

RESPONSE OF WHITE CLOVER (*Trifolium repens* L.) TO DEFOLIATION

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ABSTRACT : *Defoliation has significant effects on the plants of white clover. The effect of defoliation depends on intensity, frequency and timing of defoliation, the type of tissue removed, and whether stresses of competition have occurred before, during, or after the defoliation, and also plant stage and variety. Defoliation causes the important changes in the morphological, physiological and biochemical aspects and significantly affects the yield of the plants. Therefore, plant defoliation management has vital effect for sustainable agricultural systems.*

AK ÜÇGÜL (*Trifolium repens* L.) 'ÜN DEFOLİASYONA KARŞI GÖSTERDİĞİ TEPKİ

ÖZET: *Defoliasyon ak üçgül üzerinde önemli etkilere sahiptir. Defoliasyonun etkisi, biçimin yoğunluk, sıklık ve zamanına, uzaklaştırılan dokunun tipine, defoliasyon öncesi, zamanı ve sonrasında rekabet stresinin ortaya çıkıp-çıkmasına, ve aynı zamanda bitkinin gelişme dönemine ve varyeteye bağlı olarak değişir. Defoliasyon, bitkinin morfolojik, fizyolojik ve biyokimyasal yapısında değişimlere neden olur ve verimini önemli şekilde etkiler. Bu yüzden bitki defoliasyon idaresi, sürdürülebilir tarım sistemi içerisinde ciddi öneme sahiptir.*

Introduction

White clover (*Trifolium repens* L.) is an indispensable component of legume grass for grazing throughout much of the world. It is an effective source of biological nitrogen (N₂) fixation in association with *Rhizobium trifolii* and has high nutritional quality. Shallow root system of white clover is suitable for pastures with high water-table. Its persistence is limited by heavy and continuous grazing and defoliation, competition with grasses, and other biotic and abiotic stress factors.

The perenniality of white clover depends on the renewal of the plant parts, rather than the existence of a single long-lived meristem (Williams, 1987), and the survival of stolon and stolon roots (adventitious roots) (Hart, 1987) rather than tap-roots (Knight, 1953a). Therefore, growth and survival of white clover depends on the continual production of meristems producing new leaves and new branches (Beinhart, 1963).

Environment of factors significantly affects plant growth and meristematic production. Defoliation, the most important one among the stress factors for forage crops, reduces the harvested forage yield, alters its nutritive value, and changes morphological appearance of the species and physiological and biochemical aspects of the plants. Today's for sustainable agricultural systems, forage crop production has increasingly important and, thus, knowledge of defoliation limits forage production and performance in plant management must increase.

Response of White Clover as Whole to Defoliation

White clover, *Trifolium repens* L., is an important forage legume in many temperate regions of the world (Frame and Newbould, 1986). It has adapted to a wide range of climatic and edaphic conditions apparently due to individual plasticity and genetic differentiation of ecotypes (Williams, 1987). It often is an indispensable component of legume-grass pasture for grazing and widely distributed in the world from arctic circle to cool, temperate sites on tropical mountains (Gibson and Cope, 1985). The white clover may have evolved in the Mediterranean region from primitive clovers (Gibson and Cope, 1985).

White clover is adaptable to diverse conditions in part, because of out-crossing that results in heterogeneous population and heterozygosity at many genetic loci (Snaydon, 1962; Turkington and Harper, 1979; Burdon, 1980). The prostrate growth with stolons, voluntary reseeding, and hardseededness are important characteristics of white clover survival with heavy grazing and competition with tall plants (Gibson and Cope, 1985; Pederson, 1995). Therefore, white clover is extensively used in mixture with grasses. It grows best under moist conditions (Gibson and Cope, 1985). In the USA, almost half of humid or irrigated pastures contain white clover (Frame and Newbould, 1986).

The perenniality of white clover depends on the renewal of plant parts rather than the existence of a single long-lived meristem (Beinhart, 1963; Williams, 1987). After death of the primary axis, rooted stolons form new growth centers that have a function similar to the seedling (Gibson and Cope, 1985). Therefore, white clover has the capability of propagating itself asexually. Individual stolons have relatively short life-spans and it has been observed that no parts of stolon survived for more than two growing seasons (Harberd, 1963). Also, Chapman

(1983) showed that less than 10 % of stolons survived for longer than a year. Besides, the tap-root of white clover persists for only 1 to 2 years under field conditions (Pederson, 1989). It dies by the end of the first year or by the middle of the next summer. Also, rooting and persistence were found not to be significantly associated (Knight, 1953b).

