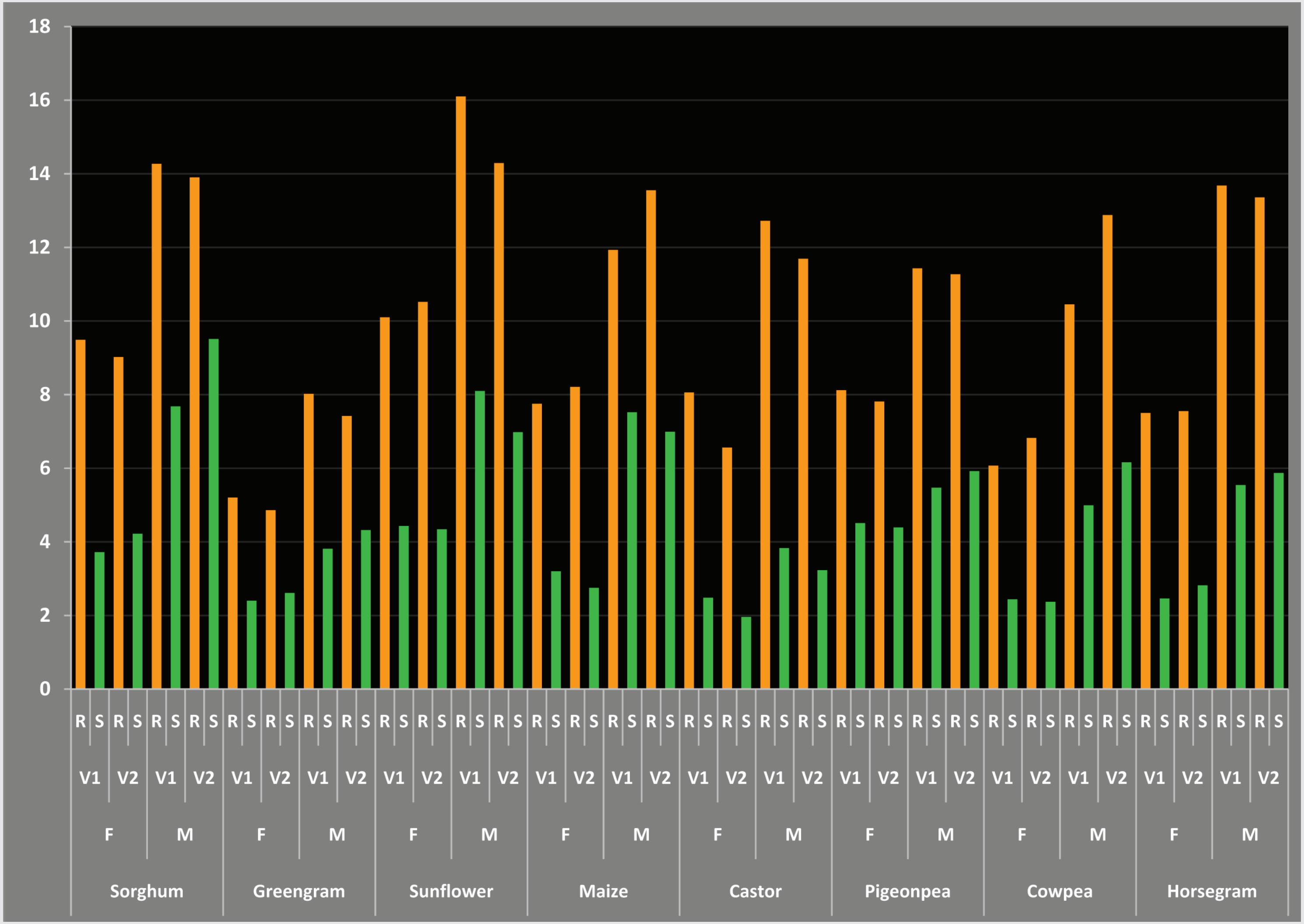


Figure 14. Lignin/N ratio of roots (R) and shoots (S) of crops and varieties (V1, V2) at late flowering (F) and maturity (M) stages

decomposition of roots may be due not only to a specific highly recalcitrant C pool but also to a reduced accessibility to decomposers. So long as this suberin–lignin complex protects the root externally, not only the macromolecular composition but also the anatomy of the tissue (location and thickness of the suberin–lignin complex) will play a role in enzyme accessibility and prevent easier decomposable compartments blocked by this complex from decomposition. Litterbag studies by Fujii and Takeda (2010) using leaves and roots of Japanese cypress (*Chamaecyparis obtuse*) revealed that mass loss of roots was considerably slower than that of leaves.

