Measuring Growth in Complex Systems: How Do Growth Regulators Alter Growth?

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GENERAL

The crop of an apple planting is the product of the interaction of two factors: the total production of dry matter per unit of land, and the partitioning of that dry matter between fruit and wood. Yield alone does not adequately describe productive efficiency. The yield must be related to vegetative growth, but, unfortunately, total vegetative growth is difficult to determine. The shoots of an apple tree are conspicuous and easily measured, but they represent only a fraction of the total vegetative growth (Forshey and McKee, 1970; Forshey et al., 1983; Mochizuki, 1962). Root growth and secondary thickening of trunk and scaffold branches account for the major part of the vegetative increment, but measurement of this growth is impractical to impossible. The assessment of growth regulator and other treatment effects is complicated by the lack of a single, simple measure that accurately characterizes vegetative growth (Forshey, 1989; Forshey and Elfving, 1989).

Shoots are the most common index of vegetative growth. While it is often assumed that shoot growth is proportional to total growth, this is not always true. Shoot growth may respond differently to treatment or stress than other parts of the tree, such as trunk or roots (Wilcox, 1937). Shoot growth is generally expressed as mean shoot length, but total shoot growth per tree is more closely related to the number of shoots than to shoot length (Barlow, 1966; Forshey, 1982b, 1989; Forshey and Elfving, 1989; Forshey and Marmo, 1985; Forshey et al., 1983; Quinlan and Preston, 1968). This point is particularly important in the vegetative growth-fruiting relationship because fruiting has a greater effect on shoot number than on shoot length (Avery, 1969, 1970; Forshey, 1982b, 1989; Forshey and Marmo, 1985; Quinlan and Preston, 1968). Total shoot growth per tree is much more meaningful than mean shoot length but is obviously difficult to determine on large trees. Where total shoot growth measurements are practical, relating yield to shoot growth

(kilograms of fruit per meter of shoot growth) provides an index of the vegetative growth-fruiting relationship (Forshey, 1982b; Forshey and Elfving, 1989). These values vary widely with cultivar and growth habit (Table 1) and are, therefore, more useful as indicators of change than as specific goals.

The leaf canopy is a reflection of the vegetative growth-fruiting relationship (Forshey, 1989; Forshey and Elfving, 1989). It is comprised of varying proportions of shoot and spur leaves. If extremes are avoided, cultural practices have little or no short-term effect on total leaf area per tree, but may result in substantial changes in the relative proportions of shoot and spur leaves (Barlow, 1964; Forshey and Marmo, 1985; Lakso, 1984; Palmer and Jackson, 1977). Total shoot leaf area is closely associated with total shoot growth, total spur leaf area is closely associated with fruitfulness, and the two (shoot leaf area and spur leaf area) are inversely related (Forshey, 1989; Forshey and Elfving, 1989; Forshey and Marmo, 1985; Forshey et al., 1983). If total leaf area per tree is determined and

Table 1. Relationship between yield of fruit and shoot growth of spur type and nonspur 'McIntosh' apple trees (Peru, N.Y.).

Year	kg of fruit/m of shoot growth	
	Spur type	Nonspur
1984 ^a	1.38**	0.78
1985	1.92**	1.02
1986 ^a	0.91**	0.27
1987	1.56**	0.62
Mean	1.37**	0.60

^aTrees were 8 years old in 1984.

^aSpring frost damage reduced the crop.

**Significantly different at $P = 0.01$ by t test. Comparisons are within years only.

the relative proportions of shoot and spur leaves are calculated, the percentage of shoot leaves is positively related to total shoot growth and negatively related to yield (Table 2). This single statistic is, therefore, an expression of both vegetative growth and of fruitfulness. Changes in the percentage of shoot leaves indicate changes in the vegetative growth-fruiting relationship (Forshey and Elfving, 1989). Since the number of shoot leaves and spur leaves is inversely related, changes in the percentage of spur leaves, or in the ratio of spur leaves : shoot leaves, similarly indicate changes in the vegetative growth-fruiting relationship. The relative proportions of shoot and spur leaves vary with cultivar, growth habit, vigor, pruning, and crop (Ferree and Forshey, 1988; Forshey and Marmo, 1985; Forshey et al., 1983, 1987; Lakso, 1984; Palmer and Jackson, 1977; Table 3). As with kilograms of fruit per meter of shoot growth, measures of the relative proportions of shoot and spur leaves are more valuable as indicators of change in the vegetative growth-fruiting relationship than as specific goals.