Therefore, growth and survival of white clover depend on continual production of meristems producing new leaves (Beinhart, 1963) and its capability to produce seed when environmental stress limits asexual reproduction, and dense stolon branching (Hart, 1987; Williams, 1987). The species produces long-lived hard seeds which may survive in large quantities in the soil for many years (Suckling and Charlaon, 1978; Williams, 1987). Persistence of white clover ecotypes was positively associated with stolon density, dry matter yield, and internode length (Piano and Annicchiarico, 1995). Also, Ahlgren and Spargue (1940) found that rapid spreading was associated with increased size of all plant organs but was generally accompanied by a reduction in number of leaves per unit area (Beinhart et al., 1963).

Williams (1987) analyzed that white clover shoot yield can be divided into a distinct horizontal component immediately above the ground surface (the stolon) with a vertical component (the leaves) above. Harvestable yield is made up almost entirely of leaf. The horizontal stolon component is largely unharvested, and provides for regrowth, plant spread, and persistence through stolon branching with the root system. White clover genotypes vary in the relative portions of leaves and stolons depending on environmental factors (Williams and Hogland, 1978).

Biochemical Response to Defoliation

White clover is normally subjected to repeated defoliations by grazing or mechanical harvesting. The removal of the assimilatory surface has large effects on the physiological, morphological and biochemical aspects of white clover. Defoliation leads to a shortage of current photosynthate supply and the plant must draw on a limited supply of storage material to produce new leaves and other photosynthetic parts (Kendall and Stringer, 1985; Dankwerts and Gordon, 1989).

Therefore, the immediate effect of defoliation is to reduce the contribution of carbon from photosynthesis to the carbon economy of the plant. Up to 100 % of net photosynthesis was lost after defoliation (Beinhart, 1963). Also, there was a decline of over 60 % in root respiration (Culvenor et al., 1989) and 30-40 % in plant respiration (Ryle et al., 1985). Furthermore, defoliation reduced the rate of N₂ fixation by over 70 % (Halliday and Pate, 1979; Ryle et al., 1985; Kang, 1991; Sanderson et al., 1997). Following severe defoliation carbon translocation to stolon tissue and roots was reduced and increased to young branches. The carbohydrate translocation to old branches ceased in severely defoliated N-deficient plants, but increased in severely defoliated N-sufficient plants (Chapman et al., 1992). Close and frequent cutting significantly decreased the content of available total carbohydrate in stolons (Tesar and Ahlgren, 1950). After defoliation, the buffer-soluble protein content of roots and stolons decreased by 32 % during the first 6 days of regrowth. About 55 % and 70 % of nitrogen contents of roots and stolons were mobilized to support the regrowth of leaves, respectively. During the first 6 days, nitrogen in growing leaves came mainly from N reserves of organs remaining after defoliation and substantial reductions in the concentration of water-soluble carbohydrates in stolon took place (Grant et al., 1991; Corre et al., 1996). Continuous defoliation reduced the percentage of total acid-soluble carbohydrate in stolon after following 7 weeks (Jones and Davies, 1988). Approximately 10 % of assimilated C was invested into long-term storage in roots and stolons (Dankwerts and Gordon, 1989). These reserves were remobilized after both partial and total defoliation, and a portion of the remobilized C was incorporated into new growth. Partly defoliated plants regrew more rapidly than totally defoliated plants, but more C reserve depletion took place in totally defoliated treatment. Reserve depletion took place from both stolons and roots, but stolon reserves were preferentially utilized.

Morphological Response to Defoliation

Defoliation has important effects on the morphological aspects of white clover. The development of an axillary bud of white clover to form a branch depends on the bud which is viable, vegetative and non-dormant, and suitable conditions for outgrowth of bud. Defoliation significantly reduces bud viability and also influences bud outgrowth because growth zones of shoots are removed as well as most or all of leaf area (Newton and Hay, 1996). Removal of the laminae and petioles reduced the rate at which branches were initiated from buds. Treatments in which petioles, or petioles plus laminae were retained branched more quickly. In addition, under the simulated continuous grazing leaf dry matter production was reduced in proportion to the leaf complement of stolon. Reduction of the leaf complement from two leaves to one leaf led to a reduction in subsidiary branch production of about 25 % and an increase in percentage dead stolon from 33 to 44 % (Jones and Davies, 1988). Shading the stolon reduced both the rate of initiation and the percentage of buds which developed, unless both petioles and laminae were retained (Davies and Evans, 1990). However, the number of growing points was