In this study, the decomposition or carbon mineralization patterns of roots and shoots (samples collected at late flowering stage) of two varieties each of the 8 crops were exponential in nature, being faster in the initial stages and slowing down with the passage of time (Figure 15). Regardless of crops and varieties, roots exhibited distinctly slower or lower carbon mineralization than their corresponding shoots. Per cent added C mineralized at the end of 120 days of incubation was markedly lower for roots than their corresponding shoots (Table 6, Figure 16). Per cent C mineralized in 120 days was lowest (29.74%) in roots of greengram LGG 460, and highest (56.69%) in sorghum CSH 16 (Table 6). Averaged across crops and varieties, per cent C mineralized in 120 days was 37.35% in roots and 50.22% in shoots (Figure 17). These results clearly indicate that roots decompose much more slowly than shoots in soil. Numerous studies conducted under different conditions confirm the slower mineralization of root C (Balesdent and Balabane, 1996; Bolinder *et al.*, 1999; Puget and Drinkwater, 2001; Lu *et al.*, 2003).

Correlations were worked out between %C mineralized in 120 days and relevant residue quality parameters. Lignin showed the best correlation ($r = 0.684^{**}$) followed by lignin/N ($r = 0.636^{**}$), both of which had a highly significant ($p = 0.01$) negative relationship with %C mineralized (Figure 18). Among the other residue quality parameters, NDF ($r = 0.417$) had a significant ($p = 0.05$) negative relationship and hemicellulose ($r = 0.357$) had a significant ($p = 0.05$) positive relationship with %C mineralized. Surprisingly, N and C/N ratio were poorly correlated with %C mineralized. Cusack *et al*. (2009) found a significant correlation between lignin content and decomposition rate of roots. In litter bag studies of roots of temperate desert vegetation in China, Zhao et al. (2015) found that the loss of root litter was strongly controlled by the initial lignin content and the lignin:N ratio, as evidenced by the negative correlations between decomposition rate and litter lignin content and the lignin:N ratio, suggesting that root litter quality may be the primary driver of belowground carbon turnover. The strong negative relationship between C mineralized and lignin content in the present study suggests that roots, which have higher lignin content than shoots, decompose more slowly and thus may contribute proportionately more to the formation of stable organic matter in soil.

Table 6: Cumulative % C mineralized from root and shoot material (late flowering stage)