The relationship between leaf area and crop load is often characterized by the leaf : fruit ratio, that is, the average number of leaves per fruit (Ferree and Cahoon, 1987; Ferree and Palmer, 1982; Hansen, 1969; Jones and Samuelson, 1983; Magness and Overley, 1930; Shen, 1941). However, the nature of the canopy, with varying proportions of shoot and spur leaves, suggests that this simple numerical ratio may be inadequate. In general, shoot leaves are $\approx 50\%$ larger than spur leaves (Forshey and Elfving, 1989; Forshey and Marmo, 1985; Forshey et al., 1983). While it is clear that spur leaves are dominant during flower development, fruit set, and early fruit growth (Arthey and Wilkinson, 1964; Hansen, 1971, 1977; Llewelyn, 1963, 1966, 1968), there is increasing evidence to indicate that the shoot leaves contribute more to fruit growth after

midsummer than the spur leaves (Myers and Ferree, 1983; Rom and Ferree, 1986; Van der Boon, 1980; Watson, et al., 1978). In fact, the consistent poor fruit size associated with spur-bound trees may be due in large part to the lack of shoot leaves. With established differences between shoot and spur leaves in both size and physiological activity, it would be more descriptive to express the ratio as leaf area per fruit, and to supplement this with a determination of the relative proportions of shoot and spur leaves.

GROWTH REGULATORS

Growth regulators such as damidazole, ethephon, chlormequat, and paclobutrazol may dramatically reduce shoot growth (Batjer et al., 1964; Edgerton and Hoffman, 1965; Forshey, 1970; Greene and Lord, 1978; Luckwill, 1968, 1970; Miller, 1988; Quinlan, 1981; Southwick et al., 1965; Steffins et al., 1983; Stinchcombe et al., 1984; Sweitlik and Miller, 1983; Volz and Knight, 1986; Williams, 1972). The response varies with chemical, application rate, timing, cultivar, and vigor. Appropriate treatments may reduce mean shoot length by one-third to one-half. With respect to leaf area, this can be somewhat deceptive. The reduction in shoot growth may be largely due to reduced internode length with relatively little effect on the number of shoot leaves or their size (Filipovich and Rowe, 1977). As a result, the effect on total shoot leaf area may be proportionately less than the effect on shoot growth. A growth regulator-induced reduction in shoot growth is often followed by increased flowering the next year (Luckwill, 1970, 1974; Mika et al., 1983; Miller, 1988; Quinlan and Preston, 1978; Volz and Knight, 1986; Williams, 1972). This response may be useful in encouraging earlier commercial fruit production in strongly vegetative, sparingly fruitful young trees (Batjer et al., 1964; Miller, 1988; Williams, 1984). The response is reflected in corresponding changes in the relative proportions of shoot and spur leaves. However, effective shoot growth control does not always increase flowering, and flowering is sometimes increased with little or no reduction in shoot growth (Batjer et al., 1964; Green and Lord, 1978; Looney and Kamienska, 1978; Luckwill, 1970; Tromp, 1972, 1973). As a result, reduced shoot growth and increased flowering the following year may be frequently associated, but are not necessarily directly related (Batjer et al., 1964; Luckwill, 1970; Tromp, 1972, 1973; Tromp and Wertheim, 1980). In contrast to growth retardants, chemicals such as BA may increase shoot growth and shoot leaf area (Table 4). Appropriate rates and timing of BA can stimulate branching in cultivars that characteristically make limited lateral growth. This is useful in improving the structure and increasing the bearing surface of young trees (Elfving, 1984; Forshey, 1982a; Miller, 1988; Quinlan and Preston, 1978). Other possible effects include paclobutrazol-induced reductions in leaf size with the spur leaves affected more than the shoot leaves (Greene and Murray, 1983; Steffins et al. 1983). Conversely, gibberellins may increase leaf size (Greene and Murray, 1983; Williams, 1984).

Growth regulators can obviously affect the leaf canopy in various ways. Significant changes in shoot growth, either increases or decreases, or in flowering can alter the leaf canopy quantitatively and/or qualitatively.

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Table 2. Correlation of percent shoot leaves with yield or shoot growth of 'McIntosh' apple trees (Peru, N.Y.).

Year	Percent shoot leaves with:	r
1984 ^a	Yield/tree	-0.80**
	Total shoot growth/tree	0.86**
1985	Yield/tree	-0.88**
	Total shoot growth/tree	0.82**
1986	Yield/tree	-0.83**
	Total shoot growth/tree	0.80**

^aTrees were 8 years old in 1984.

**Statistically significant at $P = 0.01$.

Table 3. Effects of pruning and growth habit on the percentage of shoot leaves of three apple cultivars (Hudson Valley, N.Y., 1988).

Cultivar	Variable	Shoot leaves, % total leaf area
Empire	Conventional pruning	14.1
	Extensive heading-back	39.5*
Starkrimson Delicious	Conventional pruning	8.5
	Spur pruning	14.8*
McIntosh (nonspur)	Thinning-out pruning	39.2
	Heading-back pruning	57.1*
McIntosh	Spur type growth habit	20.0
	Nonspur growth habit	49.8*

*Significantly different at $P = 0.05$ by t test.

Table 4. Effects of BA applications on shoot growth and relative proportion of shoot leaves of 'Empire' apple trees (Germantown, N.Y., 1984).

BA concn ^a (ppm)	No. shoots/cm branch circumference	Shoot leaves, % total leaf area
0	0.80	14.7
50	1.04	17.9
150	1.36	22.8
450	1.89	30.1
Coefficient of correlation ^b	0.81**	0.84**

^aN-(phenylmethyl)-H-purin-6-amine.

^bAll applications 1 week after petal fall.

^cCorrelation with BA concentration.

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