unaffected by defoliation (Marriott and Haystead, 1992). Leaf removal from the white clover reduces area of subsequently emerging leaves, dry weight, petiole length, and emergence rate, but increases the rate of development that includes leaflet unfolding and separating (Boatman and Hagggar, 1984). The reactions of white clover to severe defoliation are to develop many smaller leaves with a slightly reduced specific leaf area, more stolons, a smaller proportion of weight in leaf, root, and nodules and a greater proportion of weight in stolons, and higher branch numbers. White clover produced a prostrate network of stolon with a dense population of leaf following weekly defoliation. It produced five times as many leaves as the uncut stands, and the most of herbage consisted of leaves (70 %) (Davidson and Brich, 1973a). The daily yield (material removed by defoliation) of dry weight and nitrogen generally decreased with severity of defoliation, as did the residual plant weight. However, the efficiency of yield (daily yield/residual weight x 100) of dry matter and nitrogen was greater in the most severely defoliated treatments, attaining a maximum of 6 % (Boatman and Hagggar, 1984; Ryle et al., 1985).

The response of white clover to clipping varies depending on the clipping time intervals. Recovery after defoliation was more rapid when plants were defoliated at 8 weeks instead of 6 or 10 weeks (Evans, 1973a). Severe defoliation affects the weight of individual leaves and petioles (Jones and Davies, 1988). The magnitude of these effects varies according to the severity of treatment. Removal of older laminae has little effect, removal of younger laminae has a similar effect to removing all laminae, but removing petiole in addition to laminae has considerably more effect (Boatman and Hagggar, 1984). Defoliation retarded leaf emergence, but partial leaf removal did not cause proportional decreases in leaf area. Removing one-third or two-thirds of the leaflets did not reduce leaf area significantly. Removing all leaflets but leaving the petiole reduced subsequent leaf area and petiole length. Also, removal of younger laminae had a similar effect to removing all laminae while removal of older laminae had little effect (Carlson, 1966; Boatman and Hagggar, 1984). Therefore, severity of defoliation is important to the growth process of white clover.

Responses in Stolons, Roots and Leaves to Defoliation

In addition, defoliation affects stolon characteristics. Stolon branching decreased considerably with relatively mild moisture deficits. Similar relationships between relative reductions in relative water content (compared with the control plants), and relative reductions in leaf area, leaf appearance rate and stolon number were observed. Short deficits (1-2 week) caused a 20 to 30 % reduction in stolon number and leaf size but no change in leaf number per stolon. Longer deficits with mild, intermediate, or severe intensities caused major reductions in stolon number, leaf size, and number of leaves per stolon (Belaygue et al., 1996). However, Knight (1953b) found that cutting the stolons of ladino clover stimulated rooting and branching at the older nodes.

Defoliation caused substantial reductions in stolon extension growth and internode and petiole elongation, a reduction in number of axillary buds developing, and in the proportion of buds which were floral, but had slightly reduced rate of leaf appearance. The differences between white clover varieties in response to treatment were small (Thomas, 1987a; Grant et al., 1991). Increasingly severe defoliation reduced the number of new nodes produced on the main stolon both by reducing the number of nodes on the main stolon and also by reducing the capacity of the axillary buds at each node to develop into new branches (Jones and Davies, 1988).

Defoliation of white clover seedlings reduced both the number and length of stolons per plant when compared with undefoliated seedlings (Wagner, 1952). Defoliating early at the three leaf stage of white clover decreased the number of growing points by 32 % and stolon weights and lengths by 50 % compared with defoliation at the nine leaf-stage. After 17 weeks, undefoliated seedlings produced ten times more stolon than early defoliated or frequently defoliated seedlings. However, the response of the varieties of white clover to leaf stage for initial defoliation and defoliation interval varies (Kang et al., 1995). It was found that total shoot dry weights were reduced by 15-30 % when 40-60 % of the leaf area was removed by single defoliations from days 7 to 19 after planting. However, the growth was reduced by almost 70 % when both cotyledons were removed (days 7 to 9) before emergence of the unifoliate leaf. The relative reduction in growth depended more on the percentage of leaf area removed, rather than on time of removal. Defoliation also reduced the size of trifoliate leaves, and the number of trifoliate leaves at harvest (Rossiter, 1992). Defoliating young plants of white clover to 25, 50 and 100 mm above the base of the shoot every second day depressed root elongation. The twenty-five mm treatment reduced root elongation to approximately 5 % of that of undefoliated plants (Evans, 1973a). Carlson (1966) hypothesized that growth regulators produced by older leaves might affect the growth and development of leaves immediately after defoliation. Therefore, defoliation has adversely much more effects on the seedlings than that on the more matured plants. After defoliation, a relatively long time is necessary to restore the root reserves before subsequent defoliation (Kendall and Stringer, 1985).