Crop	Variety	Plant part	Incubation period (Days)													
			0	4	10	18	28	38	48	58	68	78	88	98	108	120
Sorghum	SPV 462		0	8.12	15.82	23.83	28.77	34.36	38.43	41.73	43.67	45.17	46.34	47.22	48.11	48.90
		Shoot	0	11.64	23.10	30.27	34.97	40.70	44.64	47.65	49.30	50.48	51.31	51.97	53.08	54.02
	CSH 16	Root	0	7.94	16.16	23.87	29.02	34.52	37.78	40.11	41.40	42.30	43.02	43.68	44.60	45.46
		Shoot	0	11.73	23.57	31.65	36.89	42.02	45.89	49.00	51.04	52.84	54.25	55.27	56.02	56.69
Greengram	ML 267	Root	0	7.73	15.75	22.88	25.27	26.94	27.87	28.58	29.08	29.58	29.92	30.26	30.67	31.01
		Shoot	0	11.39	22.76	30.66	34.46	37.74	38.98	39.51	39.89	40.27	40.54	40.90	41.20	41.35
	LGG 460	Root	0	7.46	15.28	22.32	24.42	25.97	26.86	27.58	28.06	28.45	28.74	29.05	29.46	29.74
		Shoot	0	11.89	24.2	32.94	37.16	40.55	41.93	42.78	43.02	43.45	43.64	44.08	44.43	44.7
Sunflower	Morden	Root	0	6.00	12.07	19.36	22.27	25.48	27.58	29.39	30.52	31.51	32.28	32.9	33.53	34.11
		Shoot	0	11.54	23.32	31.65	36.51	40.77	42.01	42.79	43.27	43.68	44.05	44.39	44.84	45.20
	KBSH 44	Root	0	6.34	12.68	19.94	22.86	26.28	29.01	31.34	32.93	34.36	35.51	36.47	37.39	38.11
		Shoot	0	12.12	24.36	32.94	37.63	41.55	43.10	43.99	44.58	45.07	45.46	45.81	46.35	46.70
Maize	Varun	Root	0	11.86	22.03	26.39	28.97	30.34	31.31	31.98	32.45	32.94	33.22	33.47	34.42	34.96
		Shoot	0	11.78	24.60	37.04	42.37	45.41	47.41	49.16	50.26	51.05	51.69	52.11	53.08	53.49
	DHM 117	Root	0	11.55	18.62	22.24	24.81	26.38	27.79	28.85	29.74	30.60	31.34	31.96	33.23	34.15
		Shoot	0	12.76	25.59	35.29	40.34	44.08	46.86	48.38	49.49	50.50	51.36	51.89	53.04	54.14
Castor	Kranthi	Root	0	8.73	15.16	21.44	25.94	28.70	30.68	33.14	34.91	35.87	36.87	37.60	39.07	39.91
		Shoot	0	10.52	23.32	33.94	41.19	44.86	47.24	48.14	48.85	49.54	49.94	50.20	51.00	51.42
	PCH 111	Root	0	9.11	15.42	21.55	26.06	29.71	33.36	35.82	37.58	38.75	39.76	40.52	41.08	42.29
		Shoot	0	10.23	22.33	34.11	40.16	43.76	45.87	46.70	47.41	47.87	48.17	48.38	49.11	49.57
Pigeonpea	PRG 158	Root	0	11.22	21.09	24.60	26.44	27.55	28.74	29.84	31.09	32.30	33.59	34.62	36.25	37.14
		Shoot	0	9.99	21.26	29.30	34.99	38.72	40.90	42.37	43.51	44.24	44.76	45.18	46.03	46.46
	ICPH 2740	Root	0	9.71	18.67	22.74	25.49	27.13	28.71	30.49	32.05	33.36	34.43	35.05	36.22	36.95
		Shoot	0	8.88	20.17	28.06	34.73	39.68	42.72	44.17	45.45	46.65	47.33	47.69	48.47	48.86
Cowpea	C 152	Root	0	10.52	19.46	26.84	30.87	33.32	34.5	35.38	35.92	36.51	36.74	37.29	37.91	38.59
		Shoot	0	16.02	28.87	39.05	44.96	48.9	51.08	52.56	53.39	53.93	54.25	54.74	55.25	55.68
	APFC 10-1	Root	0	10.18	18.63	25.76	29.59	32.05	33.26	34.32	34.99	35.6	36.01	36.56	37.16	37.72
		Shoot	0	15.41	27.85	38.45	44.59	47.72	49.83	51.21	51.85	52.47	52.79	53.27	53.86	54.31
Horsegram	CRHG 4	Root	0	8.34	14.96	20.08	24.06	26.22	27.32	28.14	28.76	29.48	30.00	30.57	31.27	32.03
		Shoot	0	13.63	25.37	33.97	39.17	42.33	44.59	45.89	46.64	47.32	47.64	48.09	48.53	48.86
	CRIDA 18R	Root	0	9.31	17.27	23.21	27.39	30.38	32.06	32.93	33.73	34.51	34.79	35.31	35.91	36.51
		Shoot	0	14.58	26.32	35.74	41.31	45.5	47.77	49.12	49.93	50.55	50.86	51.26	51.73	51.99

