overlook the opportunity to determined the impact of budworm-feeding on the fibre increment in different cover types. The forest must be viewed as a mosaic of cover types in which various budworm densities and damage impacts will be acceptable with regard to protection costs and cutting policy.

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by G. L. Baskerville

Spruce Budworm: Super Silviculturist

Introduction

The essential ingredients of a spruce budworm outbreak appear to be the concurrence of a suitable food supply in the form of large continuous areas of host species and consecutive years of warm, dry, spring weather that favor high budworm survival. We know that this coincidence of events prefaced the current outbreaks in eastern Canada and suspect that it has occurred at least six times from the early 1700's. There has been a specific pattern to the concurrence of these conditions in that the budworm and the forest upon which it depends for habitat and food have evolved closely linked patterns of development. The exact relationship between forest succession and the insect varies with geographical location and host species, but the functional pattern is essentially the same.

The budworm — forest cycle

As a specified example of the linkage between budworm and forest development we can examine the historic pattern of development in the fir-spruce-birch forest of Green River, New Brunswick (Fig. 1). About a century ago, mid-1870's, there existed within this region relatively large areas of mature and overmature forest in which balsam fir predominated. Interspersed in this were areas of dense, uniform, immature forests in which balsam fir again predominated. These conditions are depicted in the top line of Fig. 1. The spruce budworm outbreak of 1877 devastated the fir component of the mature and overmature forest leaving only some of the less vulnerable spruce, the non-host white birch, and a thick mat of fir

and spruce regeneration, less than 2 feet high, growing amidst a cover of raspberry, birch, and pin cherry. The dense immature stands fared better; mortality of the fir was only fractional, although most survivors probably suffered top damage. This situation is shown on the line dated 1885. By 1912, the regeneration on areas that had supported mature forest before the 1877 outbreak had grown to an exceedingly dense pole stand. In these stands, the less tolerant birch and spruce were being suppressed by the more numerous fir trees. In the same period, the areas which had initially supported dense immature stands had developed to relatively open stands of mature and overmature trees in which the spruce and birch were still well represented by virtue of the release afforded them by the 1877 outbreak. There existed in 1912, therefore, the relatively large, contiguous areas of predominantly fir forest known to be essential for an outbreak to start. Favored by several consecutive warm dry springs, the budworm population exploded to epidemic proportions about 1913 and had virtually wiped out the fir component of the older stands by 1919.

As these mature stands were dying, however, a softwood regeneration (predominately fir) had developed at densities of several thousand to several tens of thousand stems per acre, standing less than 2 feet in height. In this same outbreak, the fir component in the immature forest (which had originated after destruction of the mature stand by the 1877 outbreak) was severely thinned and the surviving fir population sustained extensive top-killing (fourth line in Fig. 1). By 1949, these thinned stands had grown to a stately overmature fir-spruce-birch forest which again occurred over

Figure 1. Natural succession in the Green River fir-spruce-birch forest. The two columns represent two sequences both beginning in 1875 but in different initial conditions. The blackened tops represent disfiguration by intensive budworm feeding. The hatched cones represent white spruce trees, the unshaded cones are fir, and the rounded trees are hardwoods.

large contiguous areas. The stem of virtually every fir tree in these stands had a crook between 20 and 35 feet from the ground as a result of the top-kill sustained in the 1913–19 outbreak. Also, by 1949 the regeneration released by the 1913–19 outbreak had developed into dense pole-stage stands over extensive areas of the province. The conditions of a mature food supply and favorable weather coincided in the late 1940's and once again an outbreak was initiated. In the check area within New Brunswick's Kedgwick watershed where the forest was not sprayed, the 1949 outbreak resulted in almost total mortality of the fir component in mature stands by 1958. As these stands were killed, they were replaced by dense softwood regeneration established amongst the raspberry, birch, and pin cherry. Unprotected immature stands in check areas received a severe thinning, losing about half of the balsam fir stems, and sustaining top-killing in the survivors. In 1975, these check areas are once again green with thrifty fir and spruce in two age classes. Where overmature forests were wiped out, the land now supports developing dense pole stands. The immature stands have recovered so remarkably well that the casual observer has no idea of the top damage and mortality they sustained 20 years ago. The major change in the cycle is that the mature forest, which was sprayed in the 1950's, is largely intact where it has not been harvested by man

and where the normal attritions of wind and weather have not destroyed it.