Furthermore, removal of all laminae resulted in rapid reduction in root elongation in white clover (Evans, 1973b). Root weight and N accumulation were less in defoliated plants. N was remobilized from root and stolon tissues for leaf regrowth after defoliation (Marriott and Haystead, 1992). In all defoliation treatments, growth

was confined to leaves for up to 5 days. Root growth ceased in all defoliation treatments. Reestablishment of the leaf area in severely-defoliated swards was facilitated by the rapid opening of developing leaves and by changes in the allocation of carbon which favored leaf development over branch and root, and lamina over petiole growth. Movement of carbohydrate and nitrogen from roots and branches for 5-9 days was observed in the severe defoliation treatments. Branches lost 62 % of their initial carbohydrate content compared with 25 % of the roots. The roots were the principal source of mobilized nitrogen (Culvenor et al., 1989). It was found that one-third of the leaf area had sufficient photo-assimilates to maintain the tap growth processes and to increase the store of root carbohydrates (Carlson, 1966). Reducing the severity of defoliation during the first producing year resulted in less root mortality. However, cutting treatment did not affect the tap-root life of white clover (Westbrooks and Tesar, 1955).

Yield of White Clover Under Defoliation

Defoliated white clover swards yield considerably less than uncut swards (Seker, 1997). The yield loss was associated with reduced leaf area (Beinhart, 1963). It was found that yield of leaf dry matter was reduced proportional to the leaf complement of the stolon. Reduction of the leaf complement from two leaves to one leaf led to a reduction in branching by about 25 % and an increase in percentage dead stolon from 33 to 44 % (Jones and Davies, 1988). Crop growth rates are decreased by defoliation and a severe defoliation treatment reduces the plant dry matter yield. Shoot dry weights were reduced by 15-30 % when 40-60 % of the leaf area was removed by single defoliations from days 7 to 19 after planting. However, the growth was reduced by 70 % when both cotyledons were removed before emergence of the unifoliate leaf (Rossiter, 1976).

The defoliation effects depend on the strains or varieties of white clover, on harvest period and frequency (Rossiter, 1976; Boatman and Haggard, 1984) and on type of tissue removed (Sanderson et al., 1997). The responses of cultivars in growth depression varied. Defoliated swards-especially those cut every three or four days-had more but smaller leaves, and higher branch numbers than uncut swards (Rossiter, 1976). Medium-large-leaved cultivars were more productive and persistent than small-leaved cultivar with less frequent defoliation while the inverse was true under the more frequent cutting intervals (Wilman and Asiegbu, 1982). Furthermore, with infrequent defoliation, large-leaved cultivar (Osceola) is more productive than small (Aberystwith S184) and medium-small (Grasslands Huia) leaved cultivars. But with frequent defoliation, small and medium-small leaved cultivars produced the longer stolon and larger leaf area (Kang, 1991). It was determined that the total dry matter yield of clover harvested differed significantly between cultivars at all harvest and differences between cultivars were consistent throughout the season under the effect of defoliation (Williams and Hayes, 1987). Generally, the large-leaved types (Ladino) had longer petioles and the small-leaved cultivars produced a much greater length of stolon and many more nodes in both the field and controlled environments. The large-leaved cultivars were more productive than small- or medium-leaved cultivars (Wilman and Asiegbu, 1982; Goodman, 1986; Kang, 1991).

The response of white clover to the mode of defoliation varies depending on the varieties. The yields of white clover were less under grazing than cutting due to selective removal of stolon material (Evans and Williams, 1987). There were significant differences in yield between white clover cultivars to treatments that included clipping, rotational grazing by sheep and continuous grazing by sheep (Evans and Williams, 1987).

Therefore, defoliation adversely causes stresses on the plants of white clover depending on some plant and environmental conditions. Thus, the biochemical, physiological and morphological aspects of the plants significantly change having effects on yield.

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