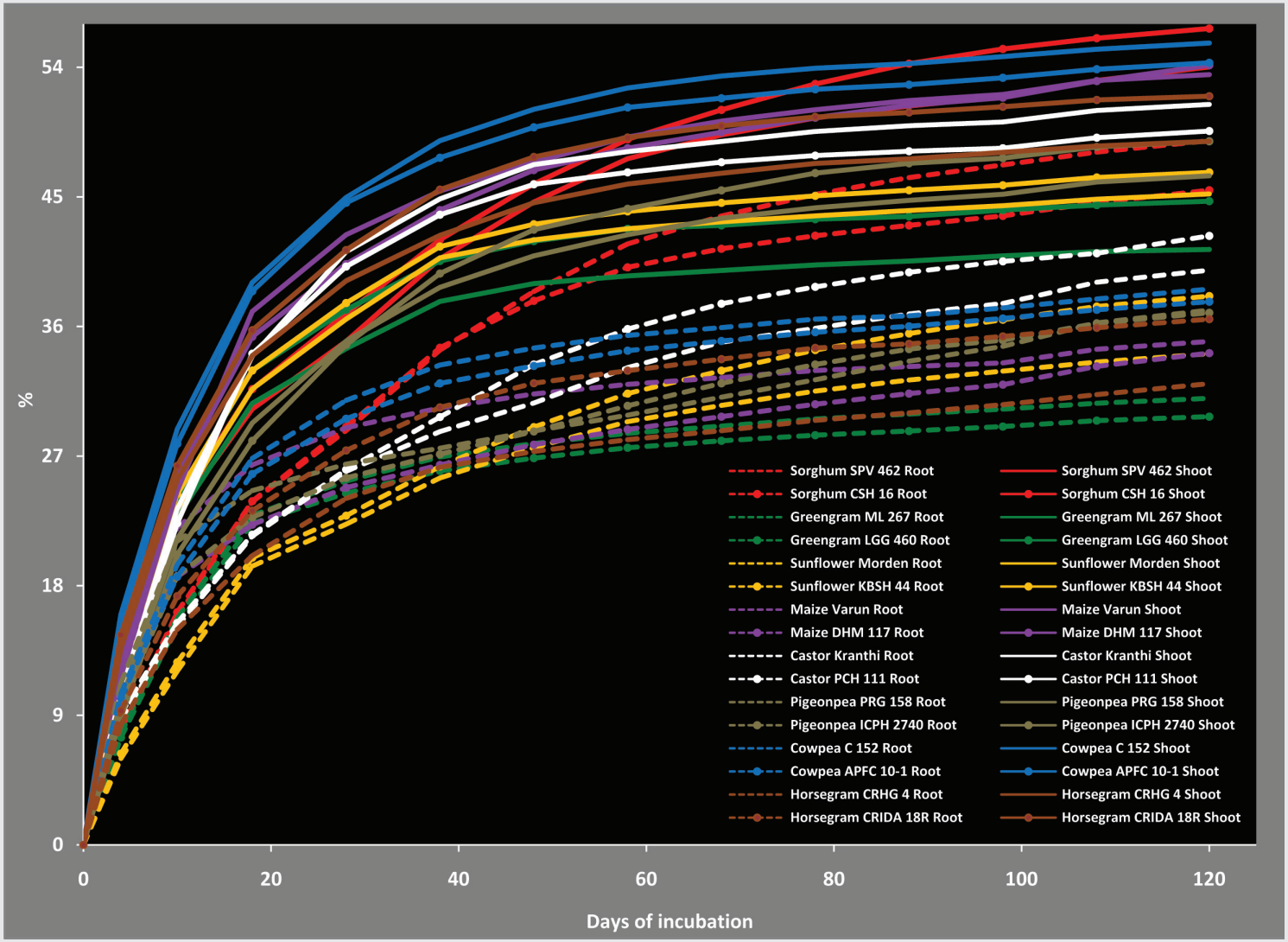


Figure 15. Cumulative % C mineralized from root and shoot material (late flowering stage)