The two recurring sequences of forest development depicted on the left and right sides of Fig. 1 are the same but are out of phase by two steps. It is evident that the budworm and this particular forest are together a self-regulating system. The budworm, wherever it reaches epidemic levels, destroys the host species in such a way as to ensure the development of a new stand of the host species suitable for future generations of budworm. The budworm is a superb silviculturist and this simply reflects the fact that the budworm and the forest in which it lives have evolved a considerable degree of interdependency. The pattern just described is specific to northwestern New Brunswick. However, equivalent patterns could be developed for any host forest within the range of budworm in eastern North America. The degree to which budworm is the driving force of forest succession depends on the extent to which it is able to devastate the forest periodically. Through Quebec and Ontario, the influence of budworm on forest history becomes less pronounced as other factors (e.g. fire) become increasingly important in determining forest succession. There are of course many variations on the theme. These depend on the abundance of favored host trees, the whims of the climate, and the like. For example, a budworm-killed forest is highly prone to fire, and generally speaking when fire occurs there is a tendency for the forest composition to move away from susceptible species (favoring black spruce, jack pine, and aspen). More recently forest harvesting activities have begun to influence the character of the forest to shift species composition towards more balsam fir.

We have direct evidence that an irregular cycle analogous to that depicted in Fig. 1 has been operating at least since the early 1700's. In all likelihood, this process has been operating for several thousand years since the end of the Ice Age. In this long period of stabilization, there have undoubtedly been major shifts in species composition. It is supposed that ecological trends strongly favored an increase in presence of susceptible species in the early stages of this evolutionary process. However, it seems likely that the content of susceptible species in these forests has been essentially stable for at least the last few centuries and possibly much longer. That is, left to their own devices, the budworm and the host forest are not changing much in long term, and contrary to commonly-held opinion, the fir content of these forests is not increasing as a result of budworm attack. In addition, there is convincing evidence that the position of more intolerant species such as white spruce and birch in this forest is maintained by the spruce budworm (Baskerville 1960). These species, being less tolerant than balsam fir, were doomed to exclusion from the extremely dense stands by the normal processes of suppression. However, with some regularity,

they were "rescued" by the budworm, which by inflicting a severe thinning on the fir in these stands, released them from fir competition. This has assured the continued position of the less tolerant species in the stand.

Human activities had no influence on the budworm-forest relationship until the late 1930's. Since that time, the most significant influence on species content of the forest has occurred through fire prevention and suppression which may have resulted in a slight increase of susceptibility. Although we have broadened our species utilization since the 1930's to include balsam fir, and although the loggers' influence on forest development has increased, our selective exploitation is not yet altering the species composition to the disadvantage of the budworm. Rather, we are competing with the insect for the right to perform the harvest of mature forests. To some extent, management policy has been counter productive; by protecting (via aerial spray) large areas of mature and overmature forests that are not being immediately harvested we are maintaining an appropriate food supply for the budworm, and we can therefore expect more frequent coincidence of suitable weather and food supply and hence more frequent outbreaks than occurred in the past when the pest periodically eliminated large areas of food supply (Blais 1974).

Stability in the budworm-forest system

Ecological examination of the budworm-forest system leads to the conclusion that free from the influences of man, it possesses self-regulating mechanisms that yield stability in biological systems. The periodic increases in budworm population from endemic to epidemic proportions are not to be regarded as a sign of instability in the forest-budworm system as a whole. On the contrary, these episodes can be seen to be an essential feature of the mechanism of maintaining the system, since by ensuring replacement of successive generations of forest, they assure a continued food supply for future generations of budworm. That is to say, ecological stability in the budworm-forest system must be measured on a time scale appropriate to the system function, namely, periods of at least 50 to 100 years. Budworm popula-

tions are not stable but the budworm-forest system possesses sufficient resilience to absorb the instability. Ecological resilience does not imply economic stability. Budworm-prone forest does not possess economic stability because of the budworm's capacity to harvest the mature forest more or less in its entirety. That is, we cannot manage the forest by taking regular small bites since this results in maintenance of conditions conducive to outbreak. In our management of this forest, we are precluded from regulating yield by either area or volume and without these we cannot maintain economic stability. Our "solution" has been to protect the host crop thus ensuring a conventional economic approach; but the price has been increased instability in an otherwise stable natural system. The longer we protect the forest in excess of what we can harvest, the more ominous the budworm's potential for large-scale sustained outbreak. We must recognize that the budworm-forest system over the long term is ecologically resilient: it possesses great long term stability in structure and species composition. Further, we should recognize that it has not been man's ecological influence in the forest that has promoted the budworm to pest level. In this case, it is our changing needs for fibre rather than changing forest management practices that result in the designation of the budworm as a pest. Budworm outbreaks were rarely mentioned before 1900 simply because balsam fir was not considered a useful species; not because there were few outbreaks or little balsam fir. Indeed, were it not for the fact that species utilization standards had been extended from the traditional pine to include spruce, the 1913-19 outbreak would have been little more than an entomological curiosity. However, in the last 40 years, industry has decided that balsam fir, red spruce, and white spruce are desirable species and consequently finds itself competing with the insect for the option to harvest.

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