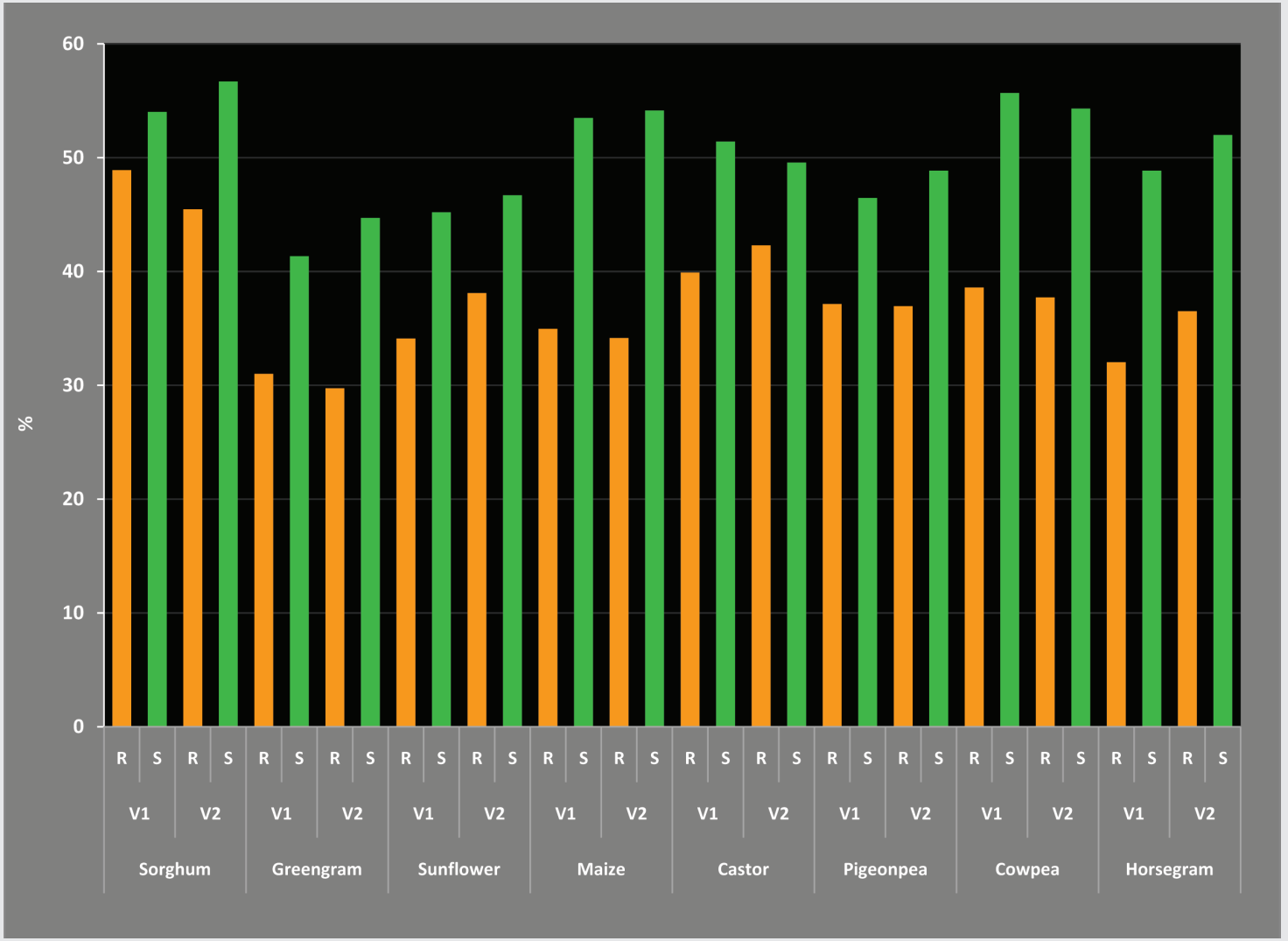


Figure 16. Per cent C mineralized from roots (R) and shoots (S) of crops and varieties (V1, V2) in 120 days of incubation

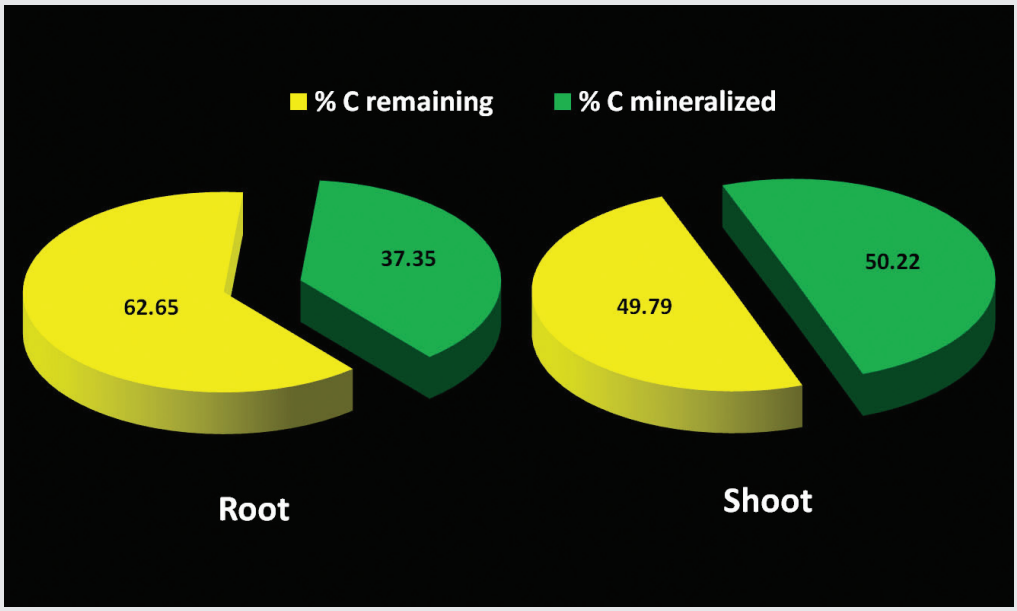


Figure 17. Per cent C mineralized from root and shoot material after 120 days of incubation

Figure 18. Pearson correlation coefficient 'r' between % C mineralized in 120 days and residue quality parameters

4. Conclusions

The results of this study bring out three key aspects - 1. root biomass of crops is substantial, roots make significant inputs of carbon to the soil, 2. roots contain greater proportion of recalcitrant constituents that make them intrinsically more difficult to decompose, 3. the rate of decomposition of root material in soil is slower and lower. These three features, coupled with several other preferential preservation mechanisms already discussed, make roots major contributors of stable soil organic matter. This makes roots a major means for sequestering carbon in soil. Any strategy that increases the quantity of C allocated belowground, enhances the recalcitrance of belowground inputs, or retards the decomposition of belowground C, will result in greater C sequestration in soil. In agroecosystems, such strategies include crop improvement through breeding or biotechnology, choice of cultivars, crops and cropping systems (intensive cropping, intercropping, mixed cropping, rotational cropping, alley cropping with tree components, etc.), and soil and crop management practices. Since potential for C sequestration in deeper soil layers is large, crop cultivars that express deeper and denser rooting characteristics will present greater opportunities for C sequestration. There is considerable scope for increasing the depth of roots by appropriate breeding strategies. Subsoil C sequestration can be achieved through greater inputs of fairly stable organic matter to deeper soil horizons. This can be achieved directly by selecting crops/cultivars with deeper and thicker root systems that are high in chemically recalcitrant compounds. Pigeonpea is a case in point. Of the eight rainfed crops included in this study, it had the highest root biomass and lignin content, and is deep rooted. Including such crops in the cropping system can lead to considerable buildup of soil organic matter and sequestration of carbon in soil. Where change of crop is not an option, varieties with greater root biomass, rooting depth and proportion of recalcitrant constituents can be selected for cultivation. Agronomic management practices that enhance root biomass and rooting depth can also enhance carbon sequestration.

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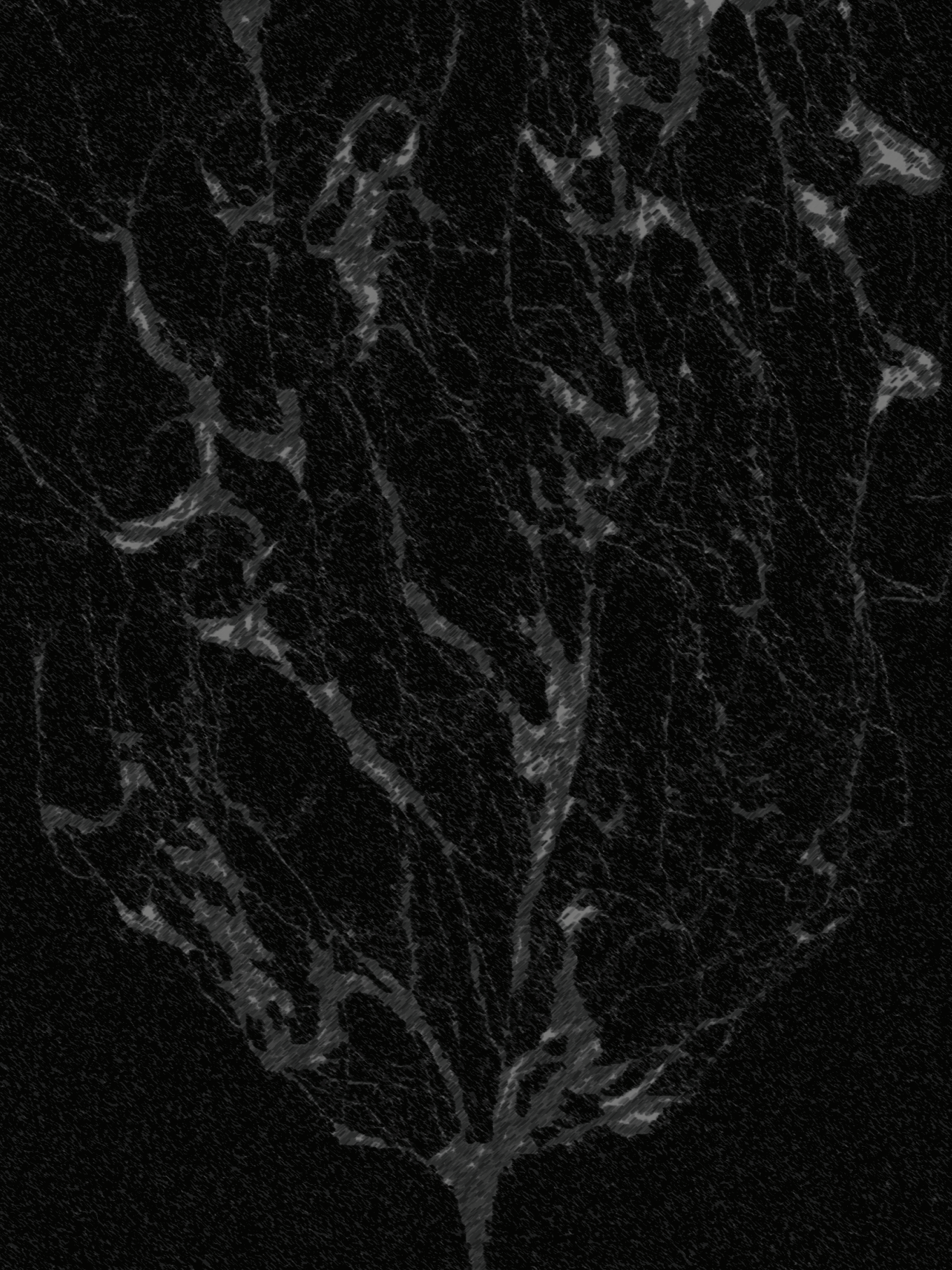

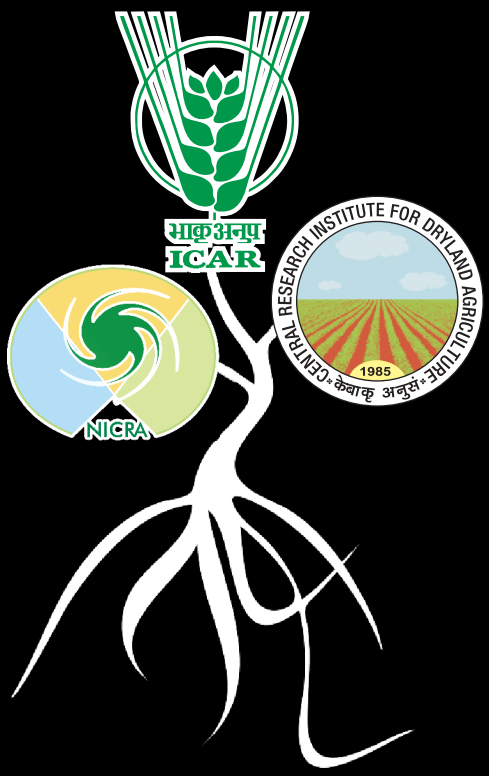

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